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Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes

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ABSTRACT

We present the energy and mass balance of cerrado *sensu stricto* (a Brazilian form of savanna), in which a mixture of shrubs, trees and grasses forms a vegetation with a leaf area index of 1·0 in the wet season and 0·4 in the dry season. In the wet season the available energy was equally dissipated between sensible heat and evaporation, but in the dry season at high irradiance the sensible heat greatly exceeded evaporation. Ecosystem surface conductance g_s in the wet season rose abruptly to 0·3 mol m^{-2} s^{-1} and fell gradually as the day progressed. Much of the total variation in g_s was associated with variation in the leaf-to-air vapour pressure deficit of water and the solar irradiance. In the dry season the maximal g_s values were only 0·1 mol m^{-2} s^{-1}. Maximal net ecosystem fluxes of CO_2 in the wet and dry season were –10 and –15 μmol CO_2 m^{-2} s^{-1}, respectively (sign convention: negative denotes fluxes from atmosphere to vegetation). The canopy was well coupled to the atmosphere, and there was rarely a significant build-up of respiratory CO_2 during the night. For observations in the wet season, the vegetation was a carbon dioxide sink, of maximal strength 0·15 mol m^{-2} d^{-1}. However, it was a source of carbon dioxide for a brief period at the height of the dry season. Leaf carbon isotopic composition showed all the grasses except for one species to be C_4, and all the palms and woody plants to be C_3. The CO_2 coming from the soil had an isotopic composition that suggested 40% of it was of C_4 origin.

Key-words: arid zone; Bowen ratio; carbon sequestration; savanna; soil respiration.

INTRODUCTION

Savannas are a major component of the world's vegetation, covering a land surface of 15×10^{12} m^2 and accounting for about 30% of terrestrial primary production (IPCC 1990). The savanna formation of South America covers $2{\cdot}5 \times 10^{12}$ m^2, of which $2{\cdot}0 \times 10^{12}$ m^2 constitutes the Brazilian *cerrado*. In Brazil it is the second most important land cover, being exceeded only by the rain forest which is $3{\cdot}5 \times 10^{12}$ m^2 (Ratter 1992).

Cerrado has many physiognomic forms, ranging from the tall *cerradão* (trees to a height of 20 m, resembling the woodland savanna of other continents), through the more common *cerrado sensu stricto* (a species-rich dense scrub of shrubs and trees, 8–10 m high, with a grass understory), to the grassland *campo* forms. The cerrado vegetation is markedly seasonal in phenology and is often burned, either naturally or as part of a management cycle (Coutinho 1990). Descriptions of cerrado vegetation can be found in Eiten (1972, 1992) and Bullock, Mooney & Medina (1995).

As a result of the large areas occupied by the savannas, and the cerrado in particular, they have the potential to influence the regional and possibly global energy, water and carbon balances. Cerrado has been somewhat neglected in this regard, although the Brazilian rain forest has been extensively studied (Shuttleworth *et al.* 1984; Shuttleworth 1988a,b; Grace *et al.* 1995a,b). There have been few micrometeorological studies of the energy and water balance of cerrado (Maitelli & Miranda 1991; Miranda & Miranda 1992), and no reports of their carbon balance. Yet the cerrado is under great economic pressure (Skole *et al.* 1994): it provides charcoal for smelting and much of the land area is likely to be converted to agriculture and pasture in the future.

In this paper we describe the first work on any savanna in which fluxes of energy, water and carbon were measured simultaneously at intervals over a year. The first objective was to explore the physiological and environmental controls of net ecosystem photosynthesis in this rather unusual system, in which proportions of C_3 and C_4 species change seasonally in concert with rainfall. This was achieved using water vapour fluxes to derive an ecosystem surface conductance g_s, so that seasonal and diurnal variations in photosynthetic CO_2 fluxes may be

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attributed to variations in light, vapour pressure deficit and stomatal behaviour of the canopy. The second objective was to examine the seasonal changes in the carbon balance of the ecosystem by making repeated measurements over the annual cycle imposed by the rainfall distribution. Such data provide the first step towards understanding the carbon economy of this widespread vegetation type, and the contribution it makes to the carbon balance of the region as a whole.

MATERIALS AND METHODS

Site

The site is at the Reserva Ecológica de Águas Emendadas (15°33' S, 47°36' W, 1000 m above sea-level) about 50 km from Brasília, DF. The average annual rainfall is 1500 mm and the mean annual temperature is 22 °C (Table 1). Leaf area indices are from 0·4 in the dry season to 1·0 in the wet season (Table 2). The tree layer is about 10 m tall with *Schlerolobium paniculatum* being the dominant species. There is a seasonal grass layer dominated by *Aristida riparia*, *Echinolaena inflexa* and *Paspalum estellatum*. The vegetation at the site is an example of cerrado *sensu stricto* which has been protected from fire. Although fires periodically occur in some areas near the borders of the Reserve, usually originating at neighbouring farms and roads, the area of the experiment is well protected by a *vereda* (a permanent grassy marsh with buriti palms, *Mauritia vinifera*) on the valley floor of the Reserve, about 2–3 km south-east of the study area. Despite protection, a rapid surface fire reached the experimental site in 1987, burning grasses and small shrubs but only scorching the leaves of the trees. The soil is a dystrophic, deep and well-drained red-yellow oxisol with a pH of < 5 (EMBRAPA 1987). The terrain has an inclination of less than 4°. A 12 m scaffolding tower was utilized to mount the instruments for the eddy covariance study.

Sensors for eddy covariance

The eddy covariance sensors for the measurement of vertical fluxes of CO_2, H_2O and momentum were mounted at 15 m above the ground on a mast at the top of the tower. In this position, it is estimated that the sensing system measures fluxes over a fetch of about 500 m (Schuepp *et al.* 1990). The same vegetation type stretches for 3 km (from south-west) to a maximum of 6 km (north-east). The prevailing winds come from the north and north-east.

Table 1. Meteorogical conditions at Brasilia, about 50 km from the study site

Month	Mean temperature (°C)	Mean vapour pressure (kPa)	Average monthly precipitation (mm)
January	21·4	1·93	250
Febuary	21·0	1·98	240
March	21·4	1·94	179
April	20·7	1·89	126
May	19·4	1·70	38
June	18·4	1·42	8
July	18·3	1·22	9
August	20·4	1·63	6
September	21·6	1·76	49
October	21·6	1·78	166
November	21·1	1·97	242
December	21·1	2·00	243

Table 2. Biomass and leaf area indices (LAI) of the site (H.S. Mirand, personal communication). Biomass of grass and dicotyledonous layers was obtained from 12 samples of 0·5 m^2; values given are means ± standard deviation. Leaf area indices of grass and dicotyledonous layers were found from the biomass data; leaf area indices of the canopy were obtained from hemispherical photographs

		Wet season (April)	Dry season (September)
Tree canopy (leaves only)	LAI	1·00 ± 0·06	0·42 ± 0·15
Grass layer (including litter)	live mass (g m^{-2})	74 ± 25	38 ± 20
	live LAI	0·4	0·2
	dead mass (g m^{-2})	101 ± 51	102 ± 36
	dead LAI	0·5	0·5
Dicotyledons (including litter)	live mass (g m^{-2})	49 ± 61	30 ± 24
	live LAI	0·1	0·1
	dead mass (g m^{-2})	279 ± 162	304 ± 128
	dead LAI	0·7	0·7

The eddy covariance system consisted of a fast-responding closed-path infrared gas analyser to measure CO_2 and H_2O (Li 6262, Li-Cor, Lincoln, NE, USA); a three-dimensional sonic anemometer to measure wind velocity and air temperature (A1002R, Solent, Lymington, UK); a pumping unit to draw air through 6 m of 5·5-mm-diameter tubing (Dekabon 1300, Deane & Co., Glasgow, UK), and a 386 laptop computer with the software EDISOL to enable the flux calculations to be made as half-hour averages in real time (Moncrieff *et al.* 1997). Air was drawn by a diaphragm pump at 4 $dm^3\ min^{-1}$ from a point 50 mm below the sonic path, passed to the sample cell of the gas analyser and vented to the atmosphere. Readings of the wind speeds and gas concentrations were made at 21 Hz, and used to compute the CO_2 and H_2O fluxes. Processing of the data to include the standard corrections for the eddy covariance system followed methods described elsewhere (Grace *et al.* 1995a; Moncrieff *et al.* 1997).

Meteorological instruments

Radiation sensors were installed on the top of the tower at a height of 13·5 m at the end of a 5 m sidewards extended arm. Measurements were made concomitantly with eddy flux data between 26 March and 2 May (wet season) and between 5 and 18 September (dry season) 1994. Shortwave (or solar) radiation, S, was measured with a Moll-Gorzynski solarimeter (Kipp & Zonen CM3, Delft, The Netherlands) and two pyranometers (Li 200B, Licor, NE, USA). One pyranometer was positioned facing skyward, and the other faced groundward to enable measurement of incoming and reflected solar radiation, respectively. All-wave radiation balance, net radiation (R_n), was measured with a Funk Type radiometer (Swissteco, Melbourne, Australia). The Kipp & Zonen solarimeter was used as a secondary standard and the radiation sensors were cross-calibrated against it in the field. Soil heat flux (G) was measured as the average value from four soil heat flux discs (Solar Radiation Instruments, Melbourne, Australia) placed about 0·03 m below the soil surface. Data were collected by two data loggers (21X, Campbell Scientific Inc., Logan, USA) every minute, and half-hourly interval averages were stored in solid memory modules (SM 192, Campbell Scientific Inc., USA).

Derived quantities

The surface roughness parameter for momentum transfer, z_{oM}, was estimated according to

$$\ln[(z-d)/z_{oM}] = ku/u_* + \Psi_M, \qquad (1)$$

where z is the measurement height, d is the zero plane displacement, k is the von Karman's constant (0·41), u is the windspeed, u_* is the friction velocity and Ψ_M is the integrated momentum profile function, calculated as outlined in Grace *et al.* (1995a). Taking near-neutral conditions (Ψ_M close to 0) and therefore assuming a logarithmic wind profile, d was first estimated by comparing the relationship between u and u_* from concurrent measurements by sonic anemometers at heights of 15 and 20 m (Lloyd, Gash & Sivakumar 1992). This yielded an estimate for d of 6·3 m and an estimate for z_{oM} of 1·2 m. Taking our estimated average vegetation height h of 9 m, this corresponds to $d = 0{\cdot}70\ h$ and $z_{oM} = 0{\cdot}13\ h$. These relationships with h are similar to those applying to other vegetation types (Monteith & Unsworth 1990).

The aerodynamic resistances for water vapour (r_{aV}) and heat (r_{aH}) transfer were calculated according to

$$r_{aV} = r_{aH} = \frac{u}{u_*^2} + \frac{\ln(z_{oM}/z_{oH})}{ku_*} + \frac{\Psi_M}{u_*} - \frac{\Psi_H}{u_*}, \qquad (2)$$

where z_{oH} is the surface roughness parameter for heat (and water vapour) transfer and Ψ_H is the integrated heat profile function. Based on the work of Garratt & Hicks (1973) in a similar vegetation type (woody savanna) we took $\ln(z_{oM}/z_{oH})$ as 2·0. Ψ_M and Ψ_H were calculated as outlined in the Appendix of Grace *et al.* (1995a). The aerodynamic conductances for heat and water vapour (g_{aH} and g_{aV}) were calculated as the reciprocals of r_{aH} and r_{aV}, respectively, and are expressed here on a molar flux basis.

Ecosystem surface conductance (g_s) was estimated by inversion of the Penman-Monteith equation using measurements of transpiration rate and vapour pressure deficit as measured by the tower instruments. Canopy surface temperature was calculated from the net radiation, g_s and g_{aH} using eqn 9·5 of Jones (1992). Canopy-to-air vapour pressure deficit was then estimated as the difference between the saturation vapour pressure at the estimated canopy temperature and the vapour pressure at the canopy surface.

Changes of CO_2 concentration in the air

Vertical profiles of CO_2 concentration and subsequent changes in the quantity of CO_2 within the airspace between the soil surface and the measurement point on the tower were made over two 24 h periods in early May (at the start of the dry season) and in November (when the dry season had recently finished). An automatic profile sampling system as described in Grace *et al.* (1995a) was employed in May, sampling air through tubing every 25 min at heights of 1, 2, 4, 8 and 12 m and passing it to an infrared gas analyser (Leybold-Binos I; Germany). This system was not available in the dry season and five tubes of equal length and diameter were used to estimate the changes in the CO_2 concentration in the air space. A pump was used to draw air at 1 $dm^3\ min^{-1}$ through the tubes into a 2 dm^3 glass mixing tank and then measured by an infrared gas analyser (Li-6262, Li-Cor, Lincoln, NE, USA). Data were taken every minute and half-hour averages were stored by using a data logger (21X; Campbell Scientific Inc., USA).

Carbon isotopic composition of cerrado CO_2

Diurnal patterns in the concentration and isotopic composition of atmospheric CO_2 were measured at 3–4 h intervals and at two heights, 1 and 13·5 m, on two occasions

(1–2 May 1993 and 1–2 November 1993). Whole air samples, pre-dried by passage through anhydrous magnesium perchlorate, were collected at each height for each time, in 0·5 dm^3 Pyrex glass cylindrical flasks with Teflon O-ring valves at each end (Glass Expansion P/l, Melbourne, Australia).

The flask and accompanying Flask Pump Unit (FPU) were developed at CSIRO Division of Atmospheric Research's GASLAB (Global Atmospheric Sampling Laboratory) as part of a global sampling network for trace gas isotopes and composition (Francey *et al.* 1990). Recent developments, employed in the Brazilian operation, included careful selection and a rigorous pre-treatment protocol for all surfaces in contact with sample air, permanent exclusion of water vapour from flasks and restricted exposure of samples to sunlight. Samples were collected by flushing for 10 min at 4 dm^3 min^{-1}, then pressurizing flasks to 100 kPa above ambient pressure. On return to GASLAB, samples were routinely analysed by gas chromatography for the concentrations of CO_2, CH_4, CO, H_2 and N_2O, and by ratio isotope mass spectrometry of extracted CO_2 for the isotope ratios $\delta^{13}C$ and $\delta^{18}O$. Only CO_2 concentration and CO_2 isotopic data are reported in this paper.

In the analysis, CO_2 in about 10 cm^3 of air is converted to CH_4 and measured on a modified CARLE (S Series) gas chromatograph with flame ionization detector. CO_2 concentrations are linked to the WMO international calibration scale via CMDL/NOAA Laboratories (Boulder, CO). Measurement precision over the concentration range 250–400 ppmv is ≤ 0·1%. Isotopic analysis involves a Finningan MAT252 ratio isotope mass spectrometer with modified MT Box-C trapping accessory for the cryogenic extraction and injection of CO_2 to the mass spectrometer. About 30 cm^3 of air is required for one $\delta^{13}C$ determination. A description of the facility is given by Allison *et al.* (1994a,b). The external precision for the $\delta^{13}C$ determination from the GASLAB/FPU flask samples is estimated to be 0·02%.

The interpretation of the isotopic results depends on the fact that the product of isotopic ratio (δ) and concentration (C) is an additive quantity (Tans 1980). Assuming a uniform source (or sink) of CO_2 of isotopic composition δ_s with a infinite background atmospheric reservoir, a simple mixing process gives:

$$\delta_a = \delta_s + \frac{M}{C_a}, \tag{3}$$

where M is a constant (related to the difference between atmospheric and source air isotopic composition), δ_a is the isotopic composition of canopy air and C_a is the associated CO_2 partial pressure.

Plant dry matter analyses

In May 1993, leaves of 50 species of plants growing around the tower were sampled for stable carbon isotopic composition and leaf nitrogen concentrations. Samples were taken from as many plants of each species as possible and pooled for analysis. The leaves were oven-dried at 80 °C until constant mass and then ground; dry samples usually exceeded 5 g.

Plant dry matter carbon isotope composition was determined on finely ground samples of 0·6 ± 0·2 mg. Samples were combusted in an elemental analyser (Carlo Erba 1108, Italy) to separate chromatographically CO_2 which was then analysed by continuous flow isotope spectrometry using a VG Isomass Spectrometer. Total leaf nitrogen content was also determined using the elemental analyser.

RESULTS

The results depended markedly on the seasonality of the environment. The weather conditions for the nearby meteorological station of Brasilia are shown in Table 1. Ninety-five per cent of the 1500 mm annual rain normally falls in the wet season, between 1 October and April.

Energy balance

The relationship between solar radiation and net radiation (Fig. 1) is approximately linear, the slope being marginally higher in the dry season (0·88) than in the wet season (0·80). Solar radiation was, overall, somewhat lower in the dry season, due to natural and anthropogenic fire in the region.

It is useful to compare the net radiation with the sum of sensible and latent heat, to assess the 'closure' of the energy balance, namely:

$$R_n - \lambda E - H - G - \partial W/\partial t = 0 \tag{4}$$

In the present study, the flux to the soil G and to the biomass store $\partial W/\partial t$ was negligibly small (10% of any hourly value), and somewhat variable from place to place. Ignoring these terms, closure of the energy balance (the condition when $R_n = \lambda E + H$) was tested by plotting net radiation against the sum of sensible and latent heat flux. This relationship was linear and data points fell around the 1:1 line, consistent with 'closure' (not shown).

The partitioning of radiation between sensible heat H and evaporation λE was different between the seasons. In the wet season, H and λE were roughly equal and linear with solar radiation S (Fig. 2). In the dry season, however, λE was linear with S only to S = 200 W m^{-2}. Thereafter, $H/\lambda E$ (the Bowen ratio) declined as the response of λE to S diminished (Fig. 2).

Mass fluxes and associated conductances

The fluxes of water and carbon were closely related to each other, and to the diurnal cycle of solar radiation. We concentrate first on the wet season, using 17/18 April as an example (Fig. 3). On this sunny day, incoming radiation rose sigmoidally to a peak of about 1000 W m^{-2}, and the air temperature rose from a pre-dawn value of 20 °C to 28 °C at noon. At this time, canopy temperature was

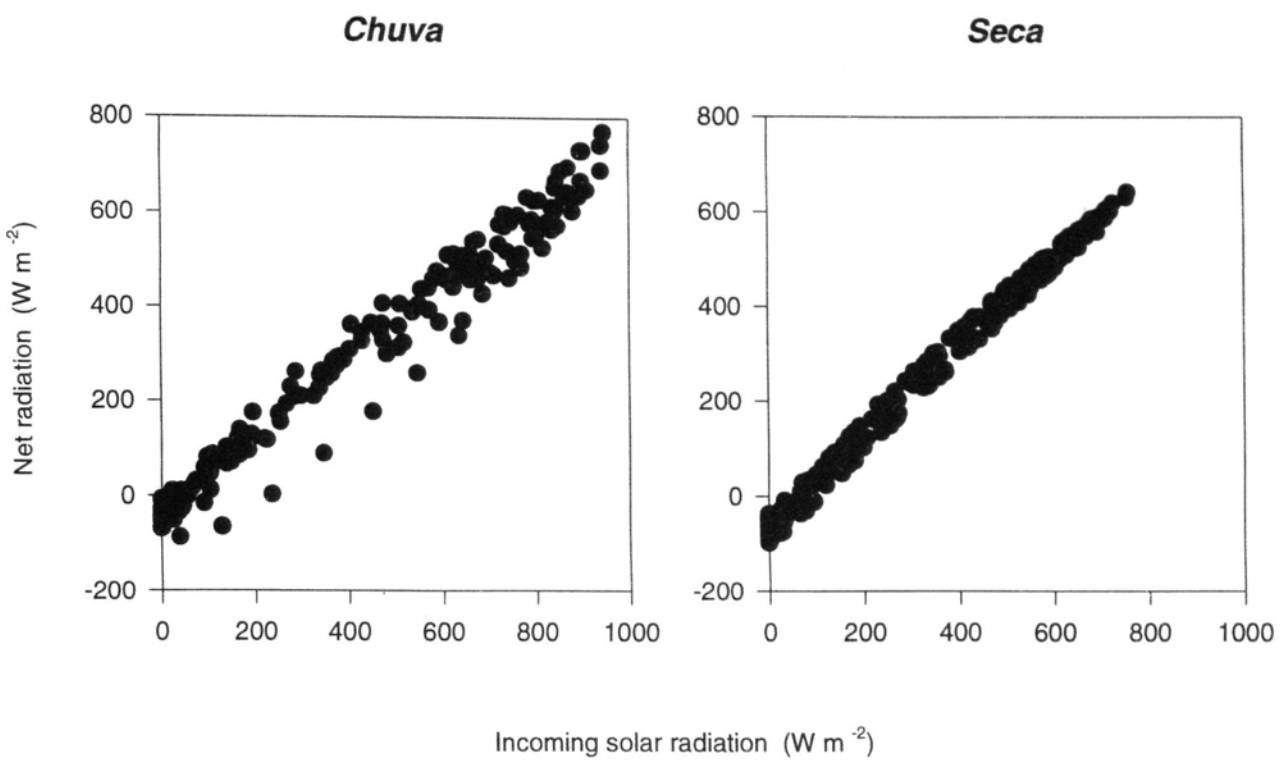

Figure 1. The relationship between solar and net radiation in the *chuva* (wet season) and *seca* (dry season). Data points are half-hour averages. The equations fitted to the data are: $R_n = 0{\cdot}80\ S - 44{\cdot}6$ ($r^2 = 0{\cdot}98$) and $R_n = 0{\cdot}88\ S - 61{\cdot}6$ ($r^2 = 0{\cdot}95$), respectively.

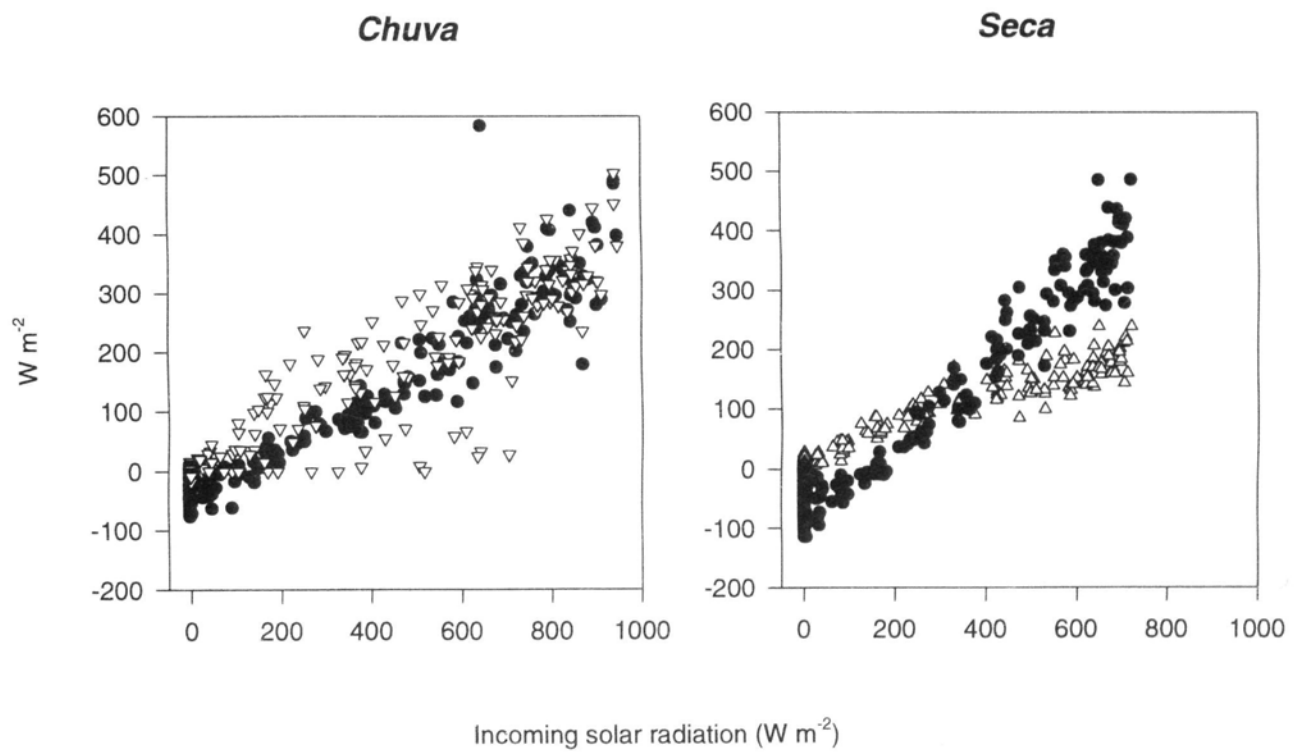

Figure 2. The relationship between incoming solar radiation and the main components of the energy balance, the sensible heat (●) and the latent heat (▽ or △) in the *chuva* (wet season) and *seca* (dry season).

6 °C above air temperature, and canopy-to-air vapour pressure difference had increased from 0 at pre-dawn to 30 mmol mol^{-1} in the early afternoon. As for fluxes of carbon and water, the sign convention used here is that negative fluxes denote a downward flux from atmosphere to canopy. The carbon dioxide efflux from the canopy at night averaged about 5 μmol m^{-2} s^{-1}, and exhibited little variability at night (between 2200 and 0400 h, Fig. 3). By day, the fluxes into the canopy were –15 μmol m^{-2} s^{-1}, reaching their maximum near the middle of the day and closely following radiation. The corresponding ecosystem surface conductance, derived from the Penman-Monteith equation, was close to zero by night, rising to 0·2–0·4 mol m^{-2} s^{-1} by day, in parallel with radiation and vapour pressure deficit.

At the end of the dry season in early September, the pattern was quite different (Fig. 4). The evaporation rate was only half that in April despite a continuing high solar irradiance and despite a much higher canopy-to-air vapour pressure deficit (60 mmol mol^{-1}). The carbon fluxes at night were only 2 μmol m^{-2} s^{-1} and the daytime fluxes into the canopy reached a maximum of only –4 μmol m^{-2} s^{-1}. This was a result of low ecosystem surface conductance, which was always below 0·15 mol m^{-2} s^{-1}.

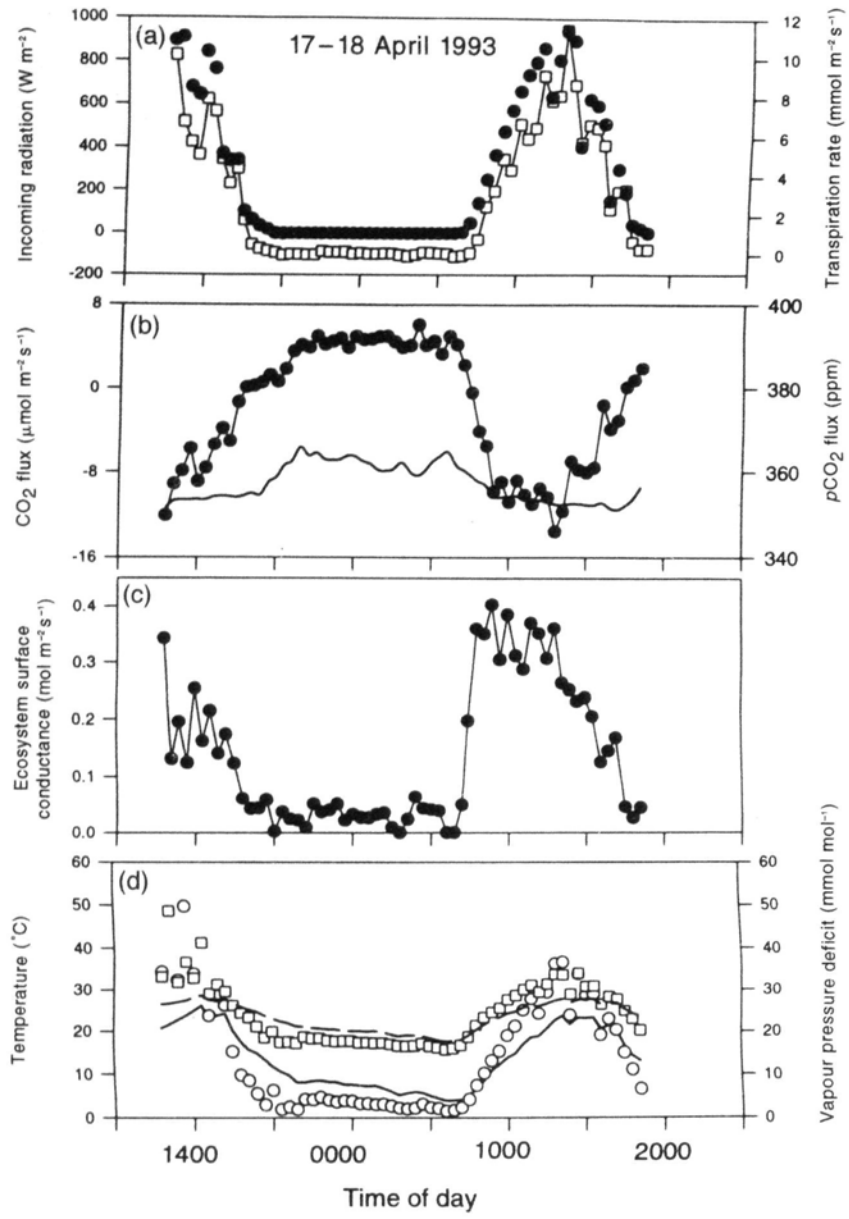

Figure 3. Water vapour and carbon dioxide fluxes in the wet season, 17–18 April. Symbols: ● is incoming solar radiation in (a), CO_2 flux in (b) and ecosystem surface conductance in (c); □ is transpiration rate in (a) and canopy-to-air vapour pressure deficit in (d); ○ is canopy temperature; —— is partial pressure of CO_2 (pCO_2) at the top of the tower in (b) and air temperature in (d); – – – is the saturation humidity deficit.

Conductances (g_s and g_a) and coupling to the atmosphere

Irrespective of the time of the year, ecosystem surface conductance g_s increased with incoming solar radiation and decreased with canopy-to-air vapour pressure difference (Fig. 5). Comparison of wet and dry season data shows that one of the marked differences between the seasons was that leaves within the cerrado canopy were exposed to different 'environmental spaces'. During the dry season canopy-to-air vapour pressure differences were much higher, but incoming radiation was lower than in the wet season. The lack of substantial overlap in 'environmental space' makes it difficult to determine whether there was any systematic difference in stomatal response to the environment. Nevertheless, there is no indication that the ecosystem surface conductances were reduced in the dry season below levels which would be expected on the basis of higher canopy-to-air vapour pressure differences.

The aerodynamic conductances were an order of magnitude larger than the ecosystem surface conductances, with lower values at night caused by lower wind speed and stable meteorological conditions (Fig. 6).

Carbon fluxes

Inspection of the data set from which these examples are drawn, and integration of the areas under the curves from data like those presented above, allow seasonal trends in photosynthesis, respiration and net ecosystem flux of cerrado to be examined. To estimate respiration from soil and non-photosynthesizing plant tissue during the day, we first examined the relationship between night time carbon efflux (mostly originating in the soil, Meir *et al.* 1996) and air temperature (Fig. 7). Respiration is higher in the wet season. This illustrates a clear temperature dependence of CO_2 efflux for the dry season, though data obtained during the wet season were less definitive in this respect. To allow for higher respiration rates during the day, as a conse-

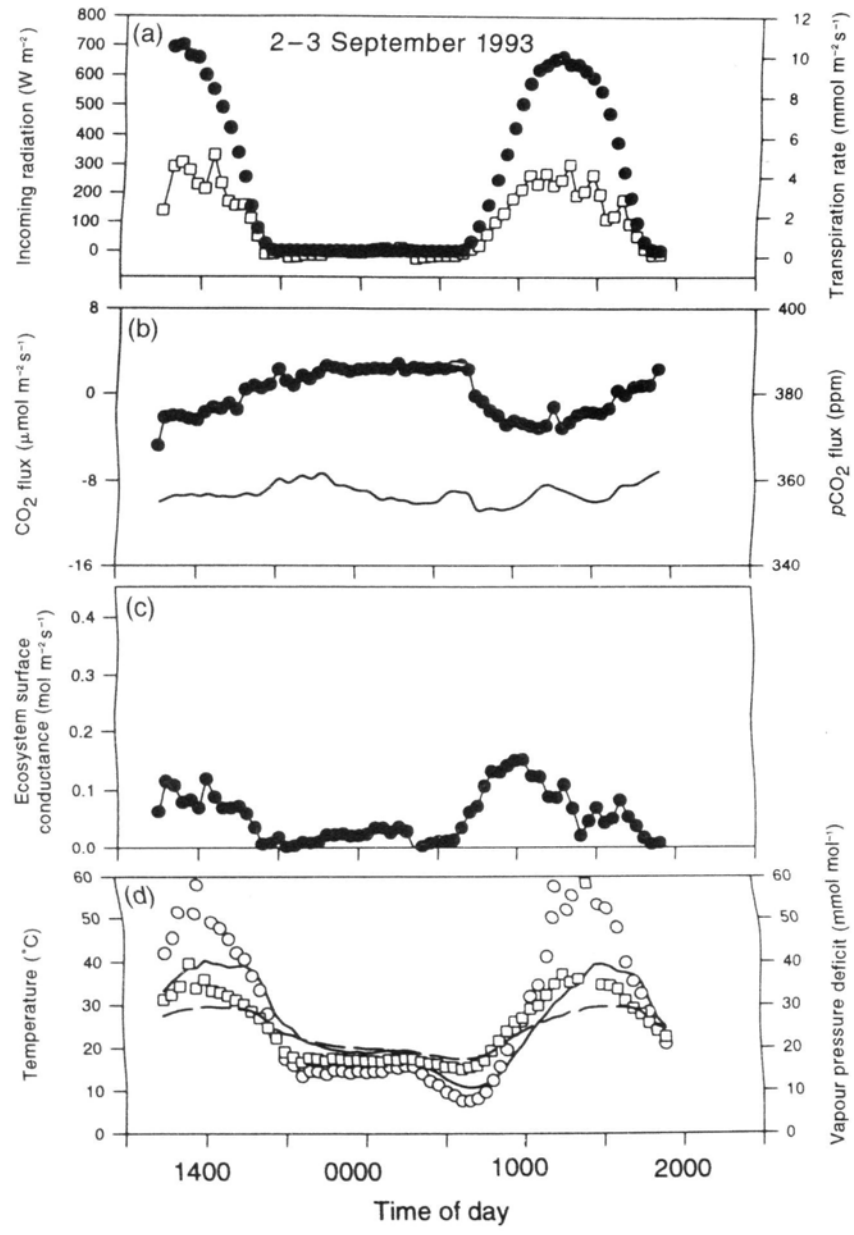

Figure 4. Water vapour and carbon dioxide fluxes in the dry season, 2–3 September. Symbols: ● is incoming solar radiation in (a), CO_2 flux in (b) and ecosystem surface conductance in (c); □ is transpiration rate in (a) and canopy-to-air vapour pressure deficit in (d); ○ is canopy temperature; ——is partial pressure of CO_2 (pCO_2) at the top of the tower in (b) and air temperature in (d); – – – is the saturation humidity deficit.

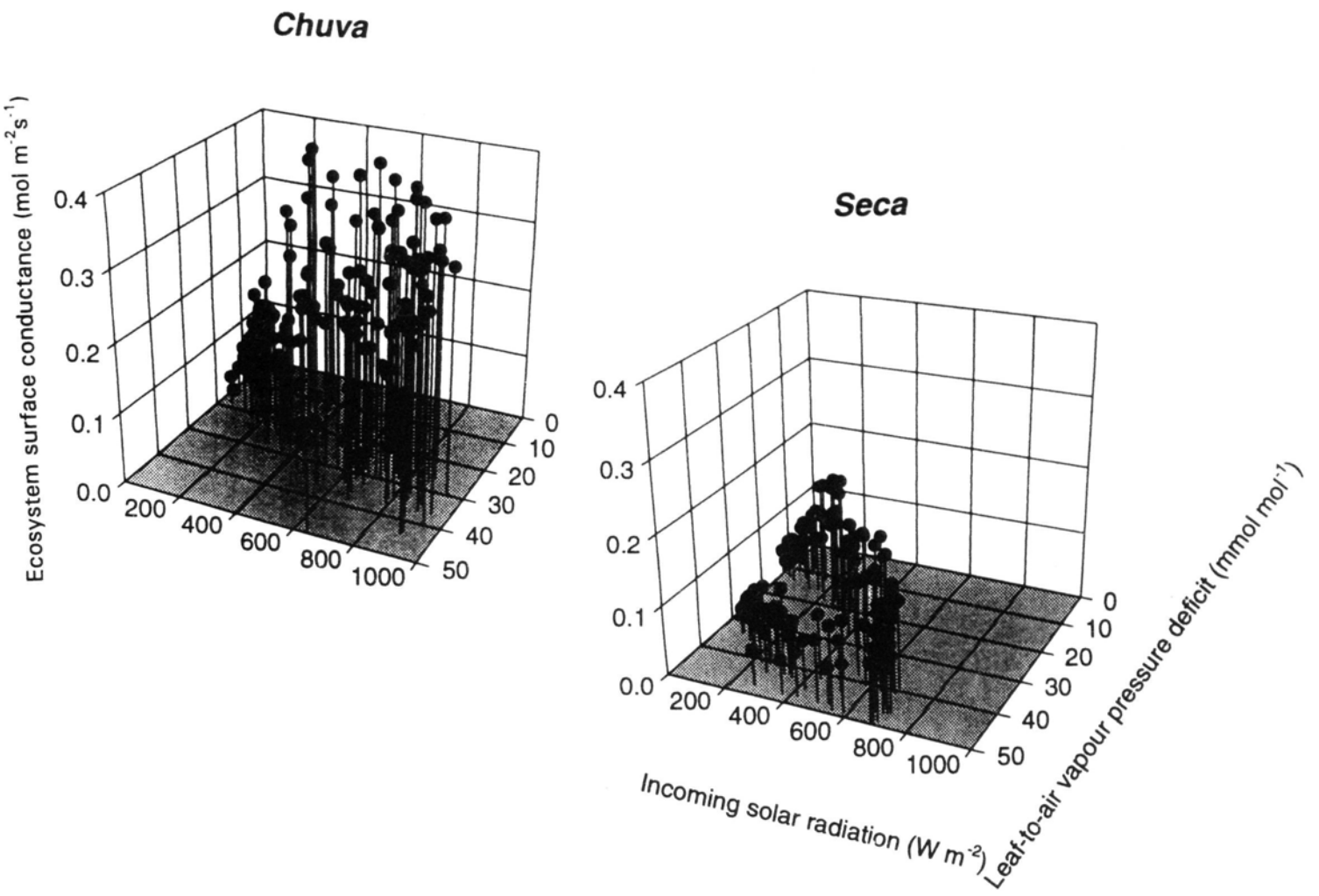

Figure 5. Ecosystem surface conductance plotted against solar irradiance and canopy-to-air vapour pressure deficit in the *chuva* (wet season) and *seca* (dry season in September).

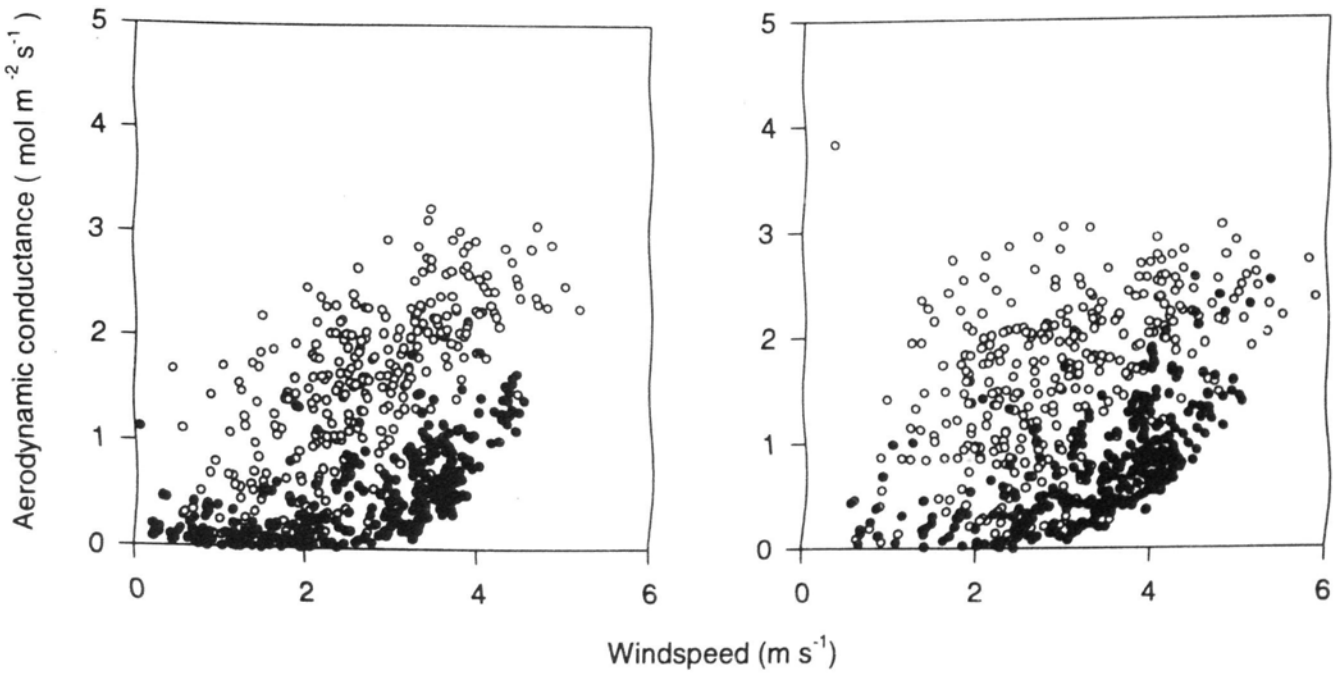

Figure 6. Aerodynamic conductance plotted against wind speed. Solid points denote nocturnal conditions in the *chuva* (wet season) and *seca* (dry season).

quence of higher temperatures, we fitted the relationship obtained by Lloyd & Taylor (1994) to the data. This relationship approximates to a straight line over such a restricted range of temperatures. This gave estimates of respiration rates at 15 °C of 1·6 and 2·3 μmol m^{-2} s^{-1} for dry and wet seasons, respectively. Using the derived dependence of respiration on air temperature, we then approximated half-hourly canopy photosynthetic rates by subtracting the estimated respiration value from the net ecosystem flux. The derived seasonal patterns in daily totals of photosynthesis, respiration and net ecosystem flux are shown in Fig. 8. On most measurement days during the dry season the cerrado was a weak source of CO_2, whilst during the wet season it was a substantial sink.

Ecosystem carbon flux data may be presented as an irradiance-response curve, in the same way as light response

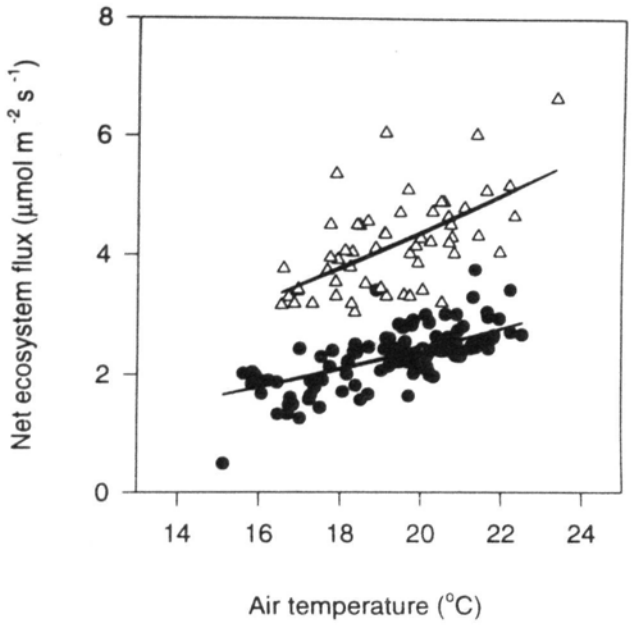

Figure 7. Nocturnal respiration as a function of temperature. The curves are the model of Lloyd & Taylor (1994) fitted to the data from the wet season (△) and dry season (●).

curves are usually shown for a leaf (Fig. 9). The curves illustrate a difference between the wet and dry periods, both in initial slopes and the point at which light saturation occurs. From fitted hyperbolic equations we obtained values for F_{resp} (the average rate of ecosystem respiration in the dark) of 2·8 μmol m^{-2} s^{-1} for the wet season and 2·1 μmol m^{-2} s^{-1} for the dry season. More marked was the variation between seasons in the maximal rate of net ecosystem photosynthesis: it declined from about –12 μmol m^{-2} s^{-1} during the wet season to –4 μmol m^{-2} s^{-1} during the dry season. There was, however, only a small effect of season of measurement on the ecosystem light compensation point (the value of solar radiation at which $F_{net} = 0$), this being 87 W m^{-2} during the wet season and 99 W m^{-2} during the dry season. Similarly, the effect of season on the initial slope of the light response curve (α, the apparent quantum efficiency) was also markedly less than for the light-saturated rate, being estimated as 68 mol photon mol^{-1} CO_2 during the wet season and 77 mol photon mol^{-1} CO_2 during the dry season. Examination of the relationship between ecosystem surface conductance and net ecosystem carbon flux (Fig. 10) showed there to be little difference between seasons in the relationship at low g_s. When the curve fitted to the wet season data is superimposed upon the dry season data it fits moderately well. This suggests that at least part of the lower daytime net ecosystem fluxes during the dry season were attributable to lower ecosystem surface conductances.

In order to examine further the interactions between the concurrent changes in ecosystem surface conductance and net ecosystem fluxes, we estimated bulk canopy values of the ratio of CO_2 partial pressure in the sub-stomatal cavity (C_{st}) to that in the ambient air (C_a) according to $C_{st}/C_a = 1 - 1{\cdot}6\,A/(C_a\,g_s)$, where A was calculated estimating the daytime respiration as described above. This showed that there was only a small effect of season on the relationship between C_{st}/C_a and canopy-to-air vapour pressure difference (Fig. 11). If anything, at a given canopy-to-air vapour pressure difference values of C_{st}/C_a were higher during the dry season than in the wet season.

Isotopic signals

The foliar carbon isotopic composition and nitrogen content of grasses and shrubs are given in Table 3. This shows that all grasses except *Echinolaena inflexa* had the C_4 pathway and all shrubs the C_3 photosynthetic mode. For C_3 shrubs the average foliar carbon isotopic composition was –28·1% and for the C_4 grasses it was –13·0%. There was a substantial difference between shrubs and grasses in the nitrogen content (dry weight basis) of foliage, with the C_4 grasses being especially low (0·2–0·4% DW).

The relationship between the partial pressure of atmospheric CO_2 (pCO_2) and its carbon isotopic composition (δ_a) is shown in Fig. 12. On the second sampling occasion (1–2 November 1993), night-time build-up of CO_2 was far more substantial than on the first (1–2 May 1993). Following Keeling (1958), plotting δ against $1/(pCO_2)$ gives an estimate of the isotopic composition of the source CO_2 (δ_s; assuming that the source is of uniform isotopic composition) of –21·8‰ for 1–2 May and –23·7‰ for 1–2 November. From mass balance considerations, the proportion of carbon originating from C_4 plant material (p_4) can be calculated (e.g. Lajtha & Michener 1994):

$$p_4 = \frac{\delta^{13} - \delta^{13}}{\delta^{13}_4 - \delta^{13}_3}, \qquad (5)$$

where $\delta_3{}^{13}$ is the average carbon isotopic composition of C_3 shrubs and $\delta_4{}^{13}$ is the average carbon isotopic composi-

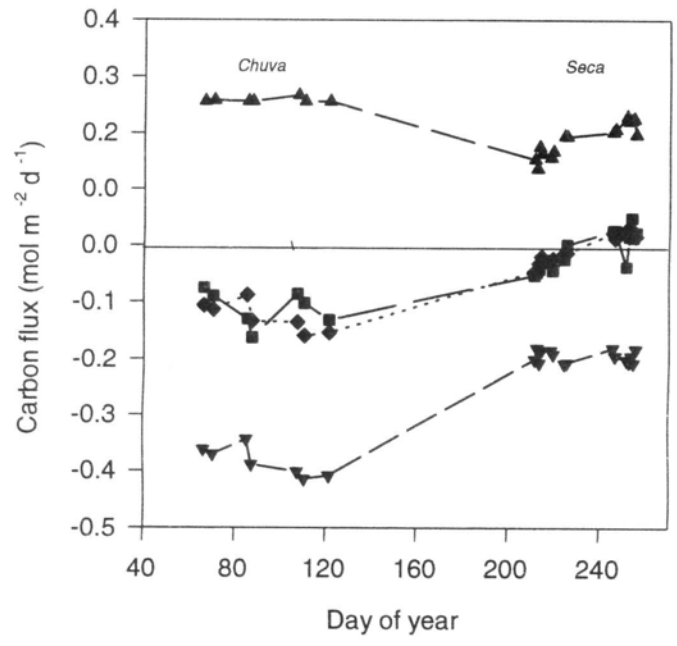

Figure 8. Daily totals of carbon flux in the *chuva* (wet season) and *seca* (dry season).The upper line denotes respiration, and it has been assumed that the respiration in the light is equal to that measured nocturnally, but adjusted for the effect of the difference in temperature. The lower data points represent the gross photosynthetic flux estimated as the net observed flux minus the respiration. The central points are the net carbon balance, as measured (■) or as estimated (◆) from the modelled respiratory and photosynthetic components.

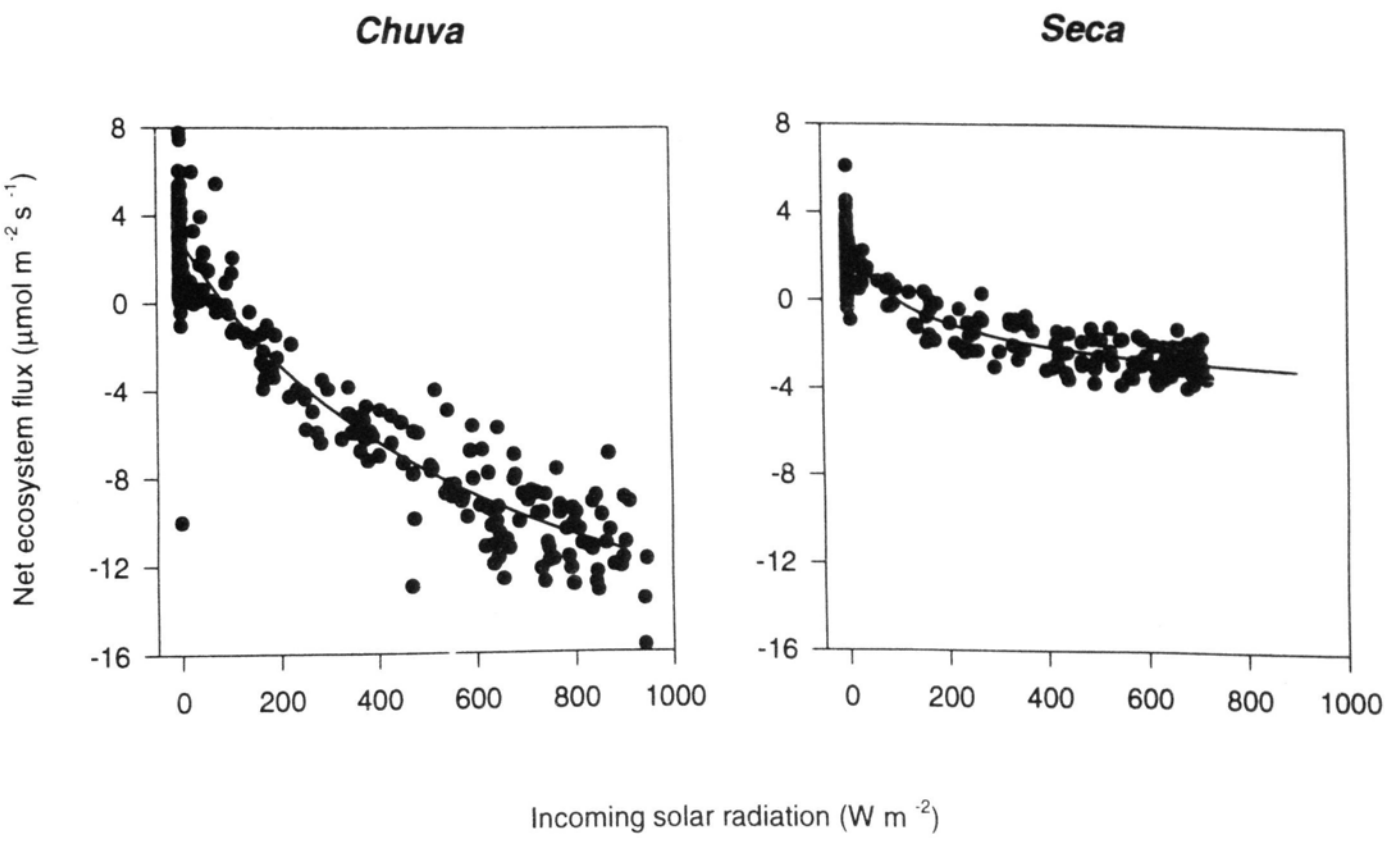

Figure 9. Net ecosystem fluxes of CO_2 as influenced by solar irradiance in the *chuva* (wet season) and *seca* (dry season).

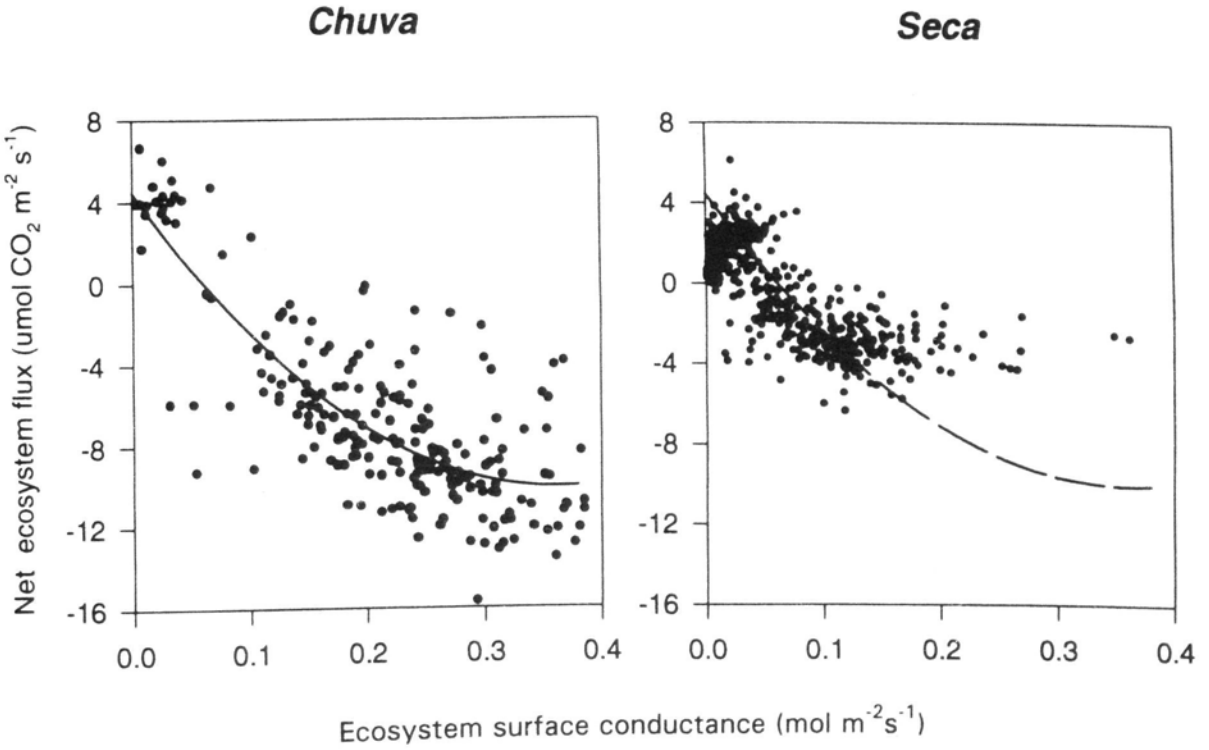

Figure 10. The relationship between ecosystem surface conductance and net ecosystem CO_2 flux in the *chuva* (wet season) and *seca* (dry season). For ease of comparison, the regression curve for wet season data is superimposed on the data illustrating the relationship in the dry season.

tion of C_4 grasses. This calculation gives $p_4 = 0{\cdot}42$ for 1–2 March and $p_4 = 0{\cdot}30$ for 1–2 November.

DISCUSSION

Cerrado compared with other ecosystems

The cerrado is a typical savanna ecosystem, showing seasonal fluctuations in leaf area index, and a seasonally varying physiology with a much-reduced surface conductance in the dry season. It is not yet clear whether the extremely low nitrogen concentrations are typical of all savannas. The lower values for the nitrogen concentration observed for the cerrado species (Table 3) may not only be a consequence of the seasonal variation (Batmanian & Haridasan 1985) but also an effect of dilution, since several species of cerrado grasses accumulate silica (Silva & Laboriau 1970). The values presented here are in agreement with the N concentration determined by Medina (1982) for tropical savanna, Foulds (1993) for species of Southwest Australia, and Borgatto (1994) for 32 species of shrubs and trees of cerrado.

The decline in photosynthesis in the dry season may be inferred from the ecosystem flux/irradiance curves (Fig. 9). They were significantly different in their initial slope, equivalent to 0·015 and 0·013 atoms C per incident

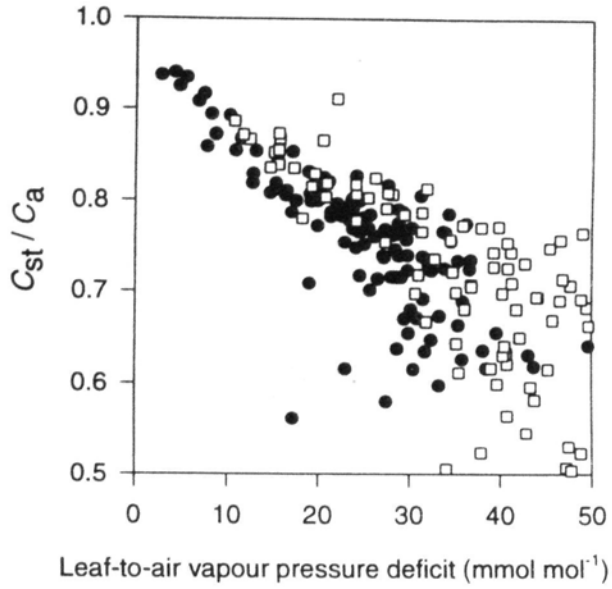

Figure 11. The relationship between estimated ecosystem values of the ratio of CO_2 partial pressure in the substomatal cavity to that in the ambient air (C_{st}/C_a) for both the wet (●) and dry (□) seasons. Data are for cases where solar radiation exceeds 100 W m^{-2}.

photon for wet and dry seasons, respectively. Re-expressed as a quantum requirement, this is 68 and 77 photons per CO_2 molecule fixed, although the difference practically disappears when these figures are re-expressed as absorbed photons, by taking into account the higher short-wave reflectance of the dry season vegetation. Corresponding apparent quantum requirements from comparable studies on 'wild' woody vegetation are: 26 photons CO_2^{-1} for the mixed deciduous Harvard Forest in the USA (Wofsy *et al.* 1993), 20–40 photons CO_2^{-1} in our own work on rain forest in Rondonia, Brazil (Grace *et al.* 1995a,b), and 45 photons CO_2^{-1} in the *Nothofagus* forest of New Zealand (Hollinger *et al.* 1994). The high quantum requirement in the present study is presumably partly the result of a sparser canopy, but might also be the result of the widespread sclerophylly. The cerrado has some similarity to the evergreen Mediterranean *machia,* described by Valentini *et al.* (1991). The CO_2 flux over the *machia* was found to be a linear function of irradiance, and the value of 63 photons per CO_2 molecule fixed by *machia* (implied by fig. 4 of Valentini *et al.* 1991) is close to the quantum requirement of the cerrado vegetation.

Net ecosystem 'dark' respiration rates from these studies may be compared, at the corresponding environmental temperatures. The rates were high in the tropical rain forests of Brazil and in the New Zealand *Nothofagus* (5–7 μmol m^{-2} s^{-1}), and rather less in the Harvard forest (2–3 μmol m^{-2} s^{-1}; Wofsy *et al.* 1993). The rates observed for the cerrado were seen to fluctuate seasonally between 1·6 and 2·3 μmol m^{-2} s^{-1}, presumably in response to the changes in soil water content.

Maximum net carbon assimilation may also be compared: –25 μmol m^{-2} s^{-1} at Harvard, –17 μmol m^{-2} s^{-1} in Rondonia, –18 μmol m^{-2} s^{-1} in Manaus, –13 μmol m^{-2} s^{-1} in New Zealand and –12 and –5 μmol m^{-2} s^{-1} in the wet and dry seasons in the present study. The reliability of such data has been discussed elsewhere (Grace *et al.* 1996; Moncrieff *et al.* 1996). From the viewpoint of statistical sampling, it seems that the amount of data presented in the present paper is sufficient to enable us to scale up to whole-year estimates (see Moncrieff *et al.* 1996). This can be achieved using process-based models of ecosystem carbon balance (e.g. Lloyd *et al.* 1995), with climatological and satellite data to estimate the intensity and extent of regional carbon sinks.

Coupling

In a similar study of tall rain forest (Grace *et al.* 1995a,b, 1996) it was found that the in-canopy CO_2 concentration usually increased at night, as a result of a high rate of soil respiration combined with poor nocturnal ventilation of the canopy. Concentrations of in-canopy CO_2 were as high as 500 ppmv, so that photosynthesis in the early morning took place at elevated CO_2. In the cerrado the situation is different. The vegetation is shorter and sparser, and soil respiration is less (Meir *et al.* 1996). Wind speeds at night did, on average, decline to some extent, but rarely fell below 0·5 m s^{-1}. In the majority of cases examined here, there was little night-time build-up of CO_2 and the storage term calculated from CO_2 profiles was always less than 1 μmol m^{-2} s^{-1}, and often much less. By contrast, in the tall forest the storage flux can amount to over 10 μmol m^{-2} s^{-1}.

Coupling between vegetation and atmosphere is measured by Ω (Jarvis & McNaughton 1986). The values of Ω indicate that this physiognomic form of cerrado is closely coupled to the air stream above it: $\Omega = 0{\cdot}32$ in the wet season and $\Omega = 0{\cdot}17$ in the dry season. These values are similar to those for heathland (Miranda, Jarvis & Grace 1984) and for coniferous forests (Jarvis & McNaughton 1986). The relatively sparse crowns of the trees make the cerrado vegetation a very aerodynamically rough surface and the eddies resulting from the transfer of momentum corrode the characteristic microclimate which could otherwise be built up around the leaves and, in this way, the regional vapour pressure deficit is largely imposed on the surface of the leaves. Near the ground, however, the leaves are less susceptible to this effect of the large mixing eddies, and local leaf surface adjustments may occur.

In the dry season, the amount of transpiring leaves is much-reduced, and the sub-canopy of grasses is especially reduced (Table 2). The ecosystem surface conductance declines correspondingly, and the cerrado becomes even more closely coupled to the atmosphere, presumably because the air movement around the remaining leaves is enhanced.

Inferences from isotope data

From comparison of the near-surface δC values of air with the known isotopic composition of C_3 and C_4 plants (Eqn 5), it appears that about 40% of the CO_2 respired at night must have been of C_4 origin. If the system were in a steady state with respect to fluxes and the above- and below-ground carbon pools, this would also reflect the relative contributions of C_3 and C_4 plants to annual photo-

Table 3. Leaf carbon isotopic composition and nitrogen contents (dry weight basis) of cerrado grasses and shrubs sampled in May 1993

	$\delta^{13}C$ (‰)	Leaf Nitrogen (%DW)
Grasses		
Andropogon sp.	–12·9	0·2
Aristida riparia Trin.	–12·9	0·2
Echinolaeana inflexa (Poir.) Chase.	–26·5	0·6
Melinis minutiflora Beauv.	–13·4	0·3
Paspalum stellatum Humb. & Bonpl.	–12·4	0·2
Palms		
Alagoptera leucocalyx (Dr.) O. Ktze	–29·6	1·0
Butia leiospatha (Mart.) Becc.	–28·6	1·3
Syagrus comosa (Mart.) Becc.	–28·8	1·3
Syagrus flexuosa (Mart.) Becc.	–27·9	1·3
Shrubs		
Anacardium humile St. Hil.	–29·3	1·0
Annona crassiflora Mart.	–30·2	1·3
Annona monticola Mart.	–29·3	2·2
Bauhinia rufa (Bong.) Steud.	–30·0	1·5
Brosimum gaudichaudii Tréc.	–29·2	2·0
Byrsonima coccolobifolia Kunth.	–29·1	1·2
Byrsonima verbascifolia (L.) DC.	–30·3	0·8
Calliandra sp.	–29·3	1·1
Caryocar brasilienese Camb.	–28·4	0·9
Cassia sp.	–29·7	1·7
Croton goyazensis M. Arg.	–30·3	1·7
Davilla elliptica St. Hil.	–29·1	1·4
Didymopanax macrocarpum (Cham. & Schl.) Seem	–27·6	0·9
Dimophandra mollis Benth.	–29·1	3·1
Diospyros hispida DC.	–30·4	0·8
Eremanthus glomerulatus Less.	–28·4	1·0
Erythroxylum campestris St. Hil.	–27·5	1·3
Erythroxylum suberosum St. Hil.	–29·5	1·4
Erythroxylum tortuosum Mart.	–27·6	1·3
Hancornia speciosa Gomez.	–28·3	1·1
Kielmeyera coriacea Mart.	–28·4	1·4
Miconia albicans (Sw.) Triana.	–29·7	1·4
Neea theifera Oerst.	–26·7	5·0
Ouratea hexasperma (St. Hil.) Bail.	–29·0	0·9
Palicourea rigida H. B. K.	–26·1	0·7
Piptocarpha rotundifolia (Less.) Baker.	–30·7	1·3
Pisonia noxia (Netto) Lundell.	–28·5	4·3
Pouteria ramiflora (Mart.) Radlk.	–28·8	1·2
Qualea grandiflora Mart.	–28·0	1·1
Qualea parviflora Mart.	–28·9	1·0
Rapanea guianensis Aubl.	–29·8	1·3
Roupala montana Aubl.	–28·9	0·7
Salacia crassifolia (Mart.) G. Don.	–29·0	1·4
Salvertia convallariodora St. Hil.	–26·9	1·4
Sclerolobium paniculatum Vog.	–30·4	1·1
Stryphnodendron adstringens (Mart.) Civille.	–29·2	0·8
Styrax ferrugineus Nees & Mart.	–29·8	0·8
Tabebuia ochracea (Cham.) Standl.	–30·8	1·5
Vochysia elliptica Mart.	–29·5	1·3
Vochysia rufa Mart.	–30·0	1·0

synthetic productivity. However, like most cerrados, this was a stand regrowing after fire. A considerable proportion of the new C_3 biomass fixed during the 8 year regrowth period would thus have been stored as recalcitrant structural carbon in woody trunks and stems. This carbon would have negligible respiration rates and hence would not be detected using the technique employed here. This is an especially important consideration for savanna ecosystems, where the mean turnover time of carbon in the soil is quite short; about 10 years (Raich & Schlesinger 1992). Respired CO_2 from the soil would thus reflect recent litter inputs, rather than the carbon isotopic composition of the

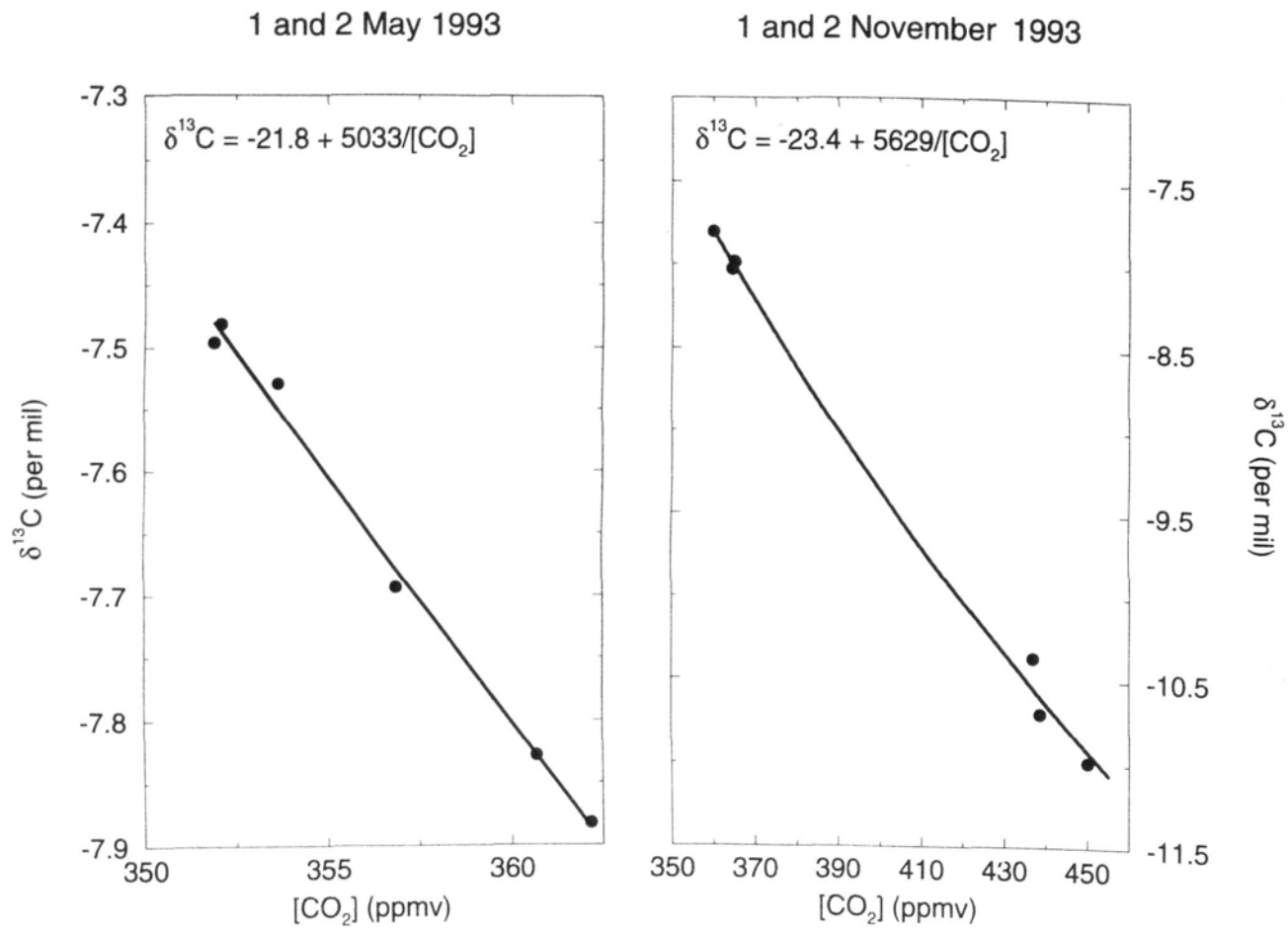

Figure 12. The relationship between the ^{13}C composition (δ_a) and the partial pressure of CO_2 above or within the canopy. For May, the range of partial pressure is so small that the relationship is indistinguishable from linear.

ecosystem as a whole. There are also uncertainties in the calculation due to differences between leaf carbon isotopic composition and other plant organs, and on the basis of what would be expected from on-line carbon isotope discrimination measurements (Henderson, Caemmerer & Farquhar 1992). Based on these considerations an estimate of somewhere between 30 and 35% of the annual sum of photosynthesis by C_4 grasses seems reasonable for this ecosystem.

At least two-thirds of the C_4 photosynthesis would have been occurring in the wet season, as the LAI of live grass foliage was half the wet season value in the dry season (Table 2). Due to physiological differences, the ratio of photosynthesis to stomatal conductance for C_4 plants is usually about twice that of C_3 plants (Farquhar & Sharkey 1982). On that basis, we can assign about 20% of the ecosystem surface conductances (averaged over a year) to C_4 grasses and about 80% to C_3 shrubs. Under the same environmental conditions, stomatal conductances of C_4 grasses are generally similar to those of C_3 grasses (Morison & Gifford 1983) with maximum stomatal conductances (leaf area basis) for C_4 grasses being of the order of 1·0 mol m^{-2} s^{-1} (Morison & Gifford 1983; Kim & Verma 1991). By contrast, even in the wet season, maximum stomatal conductances (leaf area basis) of cerrado tree species are lower (0·2–0·4 mol m^{-2} s^{-1}; Medina 1982; H.S. Miranda, unpublished results).

It should be borne in mind that the floristic composition of cerrado depends upon the season. Even in the absence of changes in environmental conditions from the wet to the dry season, the reductions in LAI for both C_4 grasses and C_3 shrubs in the dry season would be expected to cause a change in net ecosystem gas exchange characteristics. We would expect, in the absence of other changes, a reduction of about 35% in ecosystem photosynthetic rates solely by virtue of lower LAI in the dry season. The actual decrease observed was around 50%, confirming that death of grasses and abscission of leaves from some shrub species was the major cause of the lower ecosystem photosynthetic rate. Indeed, taking reduced LAI into account when ecosystem surface conductances are examined as a function of solar radiation and leaf-to-air vapour difference (Fig. 5), there is little indication of much additional reduction in ecosystem surface conductances in the dry season beyond that expected on the basis of higher leaf-to-air vapour pressure differences and lower incoming solar irradiances. This suggests that there was not a large direct effect of soil water deficit on ecosystem surface conductances during the dry season. In fact, the woody-layer plants have deep roots (some may extend up to 20 m deep) that reach perpetually humid layers in the soil (Eiten 1992).

For both C_3 and C_4 plants there is usually little variation in C_{st}/C_a with changes in irradiance, provided that leaf-to-air vapour pressure difference is held constant (Wong, Cowan & Farquhar 1985). Nevertheless, C_{st}/C_a is usually lower for C_4 plants and, as a consequence of stomatal closure, both plant types show a reduction in C_{st}/C_a with increasing leaf-to-air vapour pressure difference (Morison

& Gifford 1983). A different contribution of C_3 versus C_4 photosynthesis to total ecosystem productivity can thus also be seen in the changing pattern of the relationship between C_{st}/C_a and leaf-to-air vapour pressure difference (Fig. 11). At a given leaf-to-air vapour pressure deficit, C_{st}/C_a was higher in the dry season, indicating a smaller proportion of total ecosystem gas exchange being attributable to C_4 photosynthesis at this time. There was not a large difference between seasons in the proportions of live dicotyledonous (C_3) versus grasses (C_4) biomass (Table 2). This indicates that the grasses may have had reduced gas exchange rates per unit area of soil as a direct response to soil drying. The difference of 2‰ in the isotopic composition of (soil + plant) respired CO_2 also suggests some change in the relative activities of C_3 shrubs versus C_4 grasses, despite little change in the relative proportions of ecosystem leaf area attributable to the two photosynthetic types.

The seasonality in the physiology and morphology of the ecosystem was also reflected in changes in surface energy balance. Of the energy absorbed, a smaller fraction was partitioned to latent heat in the dry season at high solar irradiances (Fig. 2). This saturating response of latent heat flux to incoming solar radiation is consistent with stomatal closure by surviving foliage in response to the high vapour pressure deficits prevailing in the dry season.

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