

**Published in 2001 in *Tree Physiology* 21, 977 – 988.**

Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna

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**Running head: Water and CO<sub>2</sub> fluxes from a north Australian savanna**

## Summary

Daily and seasonal fluxes of carbon dioxide and water vapour above a north Australian savanna were recorded over a complete dry season-wet season annual cycle using the eddy covariance technique. Wet season rates of photosynthesis and transpiration were larger than those measured in the dry season and were dominated by the presence of the grassy understorey. As the dry season progressed and the grass understorey died, ecosystem rates of assimilation and water vapour flux declined substantially. By the end of the dry season, canopy assimilation and evapotranspiration rates were 20-25 % of wet season values. Assimilation was not light saturated in the wet but was saturated in the dry season.

Stomatal control of transpiration increased between the wet and dry season. This was revealed by the decline in the slope of  $E$  with increasing  $D$  between wet and dry seasons, and also by the significant decrease in the ratio of boundary to canopy conductance observed between the wet and dry seasons.

A simple pan-tropical modelling of leaf area index or wet season canopy  $\text{CO}_2$  flux was undertaken. It was shown that using readily available data for foliar N content and the ratio of rainfall to potential evaporation, leaf index and wet season canopy  $\text{CO}_2$  flux can be successfully estimated for a number of tropical ecosystems, including north Australian savannas.

Keywords: Savannas, eddy covariance, water vapour and  $\text{CO}_2$  flux, seasonality, photosynthesis, evapotranspiration.

## Introduction

Savannas (or miombo of Angola, cerrado and caatinga of Brazil, and llanos of Venezuela and Colombia), comprising a discontinuous tree canopy above a seasonally continuous (generally C4) grass sward, occur naturally in Australia, Africa and South America. They are important for ecological, economic, sociological, conservation and climatological reasons (Eamus 1999). They are characterised as occurring in warm (mean annual temperature above 20 °C) and seasonally dry climates. They cover approximately  $15 \times 10^{12} \text{ m}^2$  of the Earth's land surface and are expected to contribute significantly to the global carbon budget and regional hydrological cycles.

There have been many measurements of leaf scale assimilation, stomatal conductance and transpiration rate of savanna trees and grasses. Generally, stomatal conductance ( $g_s$ ) is largest in the wet season and declines in the dry season, and stomata are generally more open in the morning than the afternoon, especially in the dry season (Prior et al. 1997a, b, Eamus and Cole 1997, Pitman 1996, Franco 1998). Diurnal and seasonal patterns of soil and atmospheric water content cause these patterns. Similarly, rates of photosynthesis are larger in the wet than the dry season (Hogan et al. 1995, Le Roux and Mordelet 1995, Sobrado 1996, Eamus et al. 1999) because of seasonal patterns of soil and atmospheric water content, temperature (Prior et al. 1997a) and leaf age (Reich and Borchert 1988). Finally, at the leaf-scale, transpiration rates calculated from knowledge of  $g_s$  and leaf-to-air vapour pressure difference ( $D$ ), decline in the dry season (Sobrado 1996, Prior et al. 1997a).

Despite many leaf-scale determinations of gas exchange, there have been few attempts to determine daily and seasonal patterns of canopy-scale gas exchange in savannas (Miranda et al. 1997, Verhoef et al. 1996). This is in marked contrast to studies of boreal forest (Baldocchi et

al. 1997, Aurela et al. 1996) and rainforest (Grace et al. 1995, 1996, Williams et al. 1998) where relatively extensive canopy-scale assessments of gas fluxes have been undertaken. Furthermore, most studies of canopy gas-exchange have been undertaken where changes in temperature were the primary seasonal variable. Studies in which soil and atmospheric water content vary significantly between season are mostly neglected (Arneeth et al. 1998). Such measurements are required to estimate the contribution of savannas to the global carbon budget and also to regional hydrological cycles.

Coupling between canopy and atmosphere (Jarvis and McNaughton 1986), and hence the relative importance of boundary and stomatal conductance, varies spatially and temporally (San Jose et al. 1998, Meinzer et al. 1997). Furthermore, leaf area index (LAI) and D change seasonally. Therefore extrapolating leaf-scale gas-exchange measurements to canopy processes is likely to be very difficult. Consequently we present the results of a canopy-scale assessment of assimilation rate, stomatal conductance and transpiration rate of a north Australian savanna site.

We test the hypothesis that carbon and water fluxes do not vary markedly between season. This may be possible because more than 80 % of the tree canopy of the study site is evergreen and can access deep supplies of soil water (Cook et al. 1998, O'Grady 1999) and wet and dry season rates of water use by the evergreen trees do not differ (Eamus et al. 2000). We also hypothesise that canopy coupling increases in the dry season but because of changing LAI and prevailing climate, the ratio of aerodynamic conductance to canopy conductance declines in the wet season. Finally, we take the simple pan-ecosystem model of Baldocchi and Meyers (1998) to estimate leaf area index and wet season canopy CO<sub>2</sub> exchange rate of a number of savannas and other ecosystems in order to allow comparisons between savannas and other ecosystems with larger significantly larger LAI.

## Methods

### *Study site and climate*

The study was conducted at a site at Howard Springs (131° 5'E, 12° 30'S), approximately 35 km south-east of Darwin, in the wet-dry tropics, or seasonally dry tropics, of the Northern Territory, Australia. This is an open forest savanna site (see below) which experiences a monsoonal climate characterised by distinct wet (November to March inclusive) and dry (May – September inclusive) seasons. The wet season accounts for approximately 95% of the 1750 mm annual rainfall. Figure 1 shows daily rainfall for Howard Springs (Bureau of Meteorology, Station No. 14149). Marked on this figure are times of the field campaigns. Total rainfall of the 1996/1997 wet season was 2834 mm, the highest on record, with particularly high totals recorded in early January 1997, due to Cyclone Rachel. While reliable in occurrence, the timing of the start and end of the wet season is variable (Taylor and Tulloch 1985).

Mean daily maximum temperature at Darwin Airport (35 km from the field site) ranges from 30.4 °C (July) to 33.1 °C (October and November). Maximum and minimum temperatures have a range of 7 °C (wet season) and 11 °C (dry) (McDonald and McAlpine 1991). Daytime values of vapour pressure deficit (VPD) range from 1.5 kPa (wet season) to 3.1 kPa (June and July). Mean annual pan and potential evaporation for Darwin airport is approximately 2700 mm and 2259 mm pa respectively. Evaporation is largely aseasonal and dry season values range from 6 to 7.3 mm per day, peaking during September and October when solar inclination and radiation loads are largest (Vardavas 1987). Wet season rates are lower at 5.1 - 6 mm day<sup>-1</sup> due to increased cloud cover and water vapour pressure.

## *Vegetation and soils*

Vegetation of the catchment and region is a mosaic of Eucalypt dominated woodlands, open forests, closed forests (*sensu* Specht 1981), seasonally flooded swamps and wetlands. In the Howard River catchment open forest savanna dominates and all measurements were made in this community type. The overstorey is dominated by two evergreen species, *Eucalyptus tetrodonta* (F. Muell.) and *E. miniata* (Cunn. Ex Schauer) which form a discontinuous canopy of about 50 % cover. These two species account for approximately 90 % of the tree basal area of 8-10 m<sup>2</sup> ha<sup>-1</sup>. Overstorey LAI varies seasonally due to the presence of brevi, semi and fully deciduous tree species and ranges from 0.6 during the dry to 0.95 during the wet season. (O'Grady et al. 2000). Evergreen canopy fullness shows little seasonal variation (Williams et al. 1997). Sub-dominant tree species included *Erythrophyleum chlorostachys* (F. Muell.), *Terminalia ferdinandiana* (F. Muell.) and *Eucalyptus porrecta* (S.T. Blake). The understorey consists of semi-deciduous and deciduous small trees and shrubs with a seasonally continuous cover of annual and, to a small extent, perennial grasses. Understorey LAI changes dramatically over the wet season (2-3) with the C4 grass *Sorghum spp.* dominating. This grass senesces early in the dry season (late April) and understorey LAI remains low throughout the dry season (about 0.2).

Soils at the site are predominantly red and yellow, extensively weathered and laterised Kandosols (Isbell 1996). They are weakly acidic and low in nutrient status (Russell-Smith et al. 1995). The A horizon consists of well drained sandy loams with a massive and earthy structure, with a transition at 15-30 cm to a sandy clay loam B horizon. Rounded ferricrete gravels occur on the soil surface and throughout the profile, and are between 20 and 50 % by volume. The seasonal amplitude in volumetric soil water content is large with sandy upper

horizons (0-50 cm) ranging from 0.03 in the late dry to 0.35 at the peak of the wet season. For the clay-loam subsoils (3-3.5 m) water contents range from 0.26 to 0.45. Storage properties of these soils are poor, with only  $0.08 \text{ cm}^3 \text{ cm}^{-3}$  released between field capacity and wilting point (Cook et al. 1998). These soils overlie a surface aquifer with a seasonal amplitude of 8-10 m, bringing it to within 2 m of the land surface (Cook et al. 1998).

### *Flux measurements*

Measurements were made of whole canopy fluxes of water vapour and  $\text{CO}_2$  using eddy covariance techniques (Baldocchi et al. 1988). Four field campaigns, lasting from 8 to 14 days were made during July and September 1997, March 1998 and July 1998. These times of the year represent critical periods of the wet-dry annual cycle. Our site had adequate (1 + km) fetch in all directions, slopes of less than  $1^\circ$  and an open canopy structure (tree to tree distance was approximately 10 m), creating an aerodynamically rough surface. Eddy covariance and associated instruments were mounted on a pole supported by a tower at a height of 18 m. Tree canopy height was 14 m. Turbulent fluctuations of wind speed ( $w'$ ) and air temperature ( $T_s'$ ) were measured using a Campbell Scientific (Logan, Utah) 3-D sonic anemometer (model CSAT3) and water vapour concentration ( $q'$ ) measured using a Campbell Scientific fast-response krypton hygrometer (model KH20).

Above-canopy  $\text{CO}_2$  concentration ( $c$ ) was measured using a fast response, closed-path IRGA (LiCor 6262, Lincoln, Nebraska, USA). Sampled air for  $\text{CO}_2$  was ducted to the IRGA using 18 m of 6 mm ID Beva-Line tubing mounted on the tower at the measurement height. Air was pumped into the IRGA at flow rates of  $8 \text{ l min}^{-1}$  controlled by a mass flow controller (model FC 280, Tylan General, Torrance, California). All sensors were sampled at 10 Hz by the data logger with raw data stored on a portable computer for later processing. The IRGA was

calibrated prior to each field run using a standard CO<sub>2</sub> source. Span and zero drift was found to be small.

Using a ground-based IRGA introduced a delay of approximately 40 samples between  $w$  and  $c$ . This delay and other required corrections to the raw fluxes, as described by Webb et al. (1980) (air density effects), Moore (1986) and Moncrieff et al. (1997) (systematic sampling errors) and Leuning and Judd (1996) (tube sampling errors), were included in the post-processing of the data. Raw fluxes underestimated the 'true' flux by 4 to 15 %, with the larger corrections required for fluxes estimated at night. Spectral analysis of  $w'$ ,  $T_s'$ , and  $c'$  and co-spectral analysis of  $w'T_s'$  and  $w'c'$  were performed by way of fast Fourier transforms using the software package RAMF (Chambers et al. 1996). Time series of 8192 data points were taken from each measurement period, detrended and tapered using a Prazen type window. Log-log plots of spectral density verses normalised frequency for  $w'$  and  $T_s'$  produced slopes of  $-5/3$ , suggesting that the data were uncontaminated and well-conditioned (Stull 1988). Spectra of  $c'$  showed some high frequency noise ( $> 4$  Hz) and signal attenuation due to laminar flow within the sample tube. This loss was corrected by calculating a gain function following procedures described by Leuning and Judd (1996). However this correction was less than 5% as these high frequencies contributed little to the total flux at our site.

Instrumentation was also installed on the eddy covariance tower to measure air temperature, relative humidity. These data were supplemented by measurements from an automatic weather station located approximately 2 km from the eddy covariance tower, which monitored short wave radiation, wind speed, relative humidity and rainfall. Photosynthetic photon flux (PPFD) was not measured directly but was estimated by multiplying short wave radiation by  $1/0.456$  (Monteith and Unsworth 1990).



## *Canopy Storage of CO<sub>2</sub>*

Over forest canopies, fluxes of CO<sub>2</sub> as measured by the eddy covariance sensors does not necessarily equate to the total biotic CO<sub>2</sub> exchange, as CO<sub>2</sub> can be stored within the canopy air space beneath the measurement height (Baldocchi et al. 1988). At the Howard Springs site we did not measure storage directly, but estimated it by assuming changes in CO<sub>2</sub> at the measurement height (z) could be equated to canopy storage as;

$$F_s = \frac{V \cdot c_t}{m} \quad (1)$$

where V is the volume of air column beneath the sensors at measurement height z, c<sub>t</sub> is the change in CO<sub>2</sub> concentration per unit time and m is the molar volume (Hollinger et al. 1994). This assumption is thought to be valid for well-ventilated, aerodynamically rough surfaces (Greco and Baldocchi 1996, Hollinger 1994), which are characteristics of the open forest at our site. At another Eucalypt open-forest site in the NT (Katherine, 14° 40.28' S 132° 39.91' E), this assumption was tested by measuring the CO<sub>2</sub> profile changes over time. Both sites are structurally similar (open forest with a grassy understorey), although mean canopy height was lower (10-12 m) than the Howard Springs site. At the Katherine site, CO<sub>2</sub> concentration was measured at 2, 7, 10 and 16 m height. A regression between values of F<sub>s</sub> estimated using Equation 2 and values of F<sub>s</sub> based on the within-canopy CO<sub>2</sub> profile was highly significant (r<sup>2</sup>=0.95). However the relationship had a slope of 0.86 and an intercept of 0, suggested that evaluating F<sub>s</sub> using changes to above canopy CO<sub>2</sub> concentration alone was underestimating actual storage by approximately 15 %. Estimates of F<sub>s</sub> based on Equation 2 were corrected using the regression.

The net ecosystem exchange of CO<sub>2</sub> (canopy assimilation minus total respiration), F<sub>c</sub>, is then the sum of the eddy (F<sub>e</sub>) and storage fluxes (F<sub>s</sub>);

$$F_c = F_e + F_s \quad (2)$$

We have adopted the micrometeorological sign convention, with negative values of F<sub>c</sub>, F<sub>e</sub> and F<sub>s</sub> indicating net exchange from the atmosphere to the canopy and positive values as a loss back to the atmosphere.

#### *Open-top chamber measurements*

Estimates of understorey evapotranspiration and CO<sub>2</sub> flux were made using open-top chambers (OTC) at the end of the wet season and during the late dry of 1998. Measurements were made on bare soil, grasses and other common understorey shrubs and saplings. Evaporation and CO<sub>2</sub> flux from the substrate enclosed by the chamber was calculated by difference between gas density of air entering and exiting the chamber. The chamber consisted of 2 sections - a lower cylindrical base of 0.77 m diameter and 1.23 m height, made from clear acrylic plastic and a metal frame supporting a clear plastic cone mounted on top of this base. The upper frame had an exit port of 10.5 cm diameter, with the tapering of this upper section designed to improve mixing as air exited the chamber. Total chamber height was 2 m and the volume enclosed was 0.78 m<sup>3</sup>.

Air was pumped into the chamber using an inlet fan mounted at the base of the chamber and flow rate measured at the exit port using a propeller anemometer. Typical exit flow rates were 4 to 6 m s<sup>-1</sup>, depending on canopy drag, giving volumetric flows of 0.035 to 0.052 m<sup>3</sup> s<sup>-1</sup>. Gas concentrations of air entering and leaving the chamber were measured using a LiCor CO<sub>2</sub>/H<sub>2</sub>O

analyser (model LI 6262, Lincoln, Nebraska). Air streams were ducted to the analyser using Beva-Line tubing at flow rates of  $8 \text{ l min}^{-1}$  and controlled by a mass flow controller (model FC 280, Tylan General, Torrance, California). Output from the analyser was recorded using a data logger (21X, Campbell Scientific, Utah, USA) logging at 1 second intervals. The incoming air stream to the analyser was switched between inflow and then outflow, with the measurement of each lasting between 3 to 5 minutes until stable. Following measurement the chamber was removed from the plot to reduce its influence on plot microclimate (Denmead et al. 1993). Air temperature of the out-going air stream was between 2 and 3 °C above ambient during the wet season (March), although this chamber effect was not observed during the dry season (September/October). Plot evapotranspiration was calculated as follows:

$$E_u = V(\rho_{vo} - \rho_{vi}) / A \quad (3)$$

where  $E_u$  is the understorey evapotranspiration rate,  $\rho_{vo}$  and  $\rho_{vi}$  are the vapour densities ( $\text{g m}^{-3}$ ) of the out-going and in-coming air streams respectively,  $V$  is the volumetric flow rate ( $\text{m}^3 \text{ s}^{-1}$ ) and  $A$  is the chamber area ( $\text{m}^2$ ).

$\text{CO}_2$  fluxes were calculated analogously;

$$F_u = V(\rho_{ci} - \rho_{co}) / A \quad (4)$$

where  $F_u$  is the  $\text{CO}_2$  flux from the plot, and  $\rho_{co}$  and  $\rho_{ci}$  are the  $\text{CO}_2$  densities ( $\text{g m}^{-3}$ ) of the out-going and in-coming air streams respectively.

A fractional cover estimate for each substrate type (bare earth, grass, sapling) was used to weight estimates of  $E_u$  and  $F_u$  derived from the OTC. Line intercept methods were used to estimate fractional cover occupied by each substrate type on 10, 50 m transects (Kelliher et al. 1994). These fractions were combined with chamber data to give spatially averaged fluxes of  $E_u$  and  $F_u$ . During the wet season, 6 plots were measured (20 to 22 March 1998), including 3 of mixed *Sorghum spp* grass clumps, bare soil, plus common understorey species *Planchonia careya* (F. Muell.) R. Knuth and *Terminalia ferdinandiana*. During the late dry/build-up measurement, 4 plots were monitored (29 to 30 September 1998) and included bare soil with a small amount of dead *Sorghum spp.* cover, one *E. tetradonta* sapling, or *Cycad armstrongii* (Miq.) or *P. careya* saplings. These substrates represented more than 95% of the cover in the understorey at each measurement time. During the week prior to the dry season chamber measurement, the site received 14.2 mm of rainfall.

## Results

Figure 1 shows a typical cycle of wet and dry seasons. Effective rainfall ( $>10 \text{ mm d}^{-1}$ ) was absent between April 1<sup>st</sup> and October 1<sup>st</sup> and peak rainfall occurred in January and February. Cyclone Rachel resulted in high rainfall intensities and daily totals of up to 250 mm per day in late December 1996. Typical annual rainfalls are ca  $1700 \text{ mm yr}^{-1}$  but the wet seasons of 1996/1997 and 1997/1998 have been unusually large ( $> 2000 \text{ mm yr}^{-1}$ ).

### *Patterns of CO<sub>2</sub> Fluxes*

Daytime values of  $F_e$  represent canopy net photosynthesis. These were the largest in the wet season (March '98) and declined as the dry season progressed (Figure 2). Maximum rates of  $F_e$  during the wet season ranged from  $-9$  to  $-11 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . High rates of assimilation occurred

between 9 and 11 am local time and were maintained for much of the day in the wet season. Diurnal patterns of  $F_e$  during the wet season were also influenced by the frequent occurrence of cloud and reduced PPFD (Figure 2). Wet season rates of  $\text{CO}_2$  flux from the understorey as measured using the open-top chambers ranged from  $-33 \mu\text{mol m}^{-2} \text{s}^{-1}$  from plots dominated by dense patches of *Sorghum* to  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  for bare soil. Using fractional cover for each plot type measured, the area-averaged mid-day  $\text{CO}_2$  flux from the understorey as measured with the OTC was  $-7.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In contrast, maximum photosynthetic rates developed later and declined earlier in the day as the dry season progressed (Figure 2). By the end of the dry season (September),  $F_e$  had declined to  $-2 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 2). Maximum daytime values of  $F_e$  during July or the mid dry season ranged between these seasonal extremes at  $-4 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Similarly,  $F_u$  declined significantly by the end of the dry season, with maximal rates ranging from  $-10.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  for an *E. tetradonta* sapling to  $0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  for bare soil. The area-averaged maximum value of  $F_u$  for the dry season was  $0.66 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

Storage fluxes,  $F_s$  were large during the wet season but declined in importance as the dry season progressed (Figure 3). Early morning values of  $F_s$  during the wet season were typically  $-3$  to  $-5 \mu\text{mol m}^{-2} \text{s}^{-1}$  and were of similar magnitude or larger than  $F_e$  giving values of  $F_c$  during these early morning periods between  $-10$  to  $-16 \mu\text{mol m}^{-2} \text{s}^{-1}$ . By early afternoon,  $F_s$  was near zero and a small fraction of the turbulent flux. By the end of the dry season, early morning storage fluxes were evident, but smaller than those of the wet season and not significant for most of the day (Figure 3). Nocturnal values of  $F_e$  during the wet season had a maximum of  $2.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  with a mean of 1.15. By the mid dry season this rate had declined to a maximum and a mean of 1.2 and  $0.40 \mu\text{mol m}^{-2} \text{s}^{-1}$  respectively. However by the late dry season, the mean and maximum rate had increased to 0.58 and  $1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

Canopy assimilation rate did not become fully light saturated at any time during the wet season (Figure. 4). As the dry season progressed, the slope of the relationship between incident light flux density and assimilation and the maximum rate of assimilation declined significantly so that assimilation became increasingly light saturated as the dry season progressed.

#### *Patterns of Water Vapour Fluxes*

Total evapotranspiration ( $E_a$ ) showed similar daily and seasonal patterns to those of  $\text{CO}_2$  flux. Peak rates of  $9\text{--}10 \text{ mmol m}^{-2} \text{ s}^{-1}$  occurred in the wet season and averaged about  $8 \text{ mmol m}^{-2} \text{ s}^{-1}$  between 1100 h and 1600 h (Figure 5). Such rates are equivalent to a daily total of approximately  $3.5 \text{ mm d}^{-1}$ . Like  $F_e$ , maximum rates of  $E_a$  declined as the dry season progressed. During the mid dry,  $E_a$  was typically  $3\text{--}4 \text{ mmol m}^{-2} \text{ s}^{-1}$  and this occurred between 1100 h and 1400 h, after which a gradual decline was observed (Figure 5). By September (late dry season), maximum mid-day rates of  $E_a$  had declined to approximately  $2 \text{ mmol m}^{-2} \text{ s}^{-1}$  with daily totals of  $1.2 \text{ mm d}^{-1}$  on average.

Seasonal patterns of understorey evapotranspiration,  $E_u$ , reflected patterns of understorey  $\text{CO}_2$  with wet season values of  $E_u$  dominated by *Sorghum*. Peak rates of evapotranspiration from *Sorghum* clumps were  $12 \text{ mmol m}^{-2} \text{ s}^{-1}$  and rates of evaporation from bare soil patches were  $6 \text{ mmol m}^{-2} \text{ s}^{-1}$ . By September, bare soil evaporation declined to  $0.46 \text{ mmol m}^{-2} \text{ s}^{-1}$ . At the Howard Springs site seasonal patterns of Eucalypt transpiration has been extensively measured by O'Grady et al. (1999). Using these data,  $E_a$  and  $E_u$ , daily totals of evapotranspiration have been partitioned into tree transpiration and understorey components in Table 1. These data are expressed in  $\text{mol m}^{-2}$  of ground area per day and demonstrate the large contribution of the understorey to wet season water vapour exchange. Tree transpiration was relatively constant between seasons.

Rates of  $E_a$  increased significantly as D increased during the wet season (Figure 6). There was no evidence of feed forward behaviour of stomatal conductance in response to increasing D.

As the dry season progressed stomatal responsiveness to increasing D increased and by the end of the dry season E was kept constant as D increased throughout the day. Note that all data in Figure 6 are confined to between 1000h and 1600 h when light and temperature vary little.

Ecosystem surface and boundary-layer (or aerodynamic) conductance was calculated from an inversion of the Penman-Monteith equation using measured values of  $E_a$  and atmospheric VPD. Using these bulk conductance's, the decoupling coefficient,  $\Omega$  was calculated (Jarvis and McNaughton 1986). These data are given in Table 2 and show a decline in canopy coupling from about 0.4 to approximately 0.1 between the wet and dry season. Similarly canopy conductance declined from approximately  $0.2 - 0.4 \text{ mol m}^{-2} \text{ s}^{-1}$  to less than 0.1 between wet and dry seasons (Table 2). Finally, boundary layer conductance showed moderate (approximately 30 %) declines in the dry season compared to the wet season (Table 2).

## **Discussion**

### *Photosynthesis*

Maximum rates of net ecosystem exchange ( $F_c$ ) obtained in the wet season in the present study are similar to maximum rates determined over a Scots Pine stand in Finland (Aurela et al. 1996). However rates are considerably smaller than those measured over a temperate broad-leaved forest in SE USA, a *Pinus radiata* plantation in New Zealand or a Brazilian rainforest (maximum rates *ca*  $-20$  to  $-25 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ , Baldocchi 1997, Arneth et al. 1998, Williams et al.

1998). In all cases LAI of the savanna site is considerably smaller (LAI = 1 in the wet season, O'Grady et al. 2000) than the LAI (2-5) of the other ecosystems. In comparison, Miranda et al. (1997) found a maximum rate of  $F_c$  for a Brazilian cerrado (savanna) with a wet season LAI of 1, of -12 to -15  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Similarly Hanan et al. (1998), Verhoef et al. (1996) and Monteny et al. (1997) observed peak  $\text{CO}_2$  flux rates of between -10 and -16  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a Nigerian savanna site where LAI was about 1.2. Thus peak rates of ecosystem photosynthesis for a range of savanna sites appears to be in the range -9 to -16  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , a range similar to that as measured at Howard Springs. Similarly, in all savanna sites studied, as the dry season progresses and atmospheric and soil water decline, thereby causing a decline in LAI, maximum rates of  $\text{CO}_2$  flux decline (Figure. 2, Verhoef et al. 1996, Miranda et al. 1997, Hanan et al. 1998), although seasonality at Howard Springs appears to be larger than the above studies.

This strong seasonality is attributable to three factors. First, a decline in LAI and hence photosynthetic material present. Most of this decline in the present study in both  $E_a$  and  $F_c$  is the result of the complete loss of the grass understorey, which is almost entirely composed of annual C4 species. LAI of the deciduous, semi- and brevi-deciduous components of the tree species (Williams et al. 1998) represents about 15 % of the total tree LAI and thus dry season loss of leaves from these species also contribute to the seasonal decline in LAI and hence  $\text{CO}_2$  flux. Second, a decline in stomatal and ecosystem surface conductance (Table 2, Verhoef et al. 1996, Miranda et al. 1997, Eamus et al. 1999). This is attributed to a reduction in soil water availability and increased evaporative demand (Miranda et al. 1997, Prior et al. 1997, Eamus and Cole 1997). Finally a decline in average leaf performance contributes to the decline in  $\text{CO}_2$  flux in the dry season. As the dry season progresses, average leaf age in the tree canopy increased. Old leaves perform less well than recently fully-expanded leaves (Reich and



Borchert 1988, Sobrado 1996) because of disease and reduced foliar N content as leaves export N prior to abscission.

The importance of the C4 grass understorey in determining ecosystem CO<sub>2</sub> (and water vapour) flux can also be inferred by comparing leaf, understorey and canopy scale measurements of assimilation. Wet season comparisons of maximal rates of F<sub>u</sub> and F<sub>c</sub> suggest that approximately 70% of the day time CO<sub>2</sub> flux arose from the *Sorghum*-dominated understorey. In addition, the two dominant evergreen eucalypts (*E. tetradonta* and *E. miniata*) account for more than 80 % of the tree canopy LAI and biomass (O'Grady et al. 2000). Leaf-scale measurements of assimilation rate show that there was only a 10 – 20 % decline between maximum values in the wet season and minimum values in the dry season (Eamus et al. 1999), although this is an underestimate because the leaf-scale measurements were based on the performance of the most healthy leaves in the canopy rather than a fully random selection of leaves. Therefore if these trees were the major determinant of canopy CO<sub>2</sub> flux, we should expect a similar scale of decline between wet and dry seasons. In contrast, we observed a far larger decline (almost 90 %) and again conclude that the majority of the dry season decline in ecosystem CO<sub>2</sub> flux is the result of the loss of the grass (C4) understorey, plus a decline in photosynthetic potential of a dominant evergreen eucalypts as average leaf age increased.

Tree-scale measurements of water use using sap-flow sensors showed that tree water use is essentially constant throughout the year (Hutley et al. 2000, Table 1). Therefore we should not expect a massive decline in canopy water and CO<sub>2</sub> flux between wet and dry seasons if the trees dominate ecosystem gas exchange. However, 80 % declines in both water and CO<sub>2</sub> flux between seasons were observed, further supporting the view that the C4 grasses dominate ecosystem fluxes in the wet season.

The presence of the grassy understorey also influenced storage fluxes, which were significant during the wet season. Due to soil and canopy respiration and low overnight wind speeds ( $<0.2 \text{ m s}^{-1}$ ) nocturnal build up of  $\text{CO}_2$  was large. Concentrations reached  $400 \mu\text{mol mol}^{-1}$  prior to sunrise. The onset of turbulent exchange following sunrise reduced these storage fluxes (Figure 3) and  $\text{CO}_2$  concentrations fell to  $330 - 350 \mu\text{mol mol}^{-1}$  by mid day. For a period the canopy would be subjected to a  $\text{CO}_2$  enriched air space with conditions conducive to high water use efficiencies and it was during these morning periods (sunrise to approximately 11 am) that the highest rates of  $F_c$  were achieved. In contrast, Miranda et al. (1997) found that  $F_s$  was an insignificant component of the carbon balance for Brazilian cerrado savanna. They showed that there was little build up of  $\text{CO}_2$  and nocturnal wind speeds never fell below  $0.5 \text{ m s}^{-1}$  thereby reducing the development of a stably-stratified nocturnal boundary layer.

Assimilation was never light saturated, in the wet season. The lack of light saturation in the wet season is presumed to be a result of the light response characteristics of the tightly packed C4 grasses. Rainforest and a C4 pasture grass in Brazil have similarly not shown light saturation of assimilation in the wet season. (Grace et al. 1998). The light saturation in the dry season is presumed to be a function of the loss of the grass  $\text{CO}_2$  flux so that tree canopy  $\text{CO}_2$  flux, which was light saturated, possibly all year, became apparent in the total flux estimate.

Mean respiration rates during March and July were relatively low at  $1.15$  and  $0.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$  respectively, 10 % of maximum canopy net assimilation rates. By the late dry season this ratio had increased to 30 %, possibly due to increases in air temperature and the onset of fine root growth and canopy flushing of the late dry season (Williams et al. 1997). For comparison, wet season rates of respiration for Sahelian savanna were  $3.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , in excess of our maximum measured rates at Howard Springs. Miranda et al. (1997) reported rates of 2.8 and

2.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively for the wet and dry seasons for their cerrado savanna site. It is possible that the low nocturnal wind speeds that are a feature of our site, (especially during the wet season when they were near zero), may have resulted in low nocturnal flux estimates. This has been described by Lavigne et al. (1997) and Goulden et al. (1997) who found a systematic underestimate in nocturnal fluxes as estimated from eddy covariance measurements at low wind speeds over tall deciduous forests at the Harvard Forest, USA.

### *Transpiration and coupling*

The rate of transpiration per unit leaf area of the eucalypts is larger in the dry season than the wet season (O'Grady et al. 1999). However, the proportional increase in evaporative demand in the dry season is equal and opposite to the proportional decline in leaf area per tree. Consequently tree canopy water use is very constant between wet and dry seasons (Eamus et al. 1999; Hutley et al. 2000). In contrast, at the ecosystem scale, water use showed a large seasonal decline of approximately 67 %, between wet and dry season (Figure 5, Table 1), identical to the 66 % decline observed by Miranda et al. (1997) and others (Monteny et al. 1997, Tuzet et al. 1997). This decline was the result of large declines in ecosystem LAI (mostly the grass understorey) and reduced stomatal conductance (Verhoef et al. 1996, Eamus et al. 1999). Unlike the recent modelling exercise of Williams et al. (1998), we are not able to infer that the seasonal decline in ecosystem transpiration is primarily due to an increase in soil-root hydraulic resistance. We do not conclude this because the rate of water use per tree is the same in the dry as the wet season (O'Grady et al. 1999) and because water potential gradients between root and leaf do not change between seasons (Myers et al. 1997). This suggests that root-soil hydraulic conductance did not change between seasons and was not limiting to tree water use. We have recently shown (Cook et al. 1998) that the volume of water stored in the top 6 m of soil is sufficient to supply all the water required for transpiration in the dry season.

Evapotranspiration increased with increasing evaporative demand (D) in the wet season. This indicates that despite some degree of stomatal closure, which is almost always associated with increasing D in savanna species (Eamus and Cole 1997, Prior et al. 1997, Franco 1998, Thomas et al. 1999) the extent of closure was insufficient to negate the full impact of increased D. Such increases in transpiration rate with increasing D are commonly observed for well watered plants (Thomas and Eamus (1999), Maroco et al. 1997). The increase reflects the fact that soil water availability and soil/plant hydraulic conductances do not limit supply to the leaf (Thomas and Eamus 1999, Williams et al. 1999). In Monteith's review, this corresponds to region C in the stomatal conductance *versus* transpiration response curve (Monteith 1995). In contrast, in the dry season, transpiration rate was reduced and the rate of increase of transpiration with increasing D declined as the dry season progressed. By the end of the dry season, transpiration rate was both greatly reduced and more importantly, almost insensitive to increases in D. This corresponds to region A of Monteith (1995), and corresponds to a transition in the nature of stomatal responses to increasing D. Transpiration does not increase with increasing D because the stomata are regulating transpiration to rates that can be supported by the reduced availability of soil water at the end of the dry season. Region A in the stomatal response curve represents the transitional phase between there being little or no regulation of transpiration by stomata, to complete feed forward regulation where stomatal closure in response to increasing D is larger than that required to prevent transpiration increasing. It is interesting to note that this feed forward region (region B, Monteith 1995) was not observed in this study. This supports the view that despite 6 months of zero rain, the evergreen trees in this savanna are not water stressed (Cook et al. 1998). *Eucalyptus tetradonta*, the dominant species of this savanna, will show feed forward stomatal behaviour at low values of D when severely water stressed (pre-dawn water potential below -1.9 MPa (Thomas and Eamus 1999). These results are consistent with the hypothesis that stomata are

regulating transpiration rate to maintain leaf water potential above a critical value (Sperry et al. 1998; Oren et al. 1999).

The decoupling coefficient ( $\Omega$ ) evaluates the relative importance of stomatal *versus* boundary layer conductance. In a range of broadleaved tropical forests,  $\Omega$  is in the range 0.6 – 0.9 (Meinzer et al. 1995, Meinzer et al. 1997). This indicates that leaves are relatively uncoupled from the atmosphere and that changes in stomatal conductance are relatively ineffective in determining transpiration rate. In contrast, we calculated values  $\Omega$  of between 0.36 (wet season) and 0.09 (dry season) (Table 2). This compares well with values calculated for a Venezuelan Orinoco Llanos (savanna) and a Brazilian Cerrado (range: 0.03-0.58, San Jose et al. 1998, Miranda et al. 1997) and is a function of the tall but discontinuous tree canopy that characterises savannas (Eamus and Prior 1999). It is clear that stomatal control of transpiration increased in the dry season in savannas, as revealed by the consistent decline in  $\Omega$  (Table 2, Miranda et al. 1997, San Jose et al. 1998). In addition, the ratio of aerodynamic to canopy surface conductance was significantly smaller in the wet season compared to the dry season (Table 2), further highlighting the increasing importance of stomatal control of transpiration in the dry season (Miranda et al. 1997).

#### *Modelling of carbon flux and LAI*

Baldocchi and Meyers (1998) developed a simple global empirical scaling index, for a number of boreal, temperate and tropical evergreen systems. For these systems, LAI could be predicted from knowledge of annual potential evaporation ( $E_{eq}$ ), annual precipitation (P) and foliar nitrogen content ([N]), since  $LAI = [N] P/E_{eq}$ . Leaf area index is one determinant of maximum potential for carbon and water fluxes to and from canopies. Leaf area index is also highly

correlated with a range of ecologically significant variables, including net primary productivity, site water balance and annual temperature (Waring and Schlesinger 1985, Neilson 1995).

We took the Baldocchi and Meyers equation and applied it to savannas. Such seasonally dry forests were absent from Baldocchi and Meyers' analyses. We observed that for a range of seasonally dry forests, there is a significant relationship between  $[N] P/E_{eq}$  and LAI or tree density (Figure 7a, b). Thus, for savannas of north Australia, covering a rainfall gradient of almost 1500 mm, and for other sites in Africa, tree density (which is highly correlated with leaf area and stem volume) or LAI can be predicted ( $r^2 = 0.98$ ) from the following equation:

$$\text{Tree density} = [N] P/E_{eq} \quad (5)$$

where  $[N]$  is foliar Nitrogen content in  $\text{mg g}^{-1}$ ,

$P$  = annual precipitation and

$E_{eq}$  = annual equilibrium evaporation

Foliar N content provides a simple, albeit crude, estimate of nutrient availability and is highly correlated with assimilation rate (Eamus and Prior 1999), whilst the term  $P/E_{eq}$  is a surrogate measure of water availability. The  $[N] P/E_{eq}$  relationship for tree density and LAI may be easier to use than recently developed models based upon plant available moisture and plant available nutrients since the required data are far more available (Walker and Langridge 1997).

There is also a significant relationship between LAI and canopy  $\text{CO}_2$  exchange rate for a number of very disparate ecosystems (Figure 8, data drawn from the literature). It is

noteworthy that the few savanna sites that have been studied appear to fit the same line as sites having far larger LAI. Given the simple relationship between  $[N] P/E_{eq}$  and LAI (Figure 7a) it is clear that, from a range of published data, canopy  $CO_2$  exchange rate can be predicted from a knowledge of foliar N content and the ratio of precipitation to annual equilibrium evaporation, since:

$$CO_2 \text{ flux} = 2.94 \ln(LAI) + 11.95 \quad (r^2 = 0.4, \text{ see Figure. 8}). \quad (6)$$

And

$$LAI = 0.306 * \ln([N]P/E_{eq}) + 0.277 \quad (7)$$

$$\text{Therefore } CO_2 \text{ flux} = 2.68 * \ln(0.31 * \ln([N]P/E_{eq}) + 0.277) + 11.96 \quad (8)$$

Equation 8 yields a prediction of peak growing season  $CO_2$  flux for canopies over a large range of  $[N]P/E_{eq}$  values that include values exhibited by seasonally dry woodlands and forests.

By extrapolating our flux data over time, a crude estimate of Net Ecosystem Production (NEP) can be made for our site. This can be justified by the paucity of such data for tropical savannas, however such estimates should ultimately be made using a combination of process-based models and remotely sensed data describing landscape parameters. We have assumed that the March measurement represents a  $CO_2$  flux maxima, followed by the steady decline as the influence of the dry season increases, resulting in a minimum at the end of the dry season. Mean 24 h totals of  $F_c$  have been integrated and expressed as  $mol C m^{-2} d^{-1}$  and  $tons C ha^{-1}$  per measurement period (Table 3). The selection of the assigned periods is designed to represent each seasonal period, given the available data. Site access from December to February is

difficult given the regularly occurring monsoonal systems (eg Cyclone Rachael, Figure 1) and no measurements were possible during this period. However flux rates during March are close to maximal as both the understorey and overstorey canopies would be fully matured with peaks in soil water store occurring at this time of the year.

Integrated net fluxes suggest that these open forest savannas are a C sink for the entire year, albeit weak by the late dry season. This result is supported by the analyses of tree size class distributions of these coastal open forests of the Darwin region (Wilson and Bowman 1987, O'Grady et al. 2000). Both concluded that these forests are dominated by small tree size classes and are young and actively growing following the major disturbance of Cyclone Tracey in 1974 and the recurrent impact of fire. The total annual C sequestered was approximately 2.8 t ha<sup>-1</sup> y<sup>-1</sup> or 23.5 mol C m<sup>-2</sup> y<sup>-1</sup> (Table 3). These values compare with 0.32 t ha<sup>-1</sup> y<sup>-1</sup> for Sahelian fallow savanna (Hanan et al. 1998), 1 t ha<sup>-1</sup> y<sup>-1</sup> (Grace et al. 1996) and 5.5 t ha<sup>-1</sup> y<sup>-1</sup> (Malhi et al. 1998) for Amazonian rainforest, 2-5 t ha<sup>-1</sup> y<sup>-1</sup> for temperate deciduous forest (Goulden et al. 1996 and Greco and Baldocchi 1996). The estimate of annual net C flux for Howard Springs appears to be high relative to other systems, given overstorey LAI and typical fluxes, due to low values of respiration. Despite uncertainties in reported values of respiration as described above, low rates could be a result of reduced levels of soil organic matter build-up that results from the regular occurrence of fire, which burns these systems every 1-2 years.

Savannas cover a land surface of approximately 15 x 10<sup>12</sup> m<sup>2</sup> (Miranda et al.1997). If we add xerophytic woodlands and other tropical seasonally dry ecosystems, total land area is about 25 x 10<sup>12</sup> m<sup>2</sup> (IPCC 1995). Clearly savannas and seasonally dry forests represent a significant feature in the global carbon economy, despite a low LAI and the impact of a dry season on gas exchange.



In conclusion, we note the following. Despite there being sufficient soil moisture in the top 6 m to supply the transpirational needs of the dominant evergreen eucalypts and despite the rate of eucalypt tree transpiration being the same in the wet and dry seasons, ecosystem CO<sub>2</sub> and H<sub>2</sub>O flux showed very large declines in the dry season. This was due to the large decline in grass cover in the dry season, which dominates wet season C and water fluxes. North Australian savannas are relatively tightly coupled to the atmosphere and the degree of stomatal regulation of these fluxes increased in the dry season. A simple model was able to predict canopy CO<sub>2</sub> flux and LAI for savannas and other ecosystems.

### **Acknowledgments**

This work was supported by the Land and Water Resources Research & Development Corporation (LWRRDC) and the Cooperative Research Centre for the Sustainable Development of Tropical Savannas (TS-CRC), Darwin NT. We are grateful to Ian Lancaster of the Natural Resources Division of the Department of Lands, Planning and Environment, NT Government for the provision of climate data. We also thank Dr Tom Hatton and Dr Alex Held of CSIRO Division of Land and Water for the use of dataloggers and associated meteorological sensors. Dr David Hollinger and Dr Almut Arneth provided helpful advice and the software required to implement the Moore (1986) corrections to the raw eddy covariance fluxes. Ms Georgina Kelley kindly provided water content estimates for our site.

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Table 1. Seasonal values of evapotranspiration at the Howard Springs site partitioned between the total flux,  $E_a$ , tree transpiration as measured using sap flow sensors (O'Grady 1999a) and open-top chamber estimates understorey evaporation,  $E_u$ . Values given in parenthesis are the standard deviations.

<i>Period</i>		<i>Evapotranspiration</i> <i>(mol m<sup>-2</sup> d<sup>-1</sup>)</i>		
		Total	Tree	Understorey
Mid dry	Jul-97	93.5 (6.0)	46.7	46.7
Late dry	Sep-97	68.9 (5.9)	43.5	25.4
Wet	Mar-98	187.3 (20.5)	52.2	135.1
Mid dry	Jul-98	104.9 (7.7)	52.4	52.4

Table 2. Decoupling coefficient ( $\Omega$ ), aerodynamic conductance,  $g_a$  and canopy conductance  $g_c$  for selected days during the 4 measurement periods at Howard Springs. Values are means taken from half hourly estimates for 1100 to 1500 h. Standard deviation of the means are given in parenthesis.

<i>Period</i>		$\Omega$	$g_a$ <i>(mol m<sup>-2</sup> s<sup>-1</sup>)</i>	$g_c$ <i>(mol m<sup>-2</sup> s<sup>-1</sup>)</i>
July 97	Mid dry	0.11 (0.02)	3.10 (0.80)	0.09 (0.02)
Sep 97	Late dry	0.09 (0.02)	2.49 (0.35)	0.06 (0.01)
March 98	Wet	0.36 (0.11)	2.87 (0.19)	0.38 (0.19)
July 98	Mid dry	0.13 (0.03)	3.80 (0.63)	0.11 (0.03)

Table 3. Seasonal rates of the net ecosystem exchange (NEE) of C calculated from integrated 24 h totals of  $F_c$  for the Howard Springs site. Also given is an estimate of net ecosystem production (NEP) in  $t\ ha^{-1}\ y^{-1}$ .

<i>Season</i>	<i>Period</i>	<i>No. of Days</i>	<i>NEE</i> ( $mol\ C\ m^{-2}\ day^{-1}$ )	<i>NEP</i> ( $ton\ C\ ha^{-1}\ period^{-1}$ )
Wet season	15 Dec – 15 April	122	0.11 (0.02)	1.61
Mid dry	16 April - 31 July	107	0.063 (0.01)	0.81
Late dry	1 Aug - 14 Dec	136	0.024 (0.01)	0.40
Annual total ( $t\ ha^{-1}\ y^{-1}$ )		365	23.5	2.8

Figure 1. Daily rainfall at Howard Spring, October 1996 to October 1998, which spans the period of flux measurement.

Figure 2. Diurnal patterns of eddy fluxes,  $F_e$ , for typical days during each of the 4 measurement periods, July 1997 to July 1998 at the Howard Springs site.

Figure 3. Diurnal patterns of the storage and eddy fluxes  $F_s$  and  $F_e$ , for typical days during a) March 1998, b) July 1998 and c) September 1997 measurement periods, July 1997 to July 1998. Also plotted on the right hand axis is the friction velocity ( $u^*$ ).

Figure 4. Relationship between the eddy flux  $F_e$  and PPFD for the 4 measurement periods.

Figure 5. Diurnal patterns of evapotranspiration,  $E_a$  for typical days during each of the 4 measurement periods, July 1997 to July 1998 at the Howard Springs site.

Figure 6. Relationship between evapotranspiration  $E_a$  and vapour pressure deficit, VPD for the seasonal extremes of the wet season (March 1998) and the late dry season (September 1997).

Figure 7. Relationship between a) leaf area index (LAI) and  $[N] P/E_{eq}$  (curvi-linear increase) and b) tree density and  $[N] P/E_{eq}$  (linear increase). Data points are from Schulze et al. (1998), Miranda et al. (1997), Coomes and Grubb (1998) and O'Grady (unpubl) and refer to savannas only.

Figure 8. Derived relationship between maximum wet-season canopy  $CO_2$  exchange rate and leaf area index (LAI). Data are from Schulze et al. (1998), Miranda et al. (1997), Coomes and Grubb (1998) and O'Grady (unpubl), Grace et al. 1995, Hanan et al. 1998, Baldocchi 1997 and



Hollinger et al. 1997. Data cover savannas ( $LAI < 1.5$ ) to rainforests and coniferous forests ( $LAI > 2.0$ ).

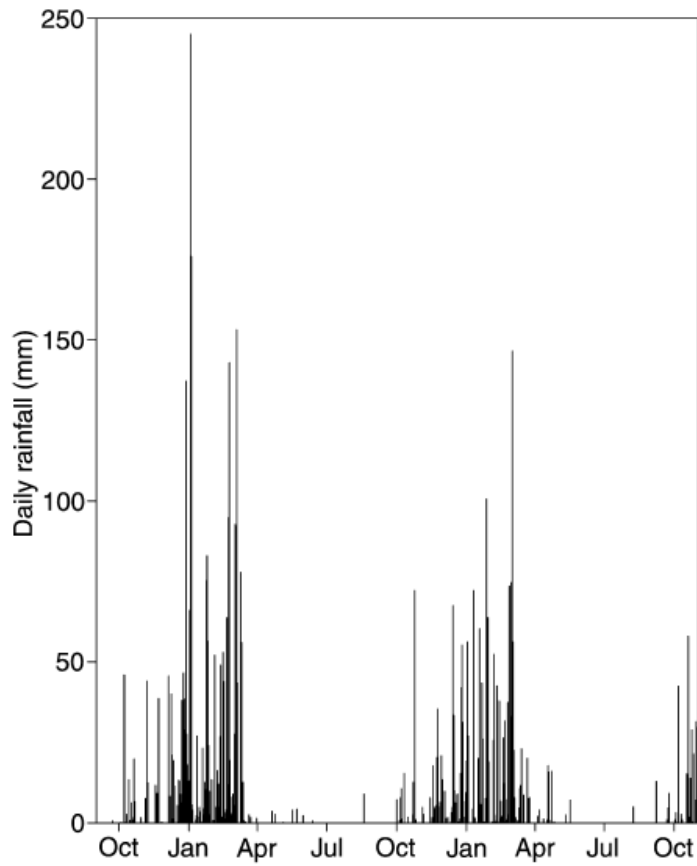


Figure 1. Daily rainfall at Howard Springs, October 1996 to October 1998, which spans the period of flux measurement.

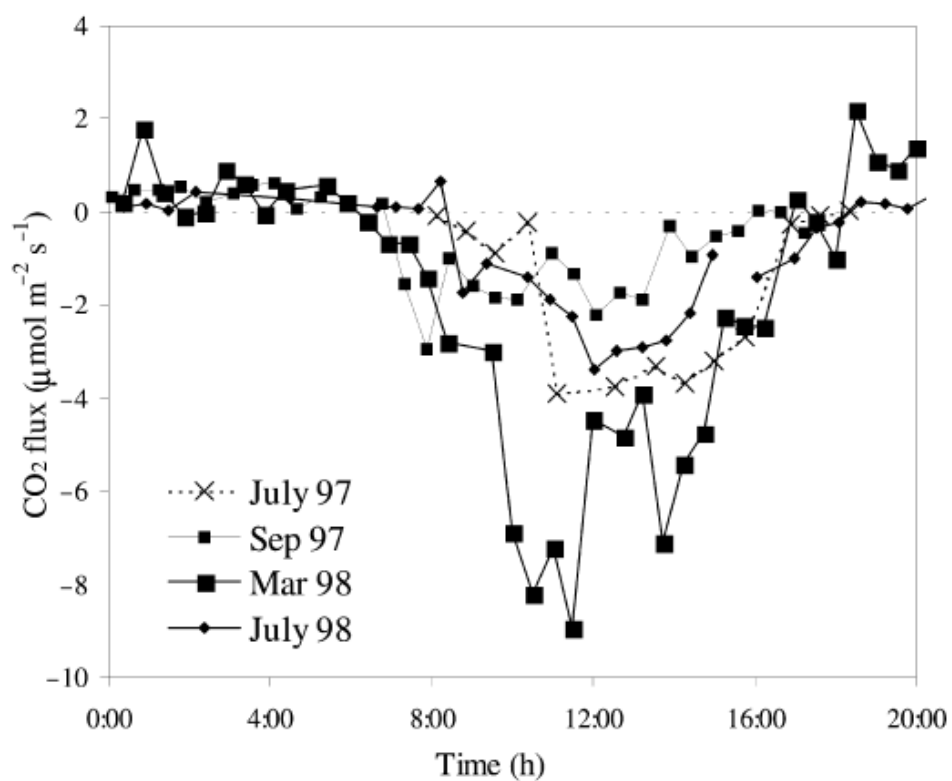


Figure 2. Diurnal patterns of eddy fluxes,  $F_e$ , for typical days during each of the four measurement periods, July 1997 to July 1998 at the Howard Springs site.

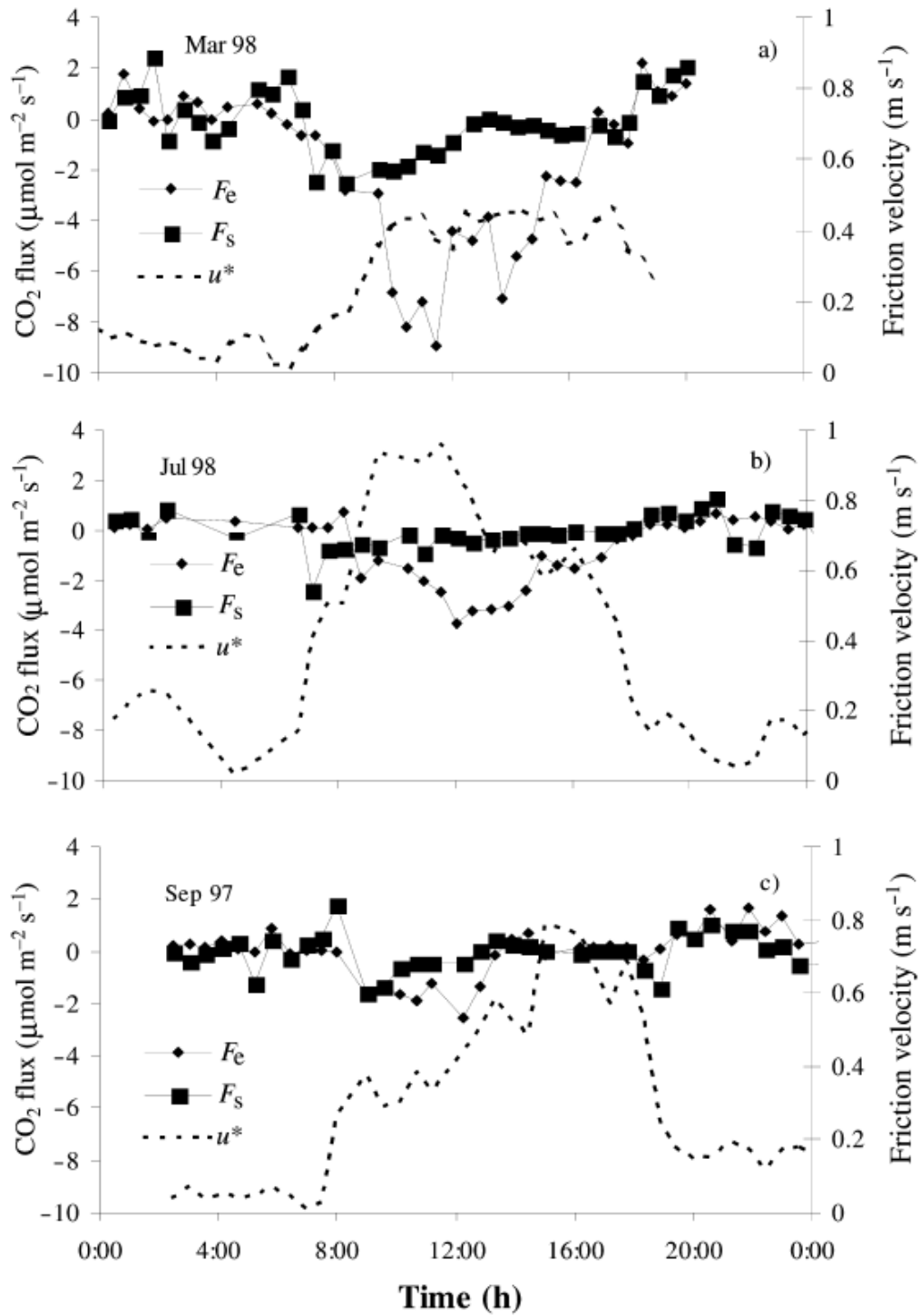


Figure 3. Diurnal patterns of the storage and eddy fluxes  $F_s$  and  $F_e$ , for typical days during (a) March 1998, (b) July 1998 and (c) September 1997. Also plotted on the right-hand axis is the friction velocity ( $u^*$ ).

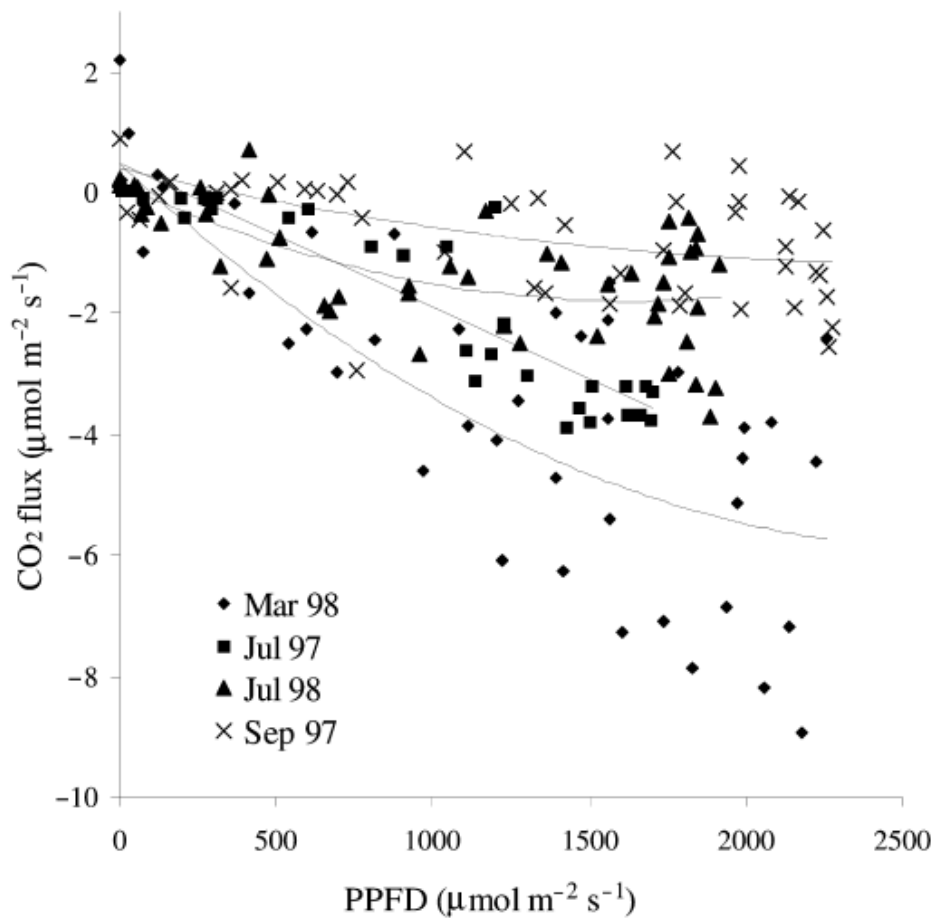


Figure 4. Relationship between the eddy flux  $F_e$  and PPFD for the four measurement periods.

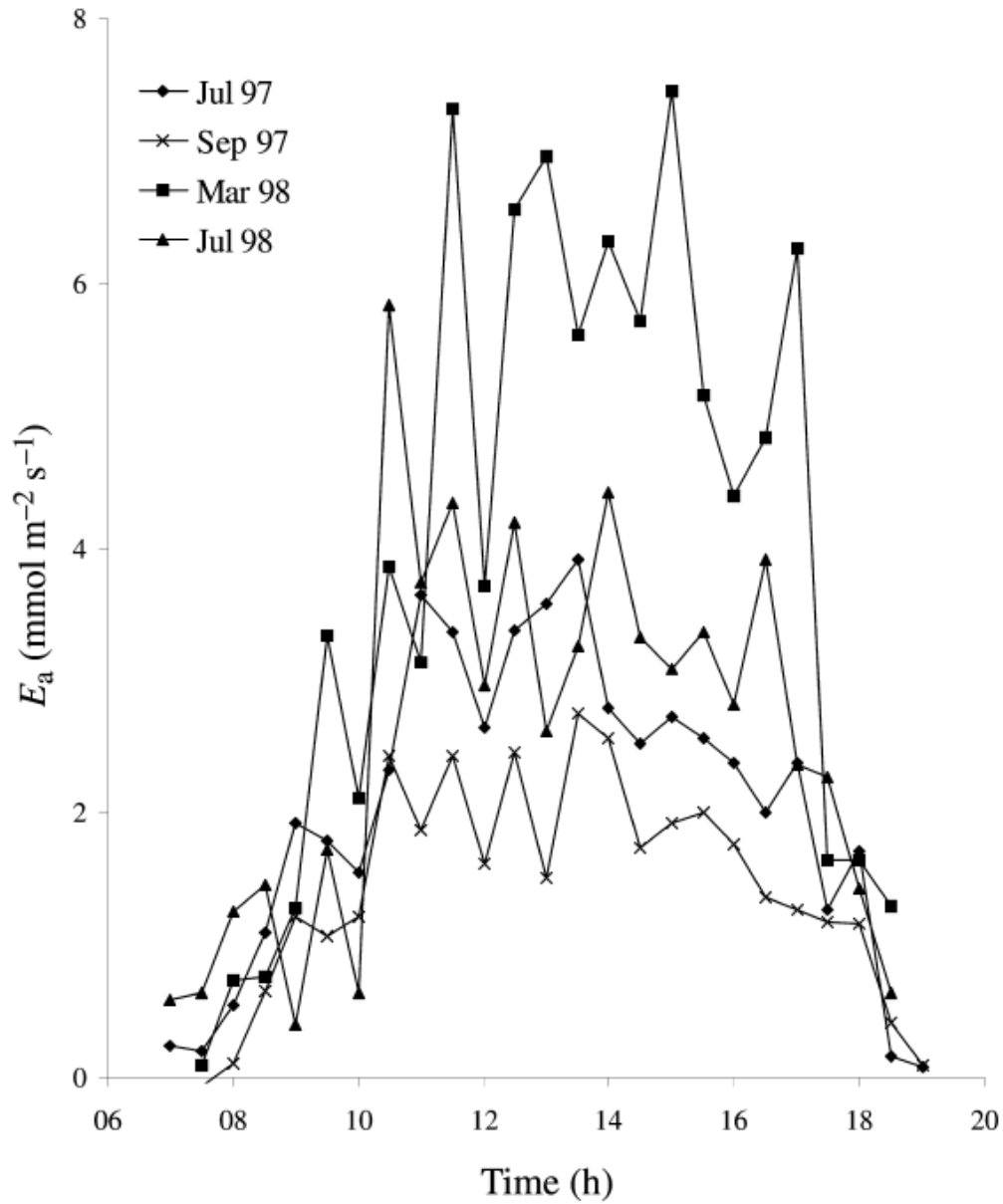


Figure 5. Diurnal patterns of evapotranspiration,  $E_a$ , for typical days during each of the four measurement periods, July 1997 to July 1998 at the Howard Springs site.

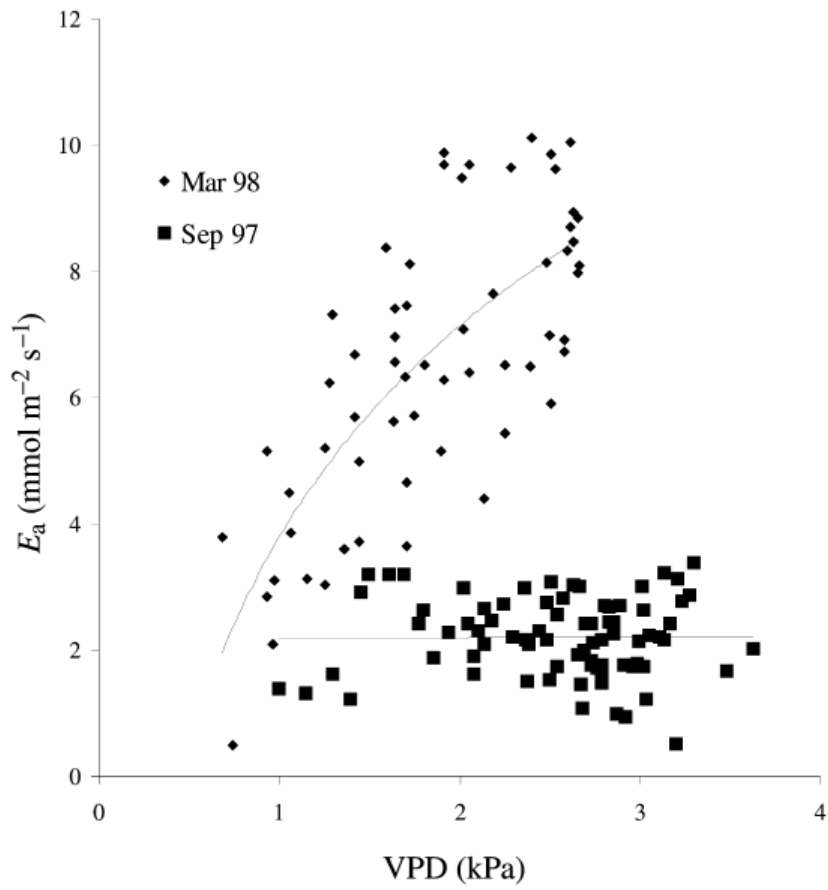


Figure 6. Relationship between evapotranspiration,  $E_a$ , and vapor pressure deficit, VPD, for the seasonal extremes of the wet season (March 1998) and the late dry season (September 1997).

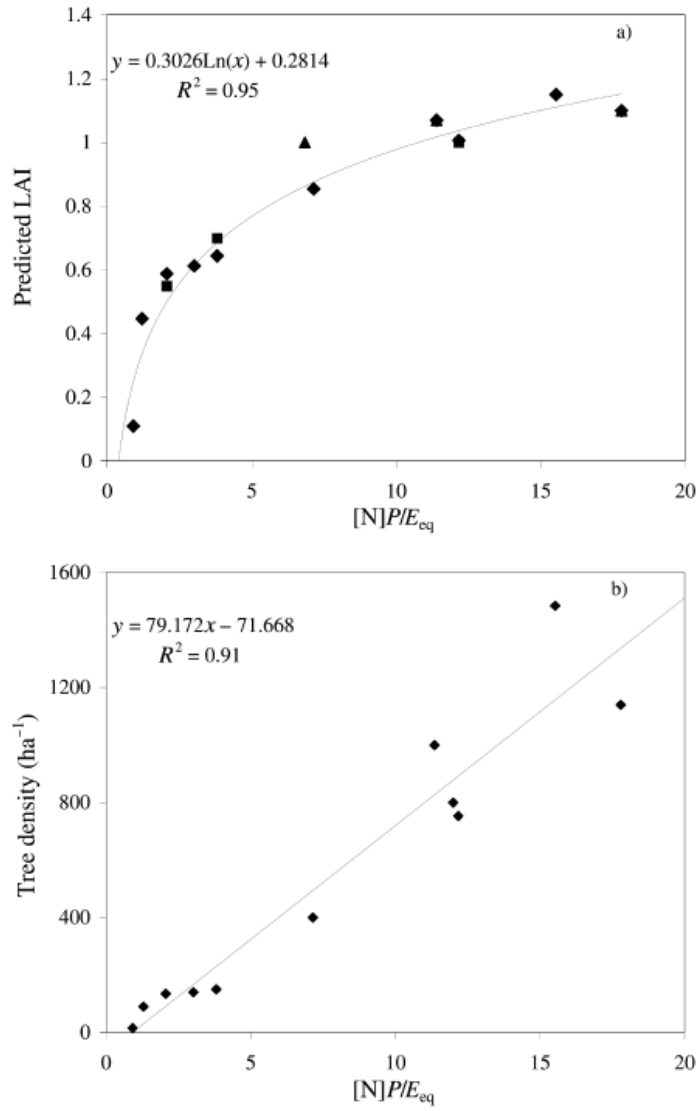


Figure 7. Relationship between (a) leaf area index (LAI) and  $[N]P/E_{eq}$  (curvi-linear increase) and (b) tree density and  $[N]P/E_{eq}$  (linear increase). Data points are from Miranda et al. (1997), Coomes and Grubb (1998), Schulze et al. (1998) and A.P. O'Grady (unpublished data) and refer to savannas only.

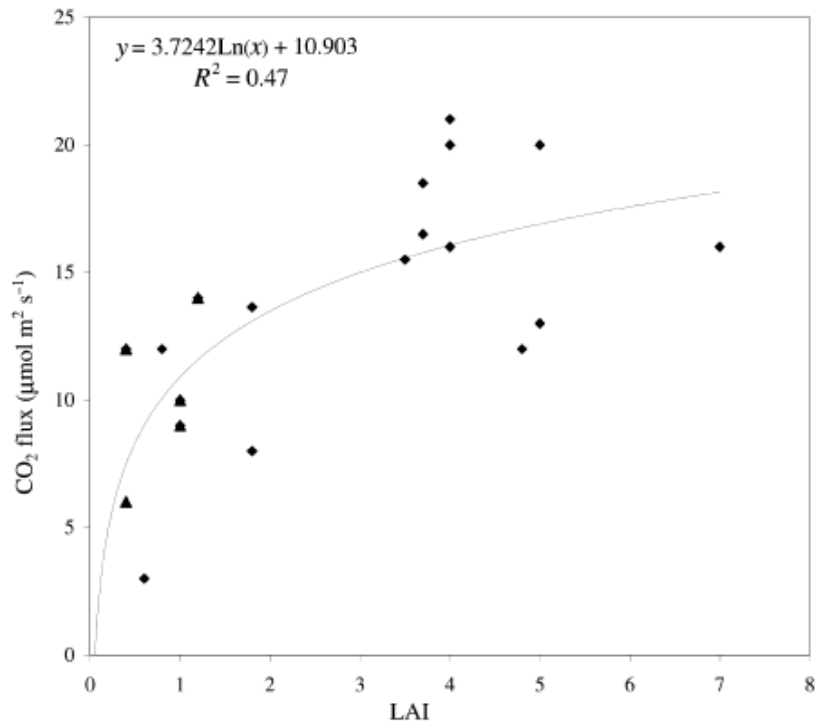


Figure 8. Derived relationship between maximum wet-season canopy CO<sub>2</sub> exchange rate and leaf area index (LAI). Data are from Hollinger et al. (1994), Grace et al. (1995), Baldocchi (1997), Miranda et al. (1997), Coomes and Grubb (1998), Hanan et al. (1998), Schulze et al. (1998) and A.P. O'Grady (unpublished data). Data cover savannas (LAI < 1.5) to rainforests and coniferous forests (LAI > 2.0).