

Savanna fires and their impact on net ecosystem productivity in North Australia

JASON BERINGER*, LINDSAY B. HUTLEY†, NIGEL J. TAPPER* and LUCAS A. CERNUSAK†¹

*School of Geography and Environmental Science, Monash University, PO Box 11A, Clayton, Vic. 3800, Australia, †School of Science and Primary Industries, Charles Darwin University, Darwin, NT 0909, Australia

Abstract

Savannas comprise a large area of the global land surface and are subject to frequent disturbance through fire. The role of fire as one of the primary natural carbon cycling mechanisms is a key issue in considering global change feedbacks. The savannas of Northern Australia burn regularly and we aimed to determine their annual net ecosystem productivity (NEP) and the impact of fire on productivity. We established a long-term eddy covariance flux tower at Howard Springs, Australia and present here 5 years of data from 2001 to 2005. Fire has direct impacts through emissions but also has indirect effects through the loss of productivity due to reduced functional leaf area index and the carbon costs of rebuilding the canopy. The impact of fire on the canopy latent energy exchange was evident for 40 days while the canopy was rebuilt; however, the carbon balance took approximately 70 days to recover. The annual fire free NEP at Howard Springs was estimated at $-4.3 \text{ t C ha}^{-1} \text{ yr}^{-1}$ with a range of -3.5 to $-5.1 \text{ t C ha}^{-1} \text{ yr}^{-1}$ across years. We calculated the average annual indirect fire effect as $+0.7 \text{ t C ha}^{-1} \text{ yr}^{-1}$ using a neural network model approach and estimated average emissions of fine and coarse fuels as $+1.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$. This allowed us to calculate a net biome production of $-2.0 \text{ t C ha}^{-1} \text{ yr}^{-1}$. We then partitioned this remaining sink and suggest that most of this can be accounted for by woody increment ($1.2 \text{ t C ha}^{-1} \text{ yr}^{-1}$) and shrub encroachment ($0.5 \text{ t C ha}^{-1} \text{ yr}^{-1}$). Given the consistent sink at this site, even under an almost annual fire regime, there may be management options to increase carbon sequestration by reducing fire frequency.

Keywords: CO₂ fluxes, eddy covariance, eucalyptus, fire, Howard Springs, net biome productivity, Savanna

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Introduction

Savanna ecosystems are characterised by the coexistence of 'carbon-rich' woody and 'carbon-poor' herbaceous plants dominated by grasses. Savannas occur in over 20 countries, mostly in the seasonal tropics, with a limited distribution in temperate regions (Hutley & Setterfield, 2007). Approximately 20% of the world's land surface is covered with savanna vegetation and this biome is responsible for almost 30% of global net primary production (NPP) (Grace *et al.*, 2006). For tropical savannas, carbon uptake from the woody com-

ponent largely occurs via the C3 photosynthetic pathway and via the C4 pathway for the grass layer. The two coexisting lifeforms (trees and grasses), thus have differing responses to available moisture and nutrient, light, changes to atmospheric CO₂ concentration and temperature and thus mechanistic modelling of savanna responses to climate change is complex. Stochastic events such as fire and climatic variation maintain tree-grass coexistence in savanna, although a unifying ecological explanation for the wide range of observed savanna physiognomy is yet to emerge (Sankaran *et al.*, 2004, 2005).

Fire is possibly the most significant driver of savanna function in Australia and modification of savanna fire regimes influences the tree and grass balance. Reductions in fire occurrence or intensity tend to enhance tree recruitment over herbaceous species, dramatically alter-

Correspondence: Jason Beringer, tel. +61 3 9905 9352, fax +61 3 9905 2948, e-mail: jason.beringer@arts.monash.edu.au

¹Present address: Smithsonian Tropical Research Institute, PO Box, 0843-03092, Balboa, Ancon, Republic of Panama.

ing ecosystem structure and increasing carbon storage in the woody components. Likewise, increased fire frequency or intensity tends to favour grassy components by suppressing tree establishment and/or subsequent growth (D'Odorico *et al.*, 2006). The water regime is also important, with high rainfall years favouring tree recruitment/growth over grasses and drought periods limiting tree recruitment and growth (Sankaran *et al.*, 2004). Therefore, climate change induced increases in rainfall variability is likely to have profound effects on savannas. Rates of herbivory are also significant, with animal grazers impacting the grassy layer and browsers the woody components. High grazing pressure leads to decreases in grass biomass and a reduction in fuel, enhancing the survival of woody seedlings and saplings. Increasing atmospheric CO₂ concentration also has the potential to shift tree–grass balance given the differential growth response to elevated CO₂ inherent in C3 and C4 plants (Bond *et al.*, 2003). Human utilization of savannas essentially involves modification of disturbance regimes as described above and sustainable savanna management requires a thorough understanding of these processes at regional scales. Long-term data sets describing carbon and energy exchange are required to more fully understand the impacts of climate variability and disturbance on savanna productivity and carbon sequestration (Grace *et al.*, 2006).

Given their size and largely tropical distribution, savanna carbon dynamics have a global impact. Savannas have a relatively high NPP with a mean global average of 7.2 tC ha⁻¹ yr⁻¹ (range 1–12 tC ha⁻¹ yr⁻¹), equivalent to 19.9 GtC yr⁻¹ for the entire savanna biome (Grace *et al.*, 2006). This NPP is comparable with that of tropical rainforests (NPP 21.9 GtC yr⁻¹; Grace *et al.*, 2006), but this significant uptake of CO₂ is offset by emissions from disturbance pathways such as herbivory and fire. Satellite-based estimates of carbon emissions due to fire in tropical and subtropical regions (38°N to 38°S) are of the order of 4 PgC yr⁻¹, approximately 10% of NPP for this region (van der Werf *et al.*, 2003). The size of this tropical flux influences interannual variation of global CO₂ concentration and is a major source of global greenhouse gas emissions (Levine *et al.*, 1995; Achard *et al.*, 2004). For savanna ecosystems in this region, the fraction of NPP consumed by fire is as much as 25% (van der Werf *et al.*, 2003). These global estimates of loss need to be matched with precise estimates of net carbon uptake. For example, enhanced biomass productivity of 30–60% after burning has been observed in some humid savanna studies (San Jose & Medina, 1975; Santos *et al.*, 2003).

In north Australia, tropical savanna is the dominant ecosystem and it covers approximately 25% of the Australian land mass. In Australian tropical savannas,

fire is the greatest natural and anthropogenic environmental disturbance, with vast tracts burnt each year ranging from 250 000 to 530 000 with an average of 373 000 km² over the period 1997–2001 (Russell-Smith *et al.*, 2003a). In order to understand the long-term carbon balance of these ecosystems, we need to understand the impact of frequent burning. Savanna fires are frequent but relatively cool (<3000 kW m⁻¹), when compared with southern Australian fires (Williams *et al.*, 1998) and the *direct* impact of fire on the carbon balance includes the carbon emissions from burning of the grassy understorey and coarse woody debris, with little combustion of the over storey canopy elements. In 1992, it was estimated that 74 000 km² of the Northern Territory (NT) burnt and consumed an estimated 29.5 × 10⁶ tonnes of biomass and associated with a likely release of more than 13 Tg of carbon products to the atmosphere (Beringer *et al.*, 1995). Williams *et al.* (2004) estimated fire emissions from the Arnhem Land Fire Abatement region, a landscape-scale fire management project area of some 60 000 km² of mesic savannas in the NT. In typical fire years, 50–60% of this highly flammable vegetation burnt; releasing approximately 3 MtC to the atmosphere each year and when scaled to include mesic savannas (>1200 mm rainfall) of the NT as a whole, 20 MtC yr⁻¹ was released. Despite these emissions of carbon, Williams *et al.* (2004) provided an estimate of savanna net biome productivity (NBP) of approximately 1 tC ha⁻¹ yr⁻¹. However, this estimate of NBP has a large degree of uncertainty as the true sink strength for this ecosystem is uncertain (Williams *et al.*, 2004) and there are no data describing interannual variation of savanna carbon sink strength as a function of climate variability or fire intensity. Nevertheless, carbon cycling is very rapid in these frequently disturbed ecosystems with carbon turnover times of approximately 5 years for mesic savannas of the NT (Chen *et al.*, 2003).

In addition to these *direct* impacts of burning (release of consumed biomass as carbon, aerosols and other trace gases), there are also *indirect* effects of burning such as the reduction in productivity following scorching due to the loss of functional leaf area and carbon costs associated with canopy rebuilding (Cernusak *et al.*, 2006). Fire also increases net ecosystem respiration (R_e) via fire-induced mortality of biomass that was not combusted but killed. This biomass enters litter pools and is subjected to microbial decomposition or serves as fuel for the following dry season fires. For north Australian savannas, this pathway is associated with post-fire leaf fall from the evergreen *Eucalyptus* dominated over storey canopy following moderate to high-intensity fires (>2000 kW m⁻¹). Leaf loss, and subsequent regeneration of the canopy represents a period of lost

productivity (Beringer *et al.*, 2003). The magnitude of this reduction is difficult to estimate, but we suggest it may be as important as the losses from ignition. At the Howard Springs flux site, Cernusak *et al.* (2006) found that young leaves associated with canopy flushing following fire had high respiration rates and took some months to regain a positive carbon balance. Given a fire frequency of 2 out of every 3 years or greater for mesic savannas of north Australia (Russell-Smith *et al.*, 2003a), the impact of fire on these ecosystems is potentially large in terms of carbon dynamics, water use, energy balance (Beringer *et al.*, 2003) and feedbacks to regional climate (Görgen *et al.*, 2006). These impacts assume even greater significance given predictions of increases of up to 30% in seasonal cumulative fire danger in parts of northern Australia under predicted climate change (Williams *et al.*, 2001).

Recently, Grace *et al.* (2006) suggested that savanna ecosystems could act as sites for global carbon sequestration if fire frequency and grazing pressures were reduced. Short-term (1 year) studies of savanna carbon dynamics following fire in central Brazil have shown that regrowth following burning can result in an enhanced carbon sink (Santos *et al.*, 2003). This question is examined in this paper by using a long-term (5 year) flux data set from the Howard Springs eddy covariance site, near Darwin, Northern Territory, Australia.

There has been an extensive suite of ecological (Bowman, 1996), eco-physiological and flux measurements previously conducted at the Howard Springs and similar sites of the surrounding region of mesic, tall-grass savannas. At the Howard Springs site, measurements have been made of vegetation structure and above-ground biomass (O'Grady *et al.*, 2000), patterns of tree transpiration (O'Grady *et al.*, 1999; Hutley *et al.*, 2000), evapotranspiration (Hutley *et al.*, 2000, 2001), soil water dynamics (Kelley, 2002), catchment water balance (Cook *et al.*, 1998), ecosystem CO₂ exchange (Eamus *et al.*, 2001), soil carbon efflux (Chen *et al.*, 2002) and measurements of stem and leaf respiration of burnt and unburnt trees (Cernusak *et al.*, 2006). An inventory-based carbon balance has also been constructed using plots at Howard Springs and similar sites in the Darwin region (Chen *et al.*, 2003).

These previous studies provide useful supporting ecological and physiological data, but most of these studies have not specifically examined the impacts of fire on savanna mass and energy exchange. Only recently have fire impacts on the surface radiation, energy balance been investigated in any detail by Beringer *et al.* (2003), who documented large changes in surface properties of savannas resulting from burning, which included a halving of surface albedo (0.12 to 0.06), a doubling of canopy resistance, an increase in surface

roughness and a resultant decrease in evapotranspiration and increase in sensible heat flux to the atmosphere.

The current study builds on previous eddy covariance studies at this site (Eamus *et al.*, 2001; Beringer *et al.*, 2003) and the inventory-based carbon balance of Chen *et al.* (2003) and provides a detailed data set describing seasonal and interannual patterns of carbon, water and energy exchanges for this frequently burnt north Australian ecosystem. In this paper, we examine seasonal and interannual variation of gross primary productivity (GPP), NPP, net ecosystem productivity (NEP) and net ecosystem respiration (R_e) to estimate the NBP of a mesic, high productivity tropical savanna site, which is impacted by frequent fire.

Materials and methods

Study site

Half-hourly fluxes of heat (H), moisture (LE) and net CO₂ flux (F_c) have been measured over a 5-year period (August 2001 to August 2006) from the Howard Springs eddy covariance site (12°29.712'S/131°09.003'E). This site is located within the Howard River catchment, 35 km south east of Darwin, NT (Fig. 1a). The Howard River catchment comprises 126 km² of gazetted water management area on the Gunn Point Peninsula near Darwin. Howard Springs is a listed Fluxnet site (www.fluxnet.ornl.gov/fluxnet/index.cfm) and data collection is on-going. The climate is wet-dry tropical, with a highly seasonal rainfall (Fig. 1b). A weather station (operated by the Australian Bureau of Meteorology since 1982) approximately 20 km from the flux tower has a mean rainfall of 1782 mm per annum, compared with the mean rainfall at the Howard Springs tower site of 1824 mm (2001–2006). Mean monthly maximum air temperature of the region varies by only 2 °C over the year, although minimum temperatures show more seasonality (Fig. 1b).

The vegetation of the catchment and region is a mosaic of Eucalypt-dominated woodland and open-forest savanna, closed forests, seasonally flooded swamps and wetlands (Wilson *et al.*, 1990). Open-forest savanna is the dominant vegetation type within the catchment, occupying ~80% of the area and flux measurements were made in this ecosystem type. Soils at the site are red-earth sands (red Kandosols, after Isbell, 1996) with an over storey dominated (in terms of leaf area and biomass) by two Eucalypt species, *Eucalyptus tetradonta* (F. Muell.) and *E. miniata* (Cunn. Ex Schauer) (O'Grady *et al.*, 2000). These and other tree species form a canopy of between 14 and 16 m in height, with over storey leaf area index (LAI) ranging from 0.95 to 0.6

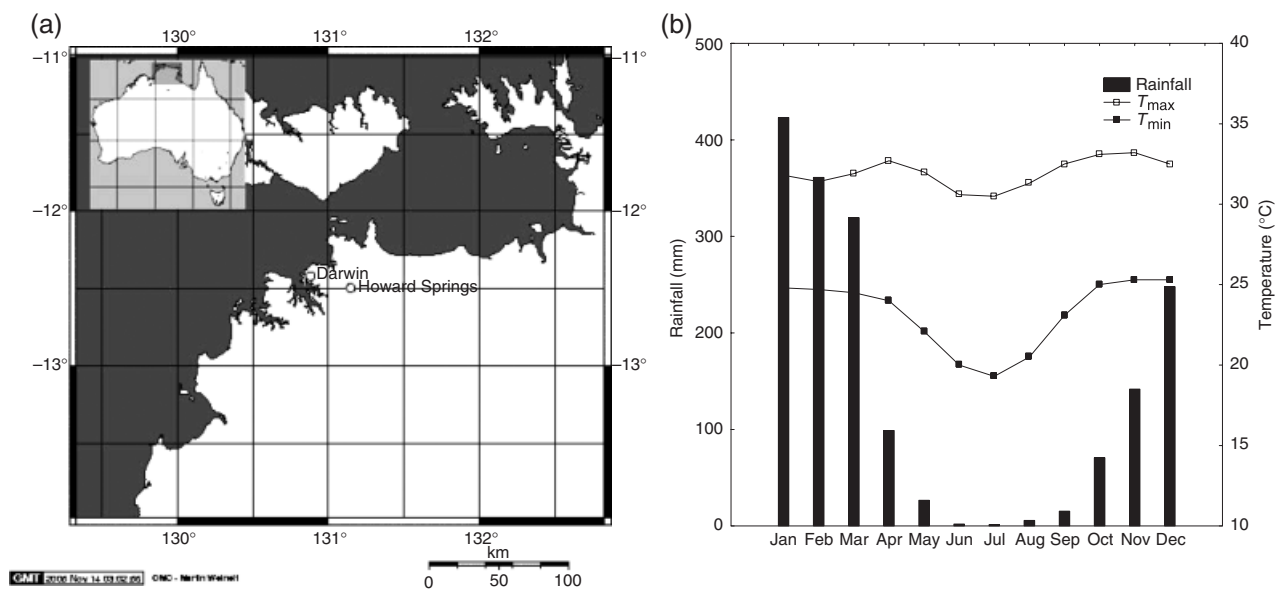


Fig. 1 (a) Savanna flux tower site at Howard Springs in the seasonal wet/dry tropics of northern Australia (12°29.712'S/131°09.003'E). (b) Monthly climate data for Darwin Airport 30 km to the north-west of Howard Springs illustrating the highly seasonal nature of rainfall but relative constancy of temperature (data from Australian Bureau of Meteorology).

between the wet and dry seasons (O'Grady *et al.*, 2000). The understorey consists of semideciduous and deciduous small trees and shrubs, but is dominated by tall C4 grasses, such as the annual species *Sarga* spp. and the perennial grass *Heteropogon triticeus*. Understorey LAI is at a maximum between January to March when it reaches 1.2–1.5 and rapidly declines during April with the senescence of annual grasses and reaches a minimum of ~0.2 by the late dry season (August–September). *E. tetradonta*, *E. miniata* and associated communities are the most widespread tall-grass savanna types in north Australia and this flux site is representative of frequently burnt savanna that occupies an area of some 132 000 km² of the NT (Fox *et al.*, 2001). This and other similar Eucalypt dominated savanna types also occur in north-western Western Australia and the Gulf of Carpentaria region of northern Queensland (Fox *et al.*, 2001).

Flux measurements

Fluxes at the site were measured using the eddy covariance technique (Baldocchi *et al.*, 1988). A 23 m guyed flux tower was located within a plot of approximately 340 ha that consists of *E. tetradonta*/*E. miniata* dominated open-forest savanna, with adequate, homogeneous fetch in all directions (>1 km) and slopes of <1°. Core instrumentation consisted of a 3-D sonic anemometer (Campbell Scientific Inc., model CSAT3, Logan, UT) and an LI-7500 open-path CO₂/H₂O analyser (Licor Inc., Lincoln, NE, USA). Flux variables were

sampled at 10 Hz, with 30 min mean fluxes calculated. The LI-7500 gas analyser was calibrated on a 6–8-week interval for the duration of the data collection period and was highly stable. From mid-2004, all raw 10 Hz data were archived in addition to the 30 min averages. All CO₂ fluxes were corrected for the effects of air density fluctuations arising from sensible and latent heat fluxes (Webb *et al.*, 1980). Daily rainfall, air temperature, relative humidity, soil heat flux and soil moisture at 10 cm depth was also measured at the tower site. The radiation balance was also measured on the tower via incoming and reflected shortwave and atmospheric and surface emitted longwave radiation.

Bulk surface resistance (*r_c*) (s m⁻¹) was determined using eddy covariance measurements and an inversion of the following Penman–Monteith equation (Wallace, 1995):

$$LE = \frac{\Delta(R_n - G) + \rho C_p [(e_s - e)/r_a]}{\Delta + \gamma[1 + r_c/r_a]}, \tag{1}$$

where ρ is air density (kg m⁻³), C_p is the specific heat of moist air (J kg⁻¹ K⁻¹), e_s is the saturated vapour pressure (mb) and e is the ambient vapour pressure (mb).

Neural network (NN) models were developed for gap-filling flux variables of F_c , R_e , LE and H using the Statistica (Statsoft, USA) software package and following the methodology of Papale & Valentini (2003). An extensive auxiliary climate and radiation database was compiled using data taken from the nearby Darwin airport (using both Australian Bureau of Meteorology and US DoE Atmospheric Radiation Measurement

Table 1 Dates of fire events along with intensity and fuel loads for dry season fires during the measurement period 2001–2006

Year	2001	2002	2003	2004	2005	2006
Julian day and date	Day 218 (6 August)	Day 230 (18 August)	Day 241 (29 August)	Day 219 (6 August)	Day 159 (8 June)	Day 146 (26 May)
Mean intensity (kW m^{-1})	3550 ± 640	~ 3000	~ 3200	3610 ± 745	1399 ± 837	1047 ± 232
Fine fuel load (t dry matter ha^{-1})	1.58 ± 0.18	2.90 ± 0.26	3.5 ± 0.76	4.26 ± 0.70	3.81 ± 2.14	3.0 ± 0.62

Standard error of measurements are shown.

(ARM) programme sites) and these data were used for gap filling missing tower meteorological data. Using directly measured data plus gap-filled records, a continuous half-hourly data set for the 5 years has been constructed for all flux, energy balance and meteorological variables.

Nocturnal values of F_c were also corrected during periods of reduced turbulent mixing by screening fluxes measured during periods of low wind speed as per Baldocchi *et al.* (2000). It was assumed that under these conditions, inadequate mixing within the canopy air space resulted in a systematic underestimation of the true respiratory flux from the ecosystem (R_e) as reported in many studies worldwide (Reichstein *et al.*, 2005). When friction velocity (u^*) values exceeded 0.15 m s^{-1} , F_c was taken to be equal to the total ecosystem respiration (R_e) and these data were used in a NN analysis to develop a model between R_e , soil temperature and moisture for the 5 years of data. Modelled R_e replaced night-time F_c data for $u^* < 0.15 \text{ m s}^{-1}$.

Much of the uncertainty in annual estimates from flux towers is derived from errors in accounting for nocturnal fluxes. In our study, the annual average NEP for 2001–2005 was estimated at $-4.3 \text{ t C ha}^{-1} \text{ yr}^{-1}$ using a u^* threshold of 0.15 m s^{-1} . We believe this estimate is robust as it is consistent with other estimates described below. However, without correcting for nocturnal periods of low u^* the annual NEP was $-5.4 \text{ t C ha}^{-1} \text{ yr}^{-1}$ and this represents the likely upper bound of estimates at our site. The impact of applying a higher u^* threshold of 0.2 m s^{-1} reduced the NEP only slightly to $-4.1 \text{ t C ha}^{-1} \text{ yr}^{-1}$ and represents the lower bound of annual estimates. NN modelling of R_e also provided a means of estimating GPP, as it can be extended to daytime periods where values of temperature and soil moisture are used to predict R_e for daylight hours. GPP was then taken to be equivalent to $F_c - R_e$. The time system used here is local Central Standard Time (CST), which is UTC + 9.5 h. Throughout this paper the term daily refers to the 24 h period from midnight to midnight and daytime refers to the period when net radiation is positive (10:00–18:00 hours). Solar noon at Howard Springs is close to 13:00 CST.

Fire regime

The Howard River catchment area has limited fire management and some part of the catchment is burnt every dry season (April to October), largely via human ignition, typical of mesic savannas of the Northern Territory. For these savannas, early dry season fires (late April to June) are typically of low intensity ($\sim 2000 \text{ kW m}^{-1}$) when compared with later dry season fires (August to September, up to 8000 kW m^{-1}) when fuel loads have accumulated and are more fully cured and when the fire weather is more extreme (Williams *et al.*, 1998). For the duration of the experimental period, the flux plot was subjected to a range of fires of varying intensity (Table 1). Initial experimental design involved the instrumentation of two adjacent 350 ha plots, with fire exclusion applied to one and a fire regime applied to the other (Beringer *et al.*, 2003). Given the fire frequency of the region, the size of the plots and a requirement to run two flux systems, this proved to be impractical mainly because excluding fire was near impossible. An ambient fire regime of annual but varying fire intensities was allowed through our single 350 ha plot, with the flux tower approximately centred within this plot. This experimental design enabled the examination of seasonal patterns of flux at our long-term site with relatively homogenous vegetation and flat terrain given a range of fire events, which represented the long-term ambient fire regime. The contemporary and pre-European 'natural' fire regime is discussed by Russell-Smith *et al.* (2003a).

Fire breaks of between 50 and 30 m width were installed around the perimeter of the flux plot to prevent late dry season fires. In addition, a narrow area immediately surrounding the tower was cleared ($< 2.5 \text{ m}$ diameter and clear of ground instruments) to protect enclosures close to the ground. The fires at the site consume fine fuels only and do not develop into crown fires, as foliage of tropical Eucalypts are low in oil content. As a result, eddy flux instruments were not directly affected by flames. However, fire fronts resulted in significant short-term pulses of heat, water vapour and CO_2 concentrations, but these did not affect the

instrument performance and the sensors maintained their calibration. The flux data from the actual fire events have been excluded and gap-filled and the emissions calculated using fuel load measurements. The data were excluded because the assumptions for the eddy covariance technique, especially stationarity of fluxes, were violated. Interestingly, these excluded flux tower measurements of CO₂ emissions during the fire event closely match those derived from fuel load estimates. Each dry season fine fuel load (grasses and leaf litter) was measured within the flux plot via harvesting within 20 m² × 1 m² quadrats. The intensity of fire events within the plot were assessed postfire according to Williams *et al.* (1997), who provides a relationship between leaf char and canopy scorch heights and fire line intensity (kW m⁻¹) for these savannas. Postfire, the plot was assessed and mean char height was measured along 100 m transects randomly established within the plot. Fuel loads and fire intensity for each fire event are given in Table 1.

Fire impacts and NN modelling

Fire events fundamentally alter mass and energy exchange at this site and Beringer *et al.* (2003) found that fire significantly impacted canopy fluxes of *H* and *LE* and for a moderate intensity fire, postfire albedo decreased from 0.12 to 0.07, the Bowen ratio increased from 1.5 to almost 10 and *F_c* was dramatically reduced (Beringer *et al.*, 2003). Clearly for gap filling a single NN model describing both burnt and unburnt conditions was not appropriate. As such, we developed NN models for both fire-free (*UnBurnt* model) and fire-impacted periods (*Burnt* model) using only quality-controlled observed tower *F_c* values. The *UnBurnt* NN model was trained using data over the 5 years, but excluded fluxes for each of the 60-day postfire recovery periods. A separate *Burnt* NN model was developed using data for the period 0–60 days postfire for each year because the fire intensities were different. In each case, the models were trained to predict *F_c* using drivers of incoming shortwave radiation, fractional of canopy absorbed photosynthetically active radiation (*fPAR*, derived from MODIS satellite data for the Howard Springs flux site), soil moisture, air temperature, vapour pressure deficit (*VPD*) and wind speed. For the *Burnt* model, an additional variable of days since the fire event was included to allow the model to account for the recovery over time since fire. The entire 5-year data set was then gap filled by replacing invalid observations using the appropriate NN model (*Burnt* or *UnBurnt*). Hence, a continuous 5-year flux tower data set including the influence of fire was created.

A unique outcome of the development of two models trained under fire-impacted and fire-free canopy conditions was that it enabled us to examine the indirect impacts of fire on carbon fluxes, simply by taking the difference between the observed (gap filled) fire affected flux data and comparing it with the *UnBurnt* NN model for the same period. The *UnBurnt* model predicts carbon fluxes for fire periods as if a fire had not occurred and is driven by the same meteorological conditions for that period and uses unburnt LAI (using *fPAR* as a surrogate). Therefore, the difference represents the loss of production due to fire-related canopy scorch, leaf death and canopy regrowth compared with a NN-modelled unburnt condition. This approach allowed us to assess the impact without the need for a replicated flux tower site unaffected by fire. NN model performance for the *UnBurnt* NN model was evaluated using a regression of daily modelled vs. observed and showed very good correlation coefficient ($R^2 = 0.57$). The slope was 0.91 and the intercept was -0.0051 and was not significantly different from 0 ($t = -1.98$, $n = 679$, $P > 0.05$). For the *Burnt* NN model, performance was similar with a good correlation coefficient ($R^2 = 0.48$). The slope was 1.01 and the intercept was 0.0022 and was not significantly different from 0 ($t = 0.52$, $n = 105$, $P > 0.05$). The results of the *Burnt* NN model can be seen in predicted values compared with observed tower data for the 2003 fire event (Fig. 2). Annual carbon flux components (*NEP*, *GPP*, *R_c*) were calculated for (1) burnt – the observed fire-affected data that were gap filled and (2) unburnt – the observed tower data but with the 60-day fire period replaced with the *UnBurnt* NN model.

Results and discussion

Seasonal and interannual patterns of productivity

Daily *NEP*, *R_c* and *GPP* for the experimental period (2001–2006) are plotted in Fig. 3, along with rainfall and the dates of fire events. A strong seasonal trend in productivity is evident, reflecting the highly seasonal pattern of available moisture and leaf phenology of this savanna (Williams *et al.*, 1997). During the wet season months of February and March the *NEP* averaged $-3 \text{ g C m}^{-2} \text{ day}^{-1}$ (negative fluxes represent a net uptake of carbon by the ecosystem) coincident with maximal LAI (2.5). The wet season fluxes (December to April) were responsible for 72% of the mean annual *NEP* of $-3.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$. This seasonal distribution of carbon exchange is almost identical to that reported by Eamus *et al.* (2001) for a similar site within the Howard Springs catchment, where much of the wet season uptake was due to the rapid growth of C4 grasses in

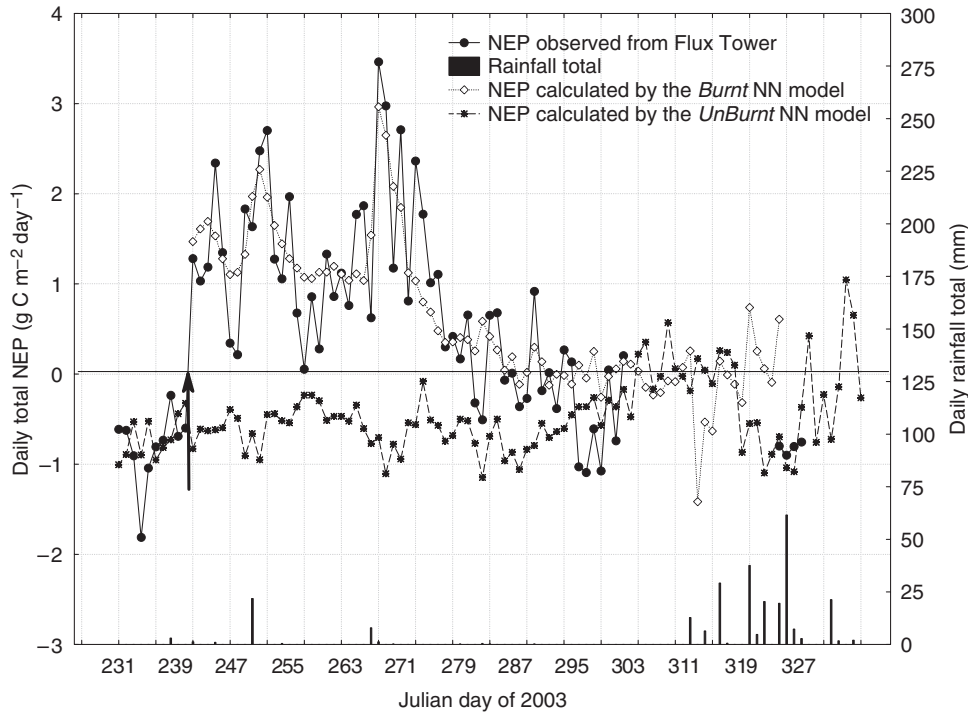


Fig. 2 Performance of the neural network (NN) model estimation of net ecosystem productivity (NEP) compared with the observed flux data using the 2003 fire event as a case study. The period shown is from 10 days preburn to 100 days postburn and the fire event is shown with an arrow. Daily averages are given. Note there are short periods of missing tower data, which have been gap filled using the Burnt NN model to construct a continuous tower based flux time series. The *unBurnt* NN gives the NEP estimate of the savanna system in fire free conditions using the same meteorological data.

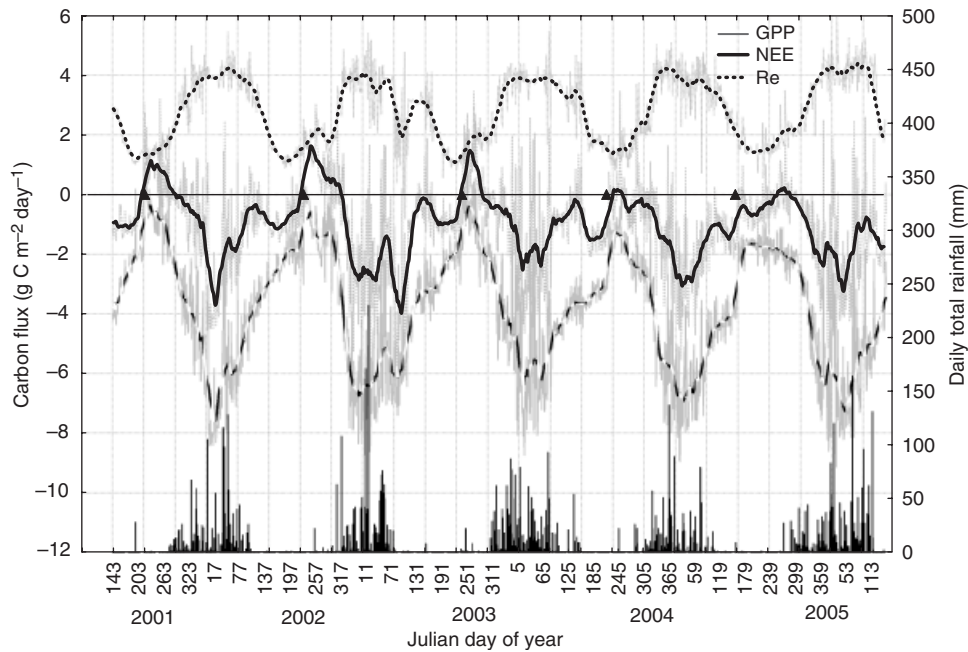


Fig. 3 Observed net ecosystem productivity values from the flux tower for the 5 years of observations (2001–2005). R_e values were calculated using a neural network model trained with nighttime F_c data and driven by soil moisture and soil temperature with gross primary productivity (GPP) shown as the residual. The thick dark lines are the 30-day moving average and the individual daily average values are shown in grey. The individual fire events are shown by the solid triangles. The fluxes vary strongly with seasonal rainfall, which is also shown.

the understorey. These grasses typically germinate at the commencement of the premonsoonal rain events after approximately 50 mm of accumulated rainfall. Rapid growth occurs through the wet season until March, when they seed and senesce. Significant wet season rainfall normally ends by April when grasses become dormant and in general, the understorey makes a smaller and smaller contribution to net carbon uptake as moisture availability reduces moving into the dry season (Fig. 3). However, a net uptake of $\sim -1 \text{ g C m}^{-2} \text{ day}^{-1}$ was maintained throughout the dry season (June) largely due to evergreen trees and shrubs, which maintain canopy leaf area (Williams *et al.*, 1997) and photosynthesis through the dry season (Eamus *et al.*, 1999) due to their ability to access deep soil water stores (Eamus *et al.*, 1999). Fire events shifted the ecosystem from this weak dry season carbon sink to a net carbon source, the duration and magnitude dependant on fire intensity and the distribution of premonsoonal rainfall events of the next wet season (e.g., see Figs 2 and 5).

Following the first rains, the ecosystem became a strong source of carbon to the atmosphere for a short period, which was likely to be associated with dramatically increased soil respiration after the prolonged dry season, a typical 'Birch type' effect (Birch, 1958). The leaf phenology of these savanna ecosystems are highly dynamic (Williams *et al.*, 1997), especially during the premonsoonal period (October to November) when tree and shrub species flush their canopies, a process that occurs with or without fire. During the wet season short spikes of 1 or 2 days duration were evident (Fig. 3) where the system reverted to a carbon source. These events were associated with heavy rainfalls after a 2 or 3-week break in the monsoon. High levels of cloud cover and low radiation during these periods reduced GPP and increased soil respiration resulting in day to day changes in the sign of NEP. Soil respiration in these savannas is particularly sensitive to soil moisture (Chen *et al.*, 2002) and this is evident in the response of ecosystem respiration to rainfall (Fig. 3). Table 2 provides annual estimates of NEP, R_e and GPP for the site.

Fire impacts

Fire will affect the carbon dynamics of the ecosystem in three ways; (a) via *direct* emissions of carbon from fuel combustion, (b) via the *indirect* impact of fire on both short- and long-term productivity and (c) via the impact of surface and vegetation change on surface-atmosphere coupling (fluxes of heat, moisture and momentum). Direct emissions are easily quantified by measuring fuel loads and combustion efficiencies (Table 1). The indirect effect is illustrated in Fig. 4 and

Table 2 Annual production indices NEP, R_e , and GPP for the Howard Springs site for each of the five experimental years of flux data

Experimental year	2001			2002			2003			2004			2005			Mean		
	B	UB	B	B	UB	B	B	UB	B	UB	B	B	UB	B	B	UB	B	UB
NEP	-2.9 (0.17)	-4.0 (0.17)	-4.0 (0.18)	-5.1 (0.17)	-2.6 (0.16)	-3.5 (0.15)	-4.4 (0.17)	-4.7 (0.17)	-4.0 (0.17)	-4.3 (0.17)	-3.6 (0.17)	-4.3 (0.17)	-4.3 (0.17)	-3.6 (0.17)	-4.3 (0.17)	-4.3 (0.17)	-3.6 (0.17)	-4.3 (0.17)
R_e	10.3 (0.05)	10.1 (0.05)	9.5 (0.06)	9.0 (0.07)	10.2 (0.05)	9.7 (0.05)	10.6 (0.06)	9.3 (0.07)	10.5 (0.05)	10.3 (0.05)	10.2 (0.05)	10.3 (0.05)	10.5 (0.05)	10.2 (0.05)	10.3 (0.05)	10.2 (0.05)	10.2 (0.05)	9.7 (0.06)
GPP	-13.2 (0.17)	-14.1 (0.16)	-13.4 (0.18)	-14.1 (0.17)	-12.9 (0.16)	-13.2 (0.14)	-14.9 (0.17)	-14.0 (0.17)	-14.5 (0.17)	-14.5 (0.17)	-14.5 (0.17)	-14.5 (0.17)	-14.5 (0.17)	-13.8 (0.17)	-14.5 (0.17)	-14.0 (0.16)	-13.8 (0.17)	-14.0 (0.16)
Rainfall (mm)	1813		2048		2085		1504		2248		1940 (129)		2248		1940 (129)		1940 (129)	

Indices are given for observed gap-filled flux tower data that includes the influence of fire (*Burnt* - B) and estimated unburnt condition using an NN model (*Unburnt* - UB). The UB data series was constructed using observed fluxes but gap filled for the 60 days postfire using a NN model trained using fire free periods. All data are $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ and have units of $\text{t C ha}^{-1} \text{ yr}^{-1}$. Values in brackets are the standard error of the mean for each year based on 30 min flux estimates. GPP, gross primary productivity; NEP, net ecosystem productivity; NN, neural network.

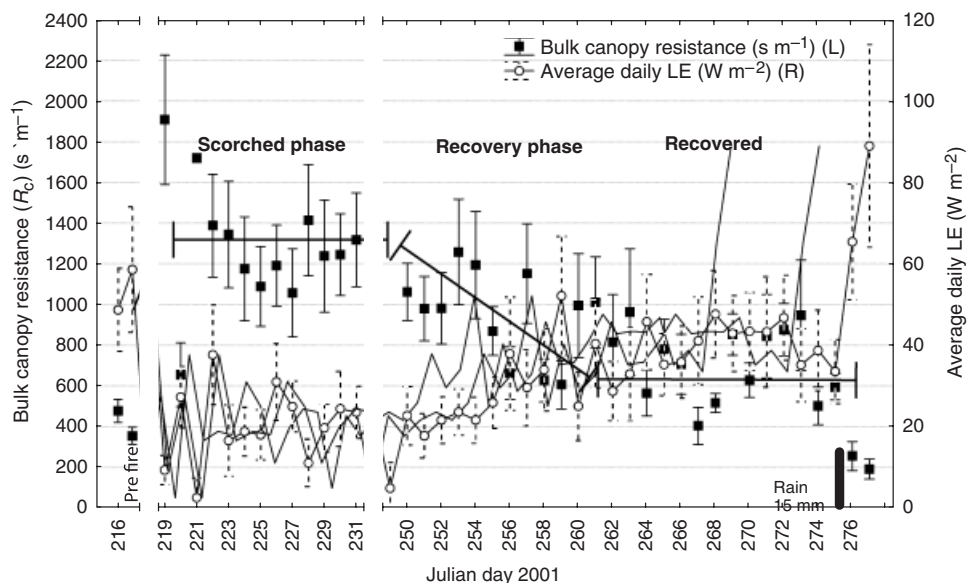


Fig. 4 Impact of fire on canopy latent energy (LE) exchange and bulk canopy resistance. The preburn data are shown as an average of the preceding 10 days. Average daily LE decreases dramatically following fire when the canopy is scorched and photosynthesis ceases (scorched phase). The canopy is rebuilt during the 'recovery phase' and LE increases. The LE and bulk canopy resistance return to preburn values approximately 40 days following fire. Also shown is the effect of the only rainfall for the period (15 mm) on day 275.

it describes shifts in canopy dynamics following the 2001 fire event. This fire resulted in approximately 80% leaf scorch and almost immediate cessation of photosynthesis and transpiration from affected leaves. The observed tower latent energy (LE) flux can be considered as mostly canopy transpiration because the soils are particularly dry (<4% volumetric soil water content) with minimal soil evaporation. Following fire the surface resistance reached 1900 s m^{-1} and LE was reduced by a factor of 3 as leaves died during this 'scorched phase'. Subsequent leaf drop occurred within the week following fire and the canopy maintained this state for approximately 20 days, which was followed by a gradual 'recovery phase' as LAI increased. After 40 days the canopy resistance was similar to prefire conditions and had 'recovered' with regard to canopy transpiration. The fire event in 2001 occurred during the late dry season and a premonsoon rainfall event of 15 mm occurred which increased LE significantly (Fig. 4).

Carbon dynamics following fire differed from water, with a longer period of recovery evident. Figure 5 describes the behaviour of NEP following the same fire in 2001 and shows that before the fire NEP was a dry season sink of approximately $-1 \text{ g C m}^{-2} \text{ day}^{-1}$ shifting to a source of $2.5 \text{ g C m}^{-2} \text{ day}^{-1}$ in the 3 days following the fire (Fig. 5). Even though the canopy had recovered in terms of transpiration within 40 days, the carbon balance remained a source for at least 70 days. The exact period of recovery is difficult to determine because of

the premonsoonal rain that begins at this time of year, which enhances soil respiration and leads to the ecosystem tending towards carbon neutral with or without fire (Fig. 5). The *UnBurnt* NN model can be used to predict carbon dynamics in the absence of this fire and for this period (70 days August to early October 2001), an unburnt canopy would have been a sink of -58.1 g C m^{-2} , whereas the burnt canopy was a source of 56.3 g C m^{-2} , a difference of 1.1 t C ha^{-1} .

We suggest that the shift from carbon sink to source for this late dry season fire event is largely due to the loss of overstorey canopy photosynthesis and enhanced respiration costs associated with canopy regeneration, both construction and maintenance respiration. Understorey grasses are completely senesced or dormant and scaling site-specific data describing woody photosynthesis and respiration (Cernusak *et al.*, 2006) provides an opportunity to examine the validity of the *UnBurnt* vs. *Burnt* NN models. During this dry season period, woody stem growth has been shown to be zero at this site (Chen *et al.*, 2003, Cernusak *et al.*, 2006) and woody stem respiration is largely maintenance respiration, which for the dominant, thick-barked Eucalypts (*E. tetradonta* and *E. miniata*) are little affected by fire (Cernusak *et al.*, 2006). Given the low soil moisture levels at this time of the year and only a moderate intensity burn, soil respiration is not likely to be influenced significantly by fire. Thus changes to ecosystem carbon dynamics postfire will be dominated by overstorey canopy dynamics, namely maintenance and con-

struction costs of canopy regeneration. The 2001 fire event resulted in approximately 80% canopy loss within the flux plot and Cernusak *et al.* (2006) provided an estimate of the construction respiration based on leaf biomass increment associated with canopy regeneration for the Howard Springs site. The LAI at the time of the 2001 fire was 0.79 (Tame, 2002) and replacement of 80% of canopy LAI following fire would be equivalent to a construction of 0.63 m^2 of foliage m^{-2} ground. The specific leaf area is $5.5 \text{ m}^2 \text{ kg}^{-1}$ for the dominant Eucalypt species (Cernusak *et al.*, 2006), with a C mass fraction of new foliage of 0.49 and a measured growth respiration coefficient for the Howard Springs site of $0.25 \text{ g C respired per gram C for new biomass}$. Combining these values gives a construction respiration associated with replacing scorched foliage of 65 g C m^{-2} ground area for the recovery period. Leaf maintenance respiration can also be estimated via dark respiration rates of foliage from burnt and unburnt trees given by Cernusak *et al.* (2006) along with a simple Q_{10} based function driven by mean daily temperature as measured by the flux tower. Assuming a Q_{10} of 2.7 gives a leaf maintenance respiration of approximately 38 g C m^{-2} , which is a total respiratory cost of approximately 1.03 t C ha^{-1} for the recovery period. This flux is similar to the 1.1 t C ha^{-1} difference between the observed fire affected fluxes and the estimated unburnt condition (from the *UnBurnt* NN model).

The data of Cernusak *et al.* for unburnt trees, both stems and foliage, can also be used in combination with August 2001 soil respiration rates of Tame (2002) to estimate a simple dry season carbon balance for an unburnt canopy. This can be compared with the *UnBurnt* NN model estimate for this same period. This calculation was made assuming respiration and mean photosynthesis rates for mature foliage at the site, with a mean photosynthesis rate of $8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for a 10 h photoperiod (Eamus *et al.*, 1999, Cernusak *et al.*, 2006), an LAI of 0.79 with no leaf construction costs and unburnt stems. These canopy properties would result in a net carbon sink of -65 g C m^{-2} , similar to the *UnBurnt* NN model estimate of -54.4 g C m^{-2} for this period. These estimates are approximations only, but suggest that tower-based measures of F_c and NN models for burnt and unburnt canopy conditions are reasonable and some faith can be placed in annual production indices for the site (Table 2).

Annual productivity and fire

The dramatic shifts in NEP following fire are evident in Fig. 3. The fire event of 2004 was estimated at 3610 kW m^{-1} , the highest recorded, but surprisingly it had a minimal impact, with the ecosystem a source for

only 20 days postfire. The early dry season event of 2006 (not shown) was the smallest, at 1047 kW m^{-1} and had no impact on NEP, which remained negative throughout the dry season. For the calendar year until September 2006, cumulative u^* star corrected NEP was already very large at -3.9 t C ha^{-1} and the annual sink is likely to be the largest recorded to date. Using the observed gap-filled flux tower data the annual NEP of the site between 2001 and 2005 was $-3.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$. There was no apparent relationship between production and rainfall of the experimental year. The highest NEP of $-4.4 \text{ t C ha}^{-1} \text{ yr}^{-1}$ was measured during 2004, the experimental year of the lowest rainfall (1504 mm). The mean difference between the observed gap-filled flux tower data and estimated unburnt condition (*UnBurnt* NN model) for the 5 years of record was $0.7 \text{ t C ha}^{-1} \text{ yr}^{-1}$ (Table 2), a measure of the *indirect* impact of fire on the ecosystem and representing the costs of lost productivity from reduced functional LAI and canopy reconstruction following fire. This value is consistent with calculations of canopy reconstruction calculated for the 2001 fire (1.1 t C ha^{-1}), which was the most intense fire event. The indirect effect of fire varied for each year dependent mainly on fire intensity (Table 2).

The eddy covariance derived estimate of NEP over 5 years at the Howard Springs flux site of $-3.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$ is very similar to the inventory and scaled flux estimates of Chen *et al.* (2003) also conducted within the Howard River catchment and at other similar savanna sites within the Darwin region. Chen *et al.* (2003) measured all component carbon stocks and fluxes and reported an NEP of $-3.8 \text{ t C ha}^{-1} \text{ yr}^{-1}$. In light of our more recent work at the Howard Springs flux site, it is likely that Chen *et al.* (2003) (1) underestimated stem respiration and (2) overestimated soil respiration (Cernusak *et al.*, 2006) and therefore overestimated GPP compared with our flux tower measurements. However, the close agreement of the tower estimates with the above scaling exercises provides confidence in these measures. Previously, Eamus *et al.* (2001) estimated NEP at a similar site within the Howard River catchment using campaign-based eddy covariance measurements over a 2-year period and reported an NEP of $-2.8 \text{ t C ha}^{-1} \text{ yr}^{-1}$. The smaller sink reported by Eamus *et al.* (2001) may reflect the fact that transition periods were not measured and annual scaling was based on a limited number of measurements (~ 30 days over differing seasonal conditions). In addition, the wet season NEP of Eamus *et al.* (2001) was estimated using March F_c rates, which the continuous data show are underestimates of peak wet season flux, which occur in January and February and hence also contributed to the underestimate of their NEP for this site.

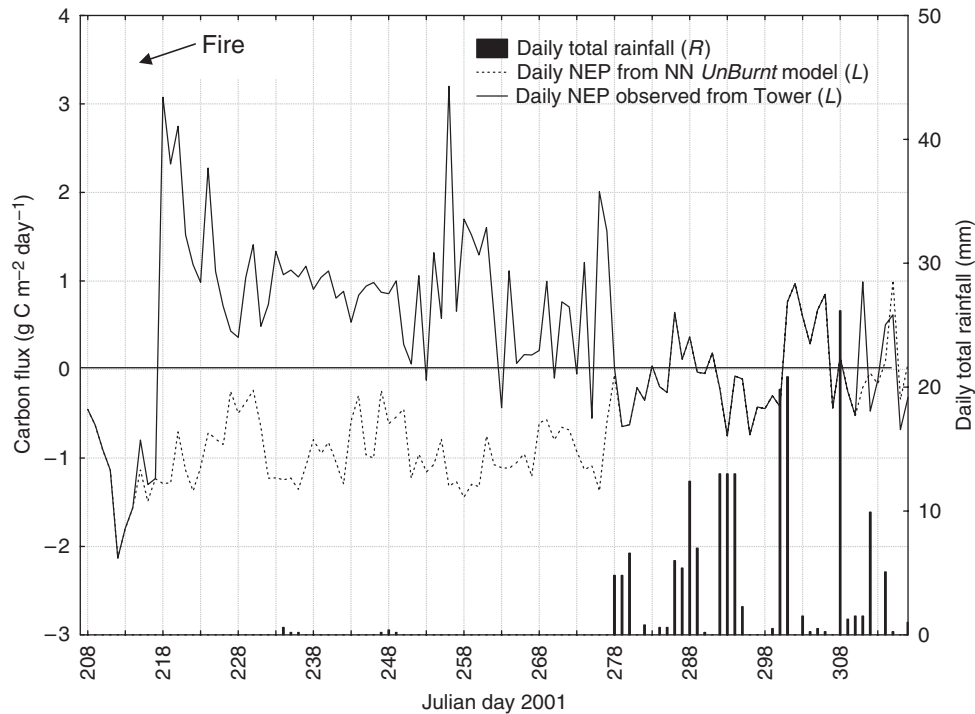


Fig. 5 Changes to net ecosystem productivity (NEP) following fire using the 2001 event as a case study. The savanna changes from sink to source after fire and remains a source for approximately 70 days despite the canopy being rebuilt and evapotranspiration returning to prefire levels after 40 days. The difference between the observed tower fluxes and the neural network (NN) model estimates of the fire free condition gives an estimate of the indirect impact of fire (the loss of canopy productivity and the cost of rebuilding the canopy) on the canopy. The integrated effect of fire is to reduce NEP over the 70 days by 1.1 t C ha^{-1} .

NBP is a longer term production index (Schulze *et al.*, 1999) that includes disturbance and in our case includes the direct (emissions) and indirect (lost productivity) effects of biomass burning but excludes grazing at our site. The fire regime at our site is ambient and similar to the surrounding region (Russell-Smith *et al.*, 2003a) and has been subject to fires of varying intensities over 5 years and, hence, we considered that our 5-year flux dataset could be used to calculate NBP for this site. We measured understorey fuel loads (Table 1) and calculated losses due to fire assuming a combustion efficiency of 0.72 (ratio of fuel pyrolyzed to fuel load within areas over which flames have passed, Russell-Smith *et al.*, 2003b). Mean emissions from fine fuel combustion were $+1.1 \pm 0.41 \text{ t C ha}^{-1}$ for the 5-year period. Recently, Rose (unpublished data) estimated combustion of coarse woody debris due to fire from the flux plot at Howard Springs to be $+0.49 \text{ t C ha}^{-1} \text{ yr}^{-1}$, giving a total carbon loss due to fire of $+1.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$. Subtracting this from the NEP of $-3.6 \text{ t C ha}^{-1} \text{ yr}^{-1}$ gives an NBP of $-2.0 \text{ t C ha}^{-1} \text{ yr}^{-1}$ indicating a carbon sink even when direct and indirect impacts of fire are included.

Other sources of carbon loss not included in this estimate of NBP include losses arising from herbivory.

However, grazing does not occur at our site, therefore invertebrate herbivory would be the main pathway. Termites and other folivores likely contribute significantly to nutrient cycling in tropical savannas with termites being responsible for up to 20% of soil carbon mineralized (Holt, 1987). Wood-consuming termites also attack dead and living woody biomass. Consumption by resident herbivores drives cycling rather than loss of carbon and fluxes of CO_2 from insect related consumption or decomposition would be captured by net ecosystem exchange measurements (F_c). However, non- CO_2 losses of carbon (methane) associated with termite activity, either grass or wood consumers, would be a net loss of carbon not measured by the flux tower. However, there are few studies quantifying this flux for these savannas. Fraser *et al.* (1986) examined six different species of termites from the United States and Australia and found positive correlation between amounts of biomass consumed and CH_4 emitted, with the average being $3.2 \text{ mg CH}_4 \text{ g}^{-1}$ of wood. Combining this with estimates of termite carbon consumption from tree hollows. (Cook *et al.* (2005) showed that for sites similar to ours with a mean basal area of $13.2 \text{ m}^2 \text{ ha}^{-1}$, $0.21 \text{ t C ha}^{-1} \text{ yr}^{-1}$ was consumed) we estimate CH_4

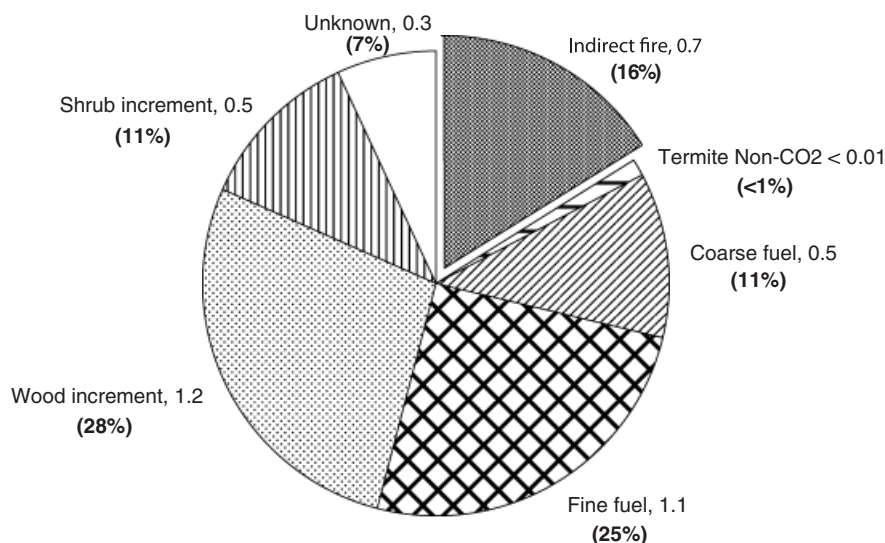


Fig. 6 Partitioning of the average annual net ecosystem productivity (NEP) at Howard Springs for 2001–2005 ($4.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$). The indirect impact of fire (loss of canopy productivity and cost of rebuilding canopy) on the canopy accounts for $0.7 \text{ tC ha}^{-1} \text{ yr}^{-1}$ and is shown as the ajar slice. The fate of the additional carbon is shown as 'best-guess' estimates, based on this study and literature values. Some carbon is missing but is likely accounted for in hydrological and soil processes as well as error associated each of the partitions.

emissions from consumption of trees at our site to be approximately $0.005 \text{ tC ha}^{-1} \text{ yr}^{-1}$. Consumption of grasses and other biomass is likely to double or triple this figure yet it remains a small fraction of NBP.

Mesic savanna carbon balance

There have been a number of studies which have examined carbon dynamics of mesic ($>1200 \text{ mm}$) north Australian savannas, both flux (Eamus *et al.*, 2001, this study) and inventory based (Chen *et al.*, 2003, Williams *et al.*, 2004, Cook *et al.*, 2005). These studies all suggest a net sink for this ecosystem, despite a high fire frequency (fire 2 in 3 years). Williams *et al.* (2004) estimated an NBP for these savannas of $\sim -1 \text{ tC ha}^{-1} \text{ yr}^{-1}$, lower than this study, as they based their estimate on a lower starting value of NEP ($-2.8 \text{ tC ha}^{-1} \text{ yr}^{-1}$, Eamus *et al.*, 2001), which was assumed to represent a fire-free NEP.

Our estimate of an NBP of $-2.0 \text{ tC ha}^{-1} \text{ yr}^{-1}$ suggests carbon is being stored in the ecosystem and this is likely to be due to woody thickening. Two tree increment studies have been conducted at the Howard Springs flux site, with Chen *et al.* (2003) reporting an increment of $1.6 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (1999–2000) with experimental trees subject to a cool fire ($<2000 \text{ kW m}^{-2}$) and Cernusak *et al.* (2006) who reported a value of $1.2 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (2004–2005). In a comprehensive study, Cook *et al.* (2005) analysed diameter increments of 453 trees in permanent plots within the Kapalaga experimental area of Kakadu National Park (Andersen *et al.*, 2003). These trees were subjected to a range of fires and stem measurements

were made twice during a 13-year period (1990–2003). Tree increment was $0.99 \text{ tC ha}^{-1} \text{ yr}^{-1}$ over this period, although a biennial fire regime was estimated to reduce this increment to $0.5 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (Cook *et al.*, 2005), lower than that recorded at Howard Springs. This may be due to the lower intensity fires and higher mean rainfall of the Howard Springs site compared with the Kapalaga site (1400 mm) and the above average rainfall over the last 10 years at Howard Springs. However, the long-term study of Cook *et al.* (2005) suggests a net tree increment of $1.2 \text{ tC ha}^{-1} \text{ yr}^{-1}$ recorded by Cernusak *et al.* (2006) at Howard Springs may be realistic. In addition, understorey shrub thickening is also important and accounts for approximately $0.5 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (Chen *et al.*, 2003).

Other sources of carbon storage could include storage in soils, while other loss pathways not quantified in this study could include loss of carbon via wind or water borne ash, carbon export to groundwater and streams, and fluxes of volatile organic carbon compounds (VOC's). We consider these as unknown. We have used the estimates above to derive a summary of carbon storage and loss pathways (Fig. 6) that accounts for an unburnt NEP estimate of $-4.3 \text{ tC ha}^{-1} \text{ yr}^{-1}$ (Table 2). Some of these parameters have been estimated in this study and others require further quantification to provide a complete carbon balance. However, fire impacts are significant via direct (fine and CWD combustion) and indirect (lost productivity through loss of functional LAI, construction and enhanced maintenance respiration) pathways.

Conclusion

Grace *et al.* (2006) compiled carbon flux data for a range of savanna studies to give a global savanna carbon sequestration rate (NBP) of $-0.14 \text{ tC ha}^{-1} \text{ yr}^{-1}$, suggesting that savannas are almost carbon neutral. This is lower than the rate estimated for the Howard Springs site ($-2.0 \text{ tC ha}^{-1} \text{ yr}^{-1}$) and reflects the high rainfall of the site which is ungrazed and dominated by evergreen Eucalypts that are superbly adapted to the wet-dry tropics (Bowman & Prior, 2005). The high NBP occurs despite an annual fire regime and is likely due to adaptations such as fire-protective bark (for the dominant species) and bimorphic root systems (shallow and deep) that maintain moisture availability (Kelley *et al.*, 2002) and allow CO_2 uptake all year. Fire clearly has a significant impact on NPP and thus NEP/NBP, supporting the notion of Williams *et al.* (2004) (for north Australian savanna) and Grace *et al.* (2006) (for the global savanna biome), that reductions in fire and grazing would increase sequestration rates. The NBP sink is accounted for almost exclusively by woody thickening and shrub growth, which has been observed previously in Australian savannas (Lewis, 2002; Bowman *et al.*, 2001; Burrows *et al.*, 2002; Sharp & Whittaker, 2003; Fensham *et al.*, 2005). These results are of significance for national carbon accounting for Australia because of the potential for carbon sequestration (Hutley *et al.*, 2005). However, the duration and robustness of this savanna sink is uncertain because a significant reduction in fire frequency may result in increased woody growth and possibly a saturation of the sink due to nutrient limitations.

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