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Carbon balance of a tropical savanna of northern Australia

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Abstract Through estimations of above- and below-ground standing biomass, annual biomass increment, fine root production and turnover, litterfall, canopy respiration and total soil CO₂ efflux, a carbon balance on seasonal and yearly time-scales is developed for a Eucalypt open-forest savanna in northern Australia. This carbon balance is compared to estimates of carbon fluxes derived from eddy covariance measurements conducted at the same site. The total carbon (C) stock of the savanna was 204±53 ton C ha⁻¹, with approximately 84% below-ground and 16% above-ground. Soil organic carbon content (0–1 m) was 151±33 ton C ha⁻¹, accounting for about 74% of the total carbon content in the ecosystem. Vegetation biomass was 53±20 ton C ha⁻¹, 39% of which was found in the root component and 61% in above-ground components (trees, shrubs, grasses). Annual gross primary production was 20.8 ton C ha⁻¹, of which 27% occurred in above-ground components and 73% below-ground components. Net primary production was 11 ton C ha⁻¹ year⁻¹, of which 8.0 ton C ha⁻¹ (73%) was contributed by below-ground net primary production and 3.0 ton C ha⁻¹ (27%) by above-ground net primary production. Annual soil carbon efflux was 14.3 ton C ha⁻¹ year⁻¹. Approximately three-quarters of the carbon flux (above-ground, below-ground and total ecosystem) occur during the 5–6 months of the wet season. This savanna

site is a carbon sink during the wet season, but becomes a weak source during the dry season. Annual net ecosystem production was 3.8 ton C ha⁻¹ year⁻¹.

Keywords CO₂ · Carbon cycling · Wet-dry tropics · Carbon source-sink relationships · Net ecosystem production

Introduction

Savannas, covering at least 16 million km² of the earth's land surface, are found in Africa, Australia, South America, India and Southeast Asia and occupy the latitudinal zone between evergreen tropical rainforest and mid-latitude deserts (Scholes and Hall 1996). Savannas are characterised by climates with distinct wet and dry seasons and this has induced correspondingly strong patterns in physiological and eco-physiological processes (Eamus and Prior 2001). Savannas account for approximately 58.7 Pg of biomass, approximately 30% the global carbon store of terrestrial ecosystems and savannas therefore have the potential to significantly influence global carbon cycling. Scurlock and Hall (1998) and Lal (2002) suggest that tropical savannas and grasslands play a more significant role in global carbon sequestration than previously thought, with soil carbon storage of particular significance.

Also of global importance is the extensive annual biomass burning that occurs in savanna ecosystems during the dry season, which results in a large quantity of carbon and other trace greenhouse gases (methane, NO_x) being released to the atmosphere (Andreae et al. 1996; Scholes et al. 1996). In the wet-dry tropics of northern Australia, tropical savanna is the dominant vegetation type and approximately 75% of Australia's total land area that is burnt annually occurs in this region (AGO-NGGI 2000). These Australian savannas occupy an area of almost 2 million km², which is 12% of the world's savannas biome and some of the world's most extensive and intact Eucalypt open forest is located here. Given the

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size of this ecosystem and the extent of burning, it is likely that savannas will have a major impact on continental-scale carbon balance.

North Australian savannas are dominated by *Eucalyptus* tree species which form an open overstorey canopy (<50% cover) and a variety of annual and perennial C₄ grasses dominating the understorey (Williams et al. 1997). These savannas have been subjected to minimal European disturbance when compared to Eucalypt dominated ecosystems of southern Australia (Tothill et al. 1985). While there is an extensive ecological literature describing savannas of Australia, plus knowledge of ecophysiological processes at leaf (Eamus et al. 1999, 2000), tree (O'Grady et al. 1999; Eamus et al. 1999; Myers et al. 1997), canopy and stand scale (Hutley et al. 2000, 2001; O'Grady et al. 2000; Eamus et al. 2001), there are no detailed studies of the carbon balance for these savannas. Most productivity studies of Australia's tropical savanna have concentrated on the herbaceous layer, with a focus on agricultural potential (e.g. Mott et al. 1985; Williams et al. 1985). There are also no studies of savanna carbon dynamics where both stocks and fluxes have been measured at the same site and over the same time period (House and Hall 2001).

In this paper, a range of measurements has been integrated to establish a carbon balance for a tropical savanna site of coastal northern Australia. Carbon pool size and fluxes have been estimated on a seasonal and annual basis to address the following questions: What are the fluxes of carbon to and from these tropical savannas? What are the allocation patterns of carbon among above- and below-ground components? Are there seasonal differences in carbon storage and carbon distribution? What are the seasonal and annual budgets of carbon for this ecosystem? For comparative purposes, we have generated data tables, providing values for a wide range of parameters, using a similar approach to that of Malhi et al. (1999).

Materials and methods

Study sites

To obtain a typical range of values for the carbon balance components, four study sites were used, all located within a 65 km radius of Darwin, Northern Territory, Australia. Sites were located at (1) Howard Springs (12°28'S, 131°08'E), (2) Humpty Doo (12°36'S, 131°10'E), (3) the Territory Wildlife Park (12°42'S, 131°0'E) and (4) a fourth site at Gunn Point (12°14'S, 131°05'E). The vegetation at all sites was Eucalypt open-forest savanna with an overstorey dominated by *Eucalyptus tetrodonta* (F. Muell) and *Eucalyptus miniata* (Cunn. ex Schauer). These two species contribute >70% to the overstorey leaf area index (LAI) and standing biomass (O'Grady et al. 2000). Sub-dominant tree species include *Erythrophyleum chlorostachys* (F. Muell), *Terminalia ferdinandiana* (F. Muell), *Eucalyptus porrecta* (S.T. Blake) and *Eucalyptus bleeseri* (Blakely). The understorey is comprised of semi-deciduous and deciduous small trees and shrubs with a seasonally continuous cover of annual and, to a small extent, perennial C₄ grasses. Overstorey LAI of these sites typically ranges from 0.6 to 1 with basal areas approximately 8–12 m² ha⁻¹

(O'Grady et al. 2000), with understorey LAI being far more seasonally dynamic and ranging from 0.2 to 1.5.

Sites used in this study are representative of the open-forest savannas of the coastal regions of the Northern Territory, which receive annual rainfalls in excess of 1,200–1,400 mm and are dominated by *E. tetrodonta* and *E. miniata* with *Sorghum* spp frequently occurring in the understorey (Wilson et al. 1990). This vegetation type occupies an area of approximately 135,000 km². This and other closely associated *Eucalypt* dominated savanna types also occur in north-western Western Australia and the Gulf of Carpentaria region of northern Queensland and occupy up to 200,000 km² in northern Australia (Fox et al. 2001). Low intensity grass fires (fire line intensities of 2,000–8,000 kW m⁻¹, Williams et al. 1999) are common, with sites burnt approximately 2 in every 3 years and annually at sites near urban settlements.

Eucalyptus tetrodonta and *E. miniata* open-forest savanna are commonly associated with well drained lateritic red and yellow earth soils, which tend to have A horizons of well drained, highly weathered sands (clay content typically <5%, Calder and Day 1982) of low nutrient status, with a massive and earthy structure. Transition at 15–30 cm to a sandy loam B horizon is gradational and can extend up to 1–2 m, where ferricrete boulders occur in a matrix of mottled, heavy clays forming a duricrust of low permeability and variable depth (Calder and Day 1982). Prominent macropores, often containing tree roots, are found in this layer. Rounded ferricrete gravels can occur on the sandy soil surface and throughout the profile up to 20% by volume. These soils are generally acidic (pH approximately 5.5, Calder and Day 1982) and low in available N and P (total N, 0.1% Schmidt et al. 1998). Dry bulk densities of these soils range from approximately 1.4 kg m⁻³ at the surface to 1.7 kg m⁻³ at depth (2 m).

The climate of the region is wet-dry tropical and rainfall is distinctly seasonal, with a wet season occurring from November to April (Cook and Heerdegen 2001). During this period, greater than 90% of the 1,700 mm annual rainfall occurs. The dry season occurs from May to October with little or no rainfall. Temperatures remain high throughout the year with mean daily maximum temperatures at the Darwin Airport (35 km from the field site) ranging from 30.4°C (July) to 33.1°C (October and November). Maximum and minimum temperatures have a range of 7°C (wet season) to 11°C (dry season) (McDonald and McAlpine 1991).

Measurements and calculations

Carbon stocks

All measures of carbon pools and fluxes were derived from the suite of measurements conducted at the four sites. A brief description of these parameters, methods and their estimation is given in Table 1. The magnitude of carbon pools (above- and below-ground biomass, soil organic matter) and fluxes between these pools (litterfall, soil respiration, root turnover, growth increment) have been integrated to calculate above- and below-ground allocation and derive a carbon balance. The range of methods used is briefly described below, with further details available in cited publications.

Above-ground biomass (AGB) was estimated from plot-based measurements of tree diameter at breast height (DBH) and tree height. Three 20×20 m plots were located at each site and biomass components (wood, bark, branch, leaf) were estimated from 48 harvested trees from 6 dominant tree species (*Eucalyptus tetrodonta*, *E. miniata*, *Erythrophyleum chlorostachys*, *T. ferdinandiana*, *Eucalyptus porrecta* and *E. bleeseri*). These species account for 95% of the standing biomass in these open-forest savannas (O'Grady et al. 2000). Allometric regression equations (power functions) relating tree DBH and biomass have been developed for these and other species at these sites (O'Grady et al. 2000; Chen 2002). The carbon content of AGB was assumed to be 49% of dry weight (Gifford 2000a) and 43% for grass fine roots.

Below-ground biomass (BGB) was estimated using the trench method (Komiyama et al. 1987). Eamus et al. (2002) provides

Table 1 Sources of data used to calculate components of the savanna carbon balance. Measurements were divided into wet (November–April) and dry (May–October) seasons

Com- ponent	Definition	Data source
ΔB_{ab}	Above-ground biomass production	Annual increment in DBH of 20 trees monitored using dendrometers Biomass components (leaf, branch and stem) calculated using regression equations (O'Grady et al. 2000) Production of all components calculated from tree DBH increment
ΔB_{cr}	Coarse root production	Derived from Johnson and Risser (1974), using AGB, ΔB_{ab} and BGB/AGB from tree harvesting (Sato and Madgwick 1982, O'Grady et al. 2000) and plot biomass sampling BGB from root trench method (Komiya et al. 1987, Eamus et al. 2002)
ΔB_{fr}	Fine root production	Root ingrowth bags and root window methods (Vogt et al. 1998)
R_{lc}	Leaf construction respiration	Derived from Ryan (1991) and Keith et al. (1997) using leaf production
R_{lm}	Leaf maintenance respiration	Derived from Ryan (1991) using average temperature (Darwin airport) and total leaf N content for dominant Eucalypt tree species (Eamus and Prichard, 1998)
R_{wc}	Wood construction respiration	Derived from Ryan (1991), Keith et al. (1997) using woody (branch and stem) production
R_{wm}	Wood maintenance respiration	Derived from Ryan and Waring (1992) using an average temperature (Darwin airport) and sapwood volume (O'Grady et al. 1999)
F_{cs}	Soil CO ₂ flux	Soil respiration was measured using close chamber technique (Chen et al. 2002)
R_r	Root respiration	Assumed to be 50% of total soil respiration (Keith et al. 1997)

details of these measurements for the Humpty Doo site, which involved root excavation from 16 trees in 8 soil trenches (4–5 m in length, up to 2 m depth). Roots were removed from excavated soil blocks of known volume and sorted into coarse (>2 mm diameter) and fine (<2 mm diameter) root fractions. The carbon content of below-ground biomass was assumed to be 49% of dry weight (Gifford 2000b).

Soil carbon stock was estimated using soil organic carbon (SOC) content and soil bulk density. At each study site, three plots were chosen for soil sampling with samples collected at 5, 20, 30, 50, 80 and 100 cm depths. SOC was determined using an improved Walkley-Black wet digestion method (Heanes 1984). Percent SOC values were converted to soil carbon stock (ton C ha⁻¹) using a bulk density for each soil layer. Bulk density was determined from pits dug at the Howard Springs site by taking 3–5 replicate soil samples using 10 cm diameter metal rings of 100 cm³ volume (A. O'Grady, personal communication). Bulk densities ranged from 1.42 at 5 cm depth to 1.7 g cm⁻³ at 1 m.

Above-ground carbon flux

Above-ground net primary production (ANPP) was estimated by summing annual increments of all components of biomass plus litterfall (Table 1). AGB was calculated from radial increments of tree diameter and an allometric regression equation relating tree diameter to AGB (O'Grady et al. 2000). Annual increment of understorey biomass was calculated from seasonal maximum and minimum values of understorey biomass, measured monthly for one year, using destructive harvests of five randomly located replicate 1 m² plots sampled at three different locations at the Humpty Doo site. Litterfall was measured using 18 litter traps over a 2-year period (1998–2000) at the Wildlife Park site. Traps, with an area of 2,463 cm² for each, were set 80 cm above the ground and litter (leaves, bark and fruit) were collected at monthly intervals and dry weight determined.

Above-ground tree respiration was divided into four sources (Table 1): leaf construction respiration (R_{lc}), leaf maintenance respiration (R_{lm}), woody components construction respiration (R_{wc}) and woody components maintenance respiration (R_{wm}). Construction respiration of leaf and woody components was calculated using leaf and woody biomass increment multiplied by the construction constant of 0.25 g C g C⁻¹ (Keith et al. 1997). This assumed that

construction respiration consumes 25% of the carbon allocated annually to each biomass component (Ryan 1991). Leaf maintenance respiration (R_{lm}) was calculated using the following equation from Ryan (1991):

$$R_{lm} = (N_{tot})[27 \exp(0.07T_a)] \quad (1)$$

where N_{tot} (g N m⁻²) is the total leaf nitrogen content obtained from leaf nitrogen concentration × leaf biomass, and T_a (°C) is the average annual temperature, although mean dry season and wet season temperatures were used. Leaf nitrogen concentration data was taken from Eamus and Prichard (1998) for both *E. tetradonta* and *E. miniata*. Wood maintenance respiration (R_{wm}) was calculated using the following equation developed by Ryan and Waring (1992):

$$R_{wm} = 0.00486V_s \exp(0.0663T_a) \quad (2)$$

where V_s (cm³) is sapwood volume. Sapwood volume for a stand was calculated using regression equations derived between sapwood basal area and tree diameter for each dominant Eucalypt species present in plots at the Howard Springs and Humpty Doo sites. These relationships (sapwood area and DBH) have been previously established at these sites for the dominate tree species by O'Grady et al. (1999). Above-ground gross primary production (AGPP) is then the sum of ANPP and above-ground tree respiration.

Below-ground carbon flux

Below-ground carbon fluxes were estimated from measures of coarse and fine root production. Fine root production was estimated using in-growth bags and coarse root production was estimated from a simple allometric equation which assumes that coarse root production is proportional to above ground NPP (Johnson and Risser 1974):

$$NPP_{cr} = (ANPP/AGB) \times B_{cr} \quad (3)$$

where NPP_{cr} is coarse root net primary production, ANPP is above-ground net primary production, AGB is above-ground biomass, and B_{cr} is coarse root biomass. Root respiration was assumed to be 50% of total soil respiration (Ewel et al. 1987; Keith et al. 1997; Haynes and Gower 1995).

Fine root production (NPP_{fr}) was estimated using in-growth bags (Smit et al. 2000) with details given by Chen et al (2003). A total of 72 in-growth bags were installed at the Howard Springs site. Soil cores were dug to a depth of 50 cm with fine roots removed and the resulting root-free soil used to fill in-growth mesh bags. Bags filled with root-free soil were then inserted into 7×50 cm deep holes and the rate of in-growth of new fine roots (productivity) determined by sequential re-sampling at 2-monthly intervals from October 1999 to January 2001.

Soil carbon efflux was measured using a closed chamber technique (Rochette et al. 1997). Chen et al. (2002) provides detailed description of measurements at the Howard Springs site, which involved the use of a polythene chamber (20×21.5×12 cm) in conjunction with portable infra-red gas analyzer (LI-6200, Licor, Lincoln, Neb., USA). Soil CO_2 efflux (F_{cs}) was calculated as the rate of change over time of CO_2 concentration in the chamber (Chen et al. 2002). Estimates of F_{cs} were made every 4 h over a 2–3 day period each month for over 2 years (September 1998 to January 2001). The 2–3 day measurement period was assumed to represent mean monthly F_{cs} and was used to calculate monthly and annual rates of soil CO_2 efflux.

Production indices

Gross primary production (GPP) is defined as the total carbon assimilated by photosynthesis, minus photorespiration. Net primary production (NPP) is defined as the difference between GPP and autotrophic respiration (R_a), representing the net result of CO_2 fixation by photosynthesis and CO_2 loss via plant respiration. Net ecosystem production (NEP) is the net carbon balance of an ecosystem over some time period (usually a year) and represents net carbon fixation by photosynthesis and losses by autotrophic plus heterotrophic respiration (respiration of soil organisms, R_h) (Kirschbaum 2001). As NEP reflects the annual change in C stored at an ecosystem scale, it indicates whether the ecosystem is a carbon “sink” or “source” for CO_2 relative to the atmosphere.

Results

Carbon stocks in tropical savanna of northern Australia

Table 2 gives the carbon stocks of different components of the savanna ecosystem. Data have been averaged using data from the three sites (Howard Springs, Humpty Doo and Territory Wildlife Park). The mean total carbon pool was 204 ton C ha⁻¹ (range 136 to 286 ton C ha⁻¹) with approximately 84% of the carbon stored below-ground (soil plus roots). Approximately 74% of the total C was stored in the mineral soil as SOC (mean 151.3 ton ha⁻¹, Table 2). Carbon stored in the tree component was the next largest pool, which accounted for 24% of the total carbon, followed by understorey (0.5%), litter-layer (0.5%) and dead stems (0.5%). Eucalypt species dominated the total carbon stored in vegetation, which was 50 ton C ha⁻¹ (range 23–76.0 ton C ha⁻¹). Above-ground woody components accounted for 64% of the total vegetation pool (53 ton C ha⁻¹, live plus dead components) with total root carbon at 19 ton ha⁻¹ or 36% of the total vegetation pool.

Table 2 Estimated stocks of carbon (ton C ha⁻¹) in Eucalypt open forest savannas of Northern Australia based on measurements at a range of sites, Howard Springs, Humpty Doo and the Wildlife Park. Multiply by 100 to convert values to g m⁻²

Parameter	Range	Mean (SD)
Above ground		
(1) Tree foliage	0.6–1.1	0.9 (0.2)
(2) Tree branches	4.2–12.2	8.2 (2.5)
(3) Tree stems	12.9–28.0	21.7 (4.8)
(4) Above-ground live tree = (1)+(2)+(3)	17.7–41.2	30.7 (7.3)
(5) Dead stems	0.2–3.2	0.9 (0.9)
(6) Understorey	0.7–1.5	1.0 (0.3)
(7) Litter-layer	0.8–1.4	1.0 (0.2)
(8) Total above-ground = (4)+(5)+(6)+(7)	19.4–47.3	33.6 (7.7)
Below-ground		
(9) Fine roots	0.2–0.8	0.5 (0.2)
(10) Coarse roots	5.2–38.8	18.9 (12.4)
(11) Total roots = (9)+(10)	5.4–39.6	19.3 (12.6)
(12) Soil organic matter	111.5–198.9	151.3 (32.9)
(13) Total below-ground = (11)+(12)	116.9–238.5	170.6 (45.5)
Ecosystem		
(14) Total live tree = (4)+(11)	23.1–80.8	50.0 (19.9)
(15) Total vegetation = (8)+(11)	24.8–86.9	52.9 (20.3)
(16) Ecosystem total = (8)+(13)	136.3–285.8	204.2 (53.2)
Ratios		
Above-ground live tree/ Total live tree = (4)/(14)		0.61
Total above-ground/ Total vegetation = (8)/(15)		0.64
Total above-ground/ Ecosystem total = (8)/(16)		0.16
Total below-ground/ Ecosystem total = (13)/(16)		0.84
Total live tree/ Ecosystem total = (14)/(16)		0.24
Soil organic matter/ Ecosystem total = (12)/(16)		0.74

Above-ground carbon flux

Table 3 provides wet and dry season and annual estimates of carbon fluxes between the various carbon pools. Total carbon flux above-ground was calculated by summing the carbon fluxes associated with tree biomass increment, litterfall, understorey biomass increment, plus construction and maintenance respiration. This sum is AGPP (Table 3). In the present study, the total carbon flux above-ground was 5.7 ton C ha⁻¹ year⁻¹, of which tree biomass increment accounted for 28%, foliage respiration accounted for 26%, wood respiration accounted for 21%, litterfall accounted for 16% and understorey biomass increment accounted for 9%.

There may be uncertainty associated with seasonal and annual estimates of leaf and stem respiration for these Eucalypt species, which were derived from equations of Ryan (1991) and Ryan and Waring (1992). These respiration equations we used in combination with site specific estimates of LAI, specific leaf area, tree sapwood area and volumes, which were derived from previous studies of leaf photosynthetic properties (Eamus and Pritchard 1998), biomass distribution and tree water use at this site (O’Grady et al. 1999, 2000; Hutley et al 2000). Stem respiration estimates using Ryan and Waring (1992)

Table 3 Seasonal and annual C fluxes (ton C ha⁻¹ season⁻¹ or ton C ha⁻¹ year⁻¹) for a Eucalypt open forest savanna of northern Australia

Processes	Dry season	Wet season	Annual
Above-ground			
(1) Net tree biomass increment	0.0	1.6	1.6
(2) Litter-fall	0.6	0.3	0.9
(3) Net understorey biomass increment	0.0	0.5	0.5
(4) Respiration of tree foliage	0.7	0.8	1.5
(5) Respiration of tree wood	0.2	1.0	1.2
(6) C allocation above-ground = (1)+(2)+(3)+(4)+(5)	1.5	4.2	5.7
Below-ground			
(7) Net coarse root biomass increment	0.0	1.0	1.0
(8) Net fine root production	1.3	5.7	7.0
(9) Respiration of roots	2.1	5.0	7.1
(10) Total soil respiration	4.2	10.1	14.3
(11) C allocation below-ground = (7)+(8)+(9)	3.4	11.7	15.1
Soil			
(12) C input = (2)+(7)+(8)	1.9	7.0	8.9
(13) C output = (17)	2.1	5.1	7.2
(14) Net soil C exchange = (12)–(13)	–0.2	1.9	1.7
Ecosystem			
(15) Total respiration = (4)+(5)+(10)	5.1	11.9	17.0
(16) Autotrophic respiration = (4)+(5)+(9)	3.0	6.8	9.8
(17) Heterotrophic respiration = (15)–(16)	2.1	5.1	7.2
(18) C allocation ecosystem total = (6)+(11)	4.9	15.9	20.8
Ratios			
(20) C allocation above-ground/ecosystem = (6)/(18)	30.6%	26.4%	27.4%
(21) C allocation below-ground/ecosystem = (11)/(18)	69.4%	73.6%	72.6%
(22) C allocation above-ground/below-ground = (6)/(11)	44.1%	35.9%	37.7%
Productivity			
(23) NPP = (1)+(2)+(3)+(7)+(8)	1.9	9.1	11.0
(24) GPP = (23)+(16)	4.9	15.9	20.8
(25) NEP = (23)–(17)	–0.2	4.0	3.8
(26) NPP/GPP = (23)/(24)	38.8%	57.2%	52.9%
Mean residence time (years)			
(27) Biomass = (8+11) ^a /(1+3+7+8)			4.8
(28) Soil and litter = (12) ^a /(2+7+8)			17
(29) Total ecosystem = (16) ^a /(1+2+3+7+8)			19

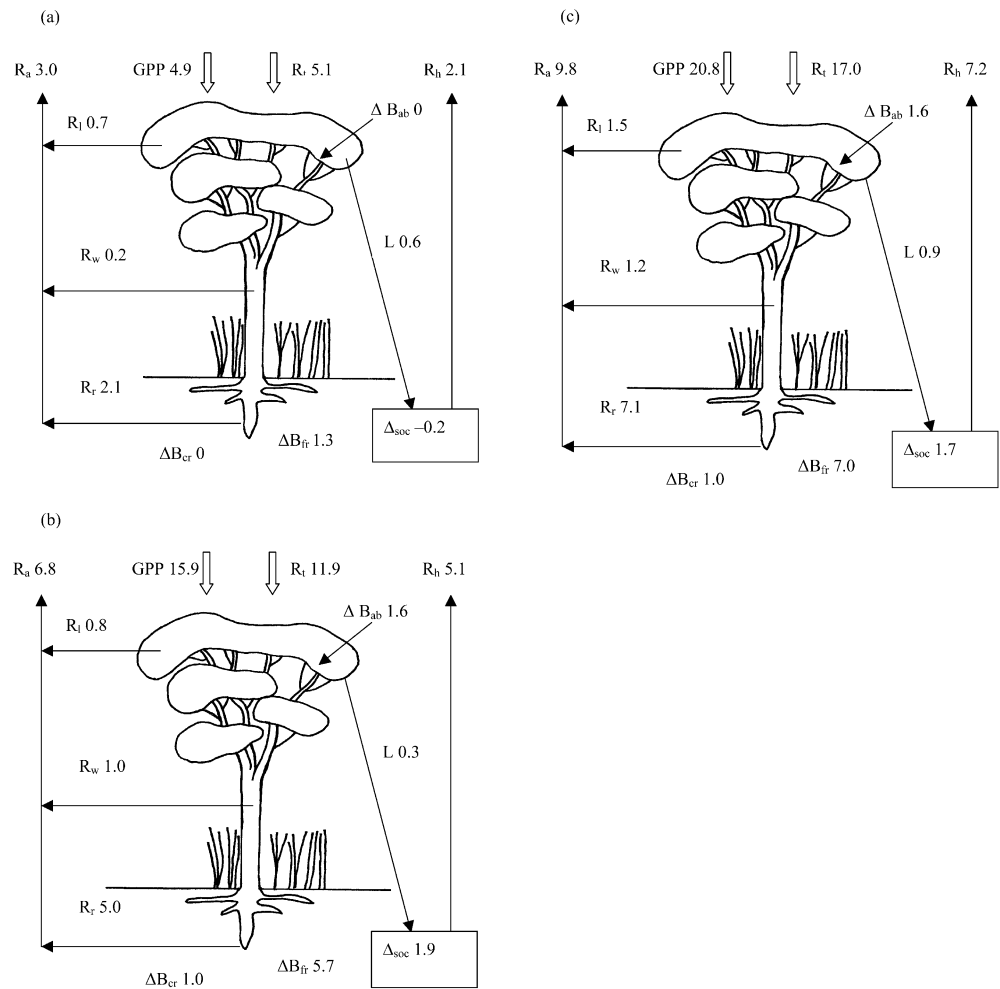
^a Values taken from Table 2, mean resident time calculated as stock/productivity

was compared to data of Tame (2002, unpublished data), who measured stem respiration of *Eucalyptus miniata*, *E. tetradonta* and *Erythrophyleum chlorostachys* at the Howard Springs site. Chambers were attached to stems of a range of individuals (13–36 cm DBH) with a mean rate of CO₂ efflux per unit stem area of approximately 0.05 mg CO₂ m⁻² s⁻¹ observed, with no statistical difference evident between species. Using our plot data (tree density, mean tree stem surface area, mean annual air temperature for the site), in combination with this stem CO₂ efflux, gives a stand-scale estimate of approximately 1.3 ton C ha⁻¹ year⁻¹, in good agreement with the estimate provided by Ryan and Waring (1992) of 1.2 ton C ha⁻¹ year⁻¹. Similarly, leaf maintenance respiration as calculated using Ryan (1991) was comparable to typical dark respiration rates of *E. tetradonta* and *E. miniata* leaves, which range from 1 to 20 nmol CO₂ m⁻² leaf area s⁻¹ (Eamus and Pritchard, unpublished data). While leaf dark respiration rates have a component of growth respiration in addition to maintenance respiration, some check of our extrapolation using Ryan (1991) is required. Converting

our R_{lm} estimate to units of CO₂ efflux per unit leaf area per second using overstorey LAI (0.9 wet season, 0.6 dry season) and specific leaf area for these species (6.1 kg m⁻²), gives a value for R_{lw} of 2.3 nmol CO₂ m⁻² s⁻¹ during the wet season and 1.4 nmol CO₂ m⁻² s⁻¹ during the dry season. These values are within the range observed by Eamus and Pritchard, although they may be an underestimate of the true value.

Mean annual tree increment (radial DBH increment) was 4.3±0.95 mm year⁻¹ (0.014±0.002 m² basal area ha⁻¹ year⁻¹), although this estimate is based on records from 10 of the original 20 stems, as dendrometers were damaged by fire during the dry season. During the dry season there was no tree growth and biomass increment was zero and on some stems, shrinkage was observed. By contrast, wet season mean stem increment was maximal at 0.71 mm month⁻¹ during December–January, and in terms of seasonal C flux above-ground, the wet season accounted for approximately 75% of the annual total. Only litterfall was larger in the dry season than in the wet season, due to canopy leaf area reductions of semi-, brevi- and fully

Fig. 1a–c Estimated seasonal and annual carbon flux in the savanna studied. All units are $\text{ton C ha}^{-1} \text{ season}^{-1}$ or $\text{ton C ha}^{-1} \text{ year}^{-1}$. **a** Dry season, **b** wet season and **c** annual. *GPP* Gross primary production, *R_t* total respiration, *R_h* heterotrophic respiration, *R_a* autotrophic respiration, *R_l* leaf respiration, *R_w* woody respiration, *R_r* root respiration, *L* litterfall, ΔB_{ab} above-ground biomass increment, ΔB_{fr} fine root biomass increment, ΔB_{cr} coarse root biomass increment, Δ_{soc} soil organic carbon change measurements



deciduous trees and shrubs and annual grass senescence during the dry season. For all other components, fluxes during the wet season were larger than during the dry season (Table 3).

Below-ground carbon flux

Total C flux below-ground (BGPP) was $15.1 \text{ ton C ha}^{-1} \text{ year}^{-1}$ (Table 3). This was calculated by summing root production of both coarse and fine root, plus root respiration. Root production and root respiration comprised approximately 53% and 47% of BGPP respectively. More than 70% of root respiration occurred during the wet season. The fine root component was the dominant contributor to total root biomass increment and accounted for more than 87% of the total root biomass production of $8 \text{ ton C ha}^{-1} \text{ year}^{-1}$.

Tropical savanna carbon balance

The savanna carbon balance is summarised in Fig. 1, using data from Table 3. Integrating all above and below

ground fluxes, production indices can be calculated. The total ecosystem carbon flux (GPP) was $20.8 \text{ ton C ha}^{-1} \text{ year}^{-1}$, of which 76% occurred in the wet season and 24% in the dry season (Table 3). Carbon flux below-ground was higher than carbon flux above-ground, and the former accounted for approximately 70% of total carbon flux. NEP was calculated by subtracting heterotrophic respiration (R_h) from NPP, which gave a value of $3.8 \text{ ton C ha}^{-1} \text{ year}^{-1}$ (Table 3). Although the NEP was positive over the entire year, net productivity was strongly seasonal and was dominated by wet season fluxes. The ecosystem was a weak carbon source during the dry season, with NEP $-0.2 \text{ ton C ha}^{-1} \text{ year}^{-1}$ (Table 3). The mean residence time for carbon for biomass, soil and the ecosystem as a whole was calculated by dividing the total carbon stock (Table 2) by rates of carbon input (Table 3). Mean carbon residence times for biomass, soil and the ecosystem were 5, 17 and 19 years respectively (Table 3).

Discussion

Savanna carbon stocks

Carbon stocks (as opposed to biomass) of the vegetation component in these savannas was 53 ton C ha⁻¹ (Table 2) and is on the lower end of the global range of carbon stocks in vegetation estimated for tropical savannas (20–150 ton C ha⁻¹, Tiessen et al. 1998). The value is significantly lower than estimates for tropical forests, where AGB carbon stocks range from 70 to 179 ton C ha⁻¹ (Delaney et al. 1997; Malhi et al. 1999). Values from the present study are closer to those given by Scholes and Hall (1996) for tropical dry forest (74.7 ton ha⁻¹), reflecting the significant woody component of these savannas. Scholes and Hall (1996) report 37.4 ton ha⁻¹ carbon density for woodlands and 11.3 ton C ha⁻¹ for 'dry savannas'.

Below-ground biomass was 19 ton C ha⁻¹, approximately 35% of the total biomass carbon stock, which is a higher percentage than that commonly observed in drought deciduous forests (20%) or moist, broad-leaved woodlands and savannas (25%) (Scholes and Hall 1996). Like the seasonal patterns of ANPP, high below-ground carbon allocation relative to above-ground at these sites reflects the annual drought of this wet-dry climate zone. There is significant investment of carbon in root systems of the dominant tree species (*Eucalyptus tetrodonta*, *E. miniata*, *Erythrophyleum chlorostachys*), via the development of large lignotubers that enable carbon storage and vegetative re-growth following frequent fires (burning 2 in 3 years, Williams et al. 2002) occurring in these savannas (Williams et al. 1999). Root biomass tends to be concentrated in the upper 50 cm of soil (Werner and Murphy 2001; Eamus et al. 2002), roots of mature trees can grow to 5 m depth (Kelley et al. 2002) and we have observed roots to 9 m (A. O'Grady, personal communication), although the biomass at these depths was small. These root systems enable extraction of water from the sub-soil (1–5 m depth, Kelley et al. 2002) during the 6 month dry season and maintain tree stand transpiration at a constant rate all year (O'Grady et al. 1999).

Dry season dormancy in stem growth of these species occurs despite the maintenance of dry season photosynthesis (Eamus et al. 1999) and transpiration (O'Grady et al. 1999). Eamus et al. (1999) observed only modest (approximately 10–15%) declines in assimilation per unit leaf area for these evergreen species during the dry season relative to the wet, although photosynthesis of semi- and brevi-deciduous species declined by 25–75%. Fully deciduous species were leafless for some period of the dry season. Despite the continuation of photosynthesis by evergreen species during the dry season, albeit at reduced rates compared to the wet season, carbon assimilated is apparently not utilised for shoot growth or significant leaf production. Below-ground storage, especially in lignotubers, and dry season flowering and fruiting (Setterfield and Williams 1996) is likely to be a significant sink for this carbon. Mucha (1979) observed a similar confine-

ment of stem increment in *E. tetrodonta* to the wet season, with growth increment of 3 mm per month occurring during January and February, higher than rates of increment observed in this study. Hoffmann (2002) also observed strongly seasonal stem growth, despite relatively aseasonal patterns of gas exchange in evergreen trees of cerrado savannas of south-central Brazil and stored carbon is likely to be used to initiate fine root growth and leaf production prior to the onset of wet season rains.

In woodlands and savannas, SOC tends to be more than three-quarters of the total ecosystem carbon stock (Scholes and Hall 1996). However, in comparison with tropical forests or temperate grasslands, savannas generally have a low SOC content due to high soil respiration rates (Chen et al. 2002) and soil carbon losses occur due to frequent burning (Kalpage 1974; Montgomery and Askew 1983; Bird et al. 2000). SOC content of savannas generally increases with increasing soil clay content, rainfall, tree cover and decreasing temperature (Scholes and Hall 1996). The SOC density in these Eucalypt open forest savannas (151±33 ton C ha⁻¹ or 15.1±3.3 kg C m⁻²) was significantly higher than the savanna mean (5.65±4.60 kg C m⁻²) and was similar to the mean for tropical woodlands (11.8±5.43 kg C m⁻²) as given by Scholes and Hall (1996). The high level of SOC of these savannas is likely to be high below-ground carbon allocation and fine root productivity in the wet season.

Savanna productivity

All productivity indices (GPP, NPP, NEP) describe a savanna ecosystem where carbon fluxes are tightly coupled to seasonal patterns of rainfall and resultant changes to soil water content. This feature has been observed at leaf (Prior et al. 1997a, 1997b; Eamus et al. 1999) and canopy scale (Hutley et al. 2000, 2001; Eamus et al. 2001) and is evident at the ecosystem scale (this study). The production efficiency of this savanna (NPP/GPP) was approximately 53% (Table 3), close to the often assumed ratio of NPP/GPP of 0.5. In a review of carbon balance of contrasting ecosystems, Malhi et al. (1999) obtained similar production efficiencies for tropical (51%), temperate (55%) and boreal (54%) ecosystems.

Murphy and Lugo (1995) reported the range of total or ecosystem NPP for tropical dry forests and savanna as 8–21 ton DM ha⁻¹ year⁻¹, with 6–16 ton DM ha⁻¹ year⁻¹ for ANPP. For total NPP, this is approximately 4–10 ton C ha⁻¹ year⁻¹, and 3–8 ton C ha⁻¹ year⁻¹ ANPP. At the Howard Springs/Humpty Doo sites, total NPP is at the top of this range, yet ANPP is near the bottom, at 3 ton C ha⁻¹ year⁻¹ (Table 4). This pattern of average to high NPP for these Northern Territory savannas, but low ANPP is also seen in Table 4, with NPP of this study comparable to other savannas and drought-deciduous woodlands, although ANPP is significantly lower. This further indicates that savannas of northern Australia have relatively high below-ground carbon allocation (see ratio of ANPP/NPP, Table 4). BNPP accounted for 70% of NPP and fine root

Table 4 Comparison of ANPP (ton C ha⁻¹ year⁻¹), NPP (ton C ha⁻¹ year⁻¹) and ratio of ANPP/NPP for savanna ecosystems, other Australian *Eucalypt* communities and tropical forests^a

Forest type	ANPP	NPP	ANPP/NPP	Rainfall (mm)	Reference
Savannas					
Eucalypt open-forest savanna, NT	3.0	11.0	0.27	1,750	This study
Drought-deciduous woodland	9.7	12.7	0.76		Menaut and Cesar (1979) ^b
Tropical savanna (global mean)	5			300	Scholes and Hall (1996)
Drought-deciduous woodland (S. America)	2.1	4.4	0.48		Scholes and Hall (1996)
Sahelian shrub savanna	2.2			450	Hanan et al. (1998)
Trachypogon savanna (S. America)	4.6			1,300	San Jose and Montes (1989)
Drought-deciduous woodland	7.5	15.7	0.48		Menaut and Cesar (1979) ^b
Drought-deciduous woodland	8.6	13.2	0.65		Menaut and Cesar (1979) ^b
Drought-deciduous woodland	6.5	12.3	0.53		Menaut and Cesar (1979) ^b
Tropical grasslands (Thailand)	7.2	10.0	0.72		Long et al. (1992) ^b
Tropical grasslands (Australia)	2.3	3.6	0.64		Christie (1978) ^b
Australian <i>Eucalyptus</i> forests					
Eucalypt woodlands, Box-ironbark forest	0.5–2.0			350–500	Grierson et al. (1992)
<i>E. regnans</i> (young)	9			1,000	Grierson et al. (1992)
<i>E. regnans</i> (mature)	6.5			1,000	Grierson et al. (1992)
<i>E. regnans</i> (regenerating)	36				Attiwill (1991)
<i>E. obliqua</i> (45 years old)	14				Attiwill (1979)
<i>E. pauciflora</i> (mature)	12	17	0.71	1,200	Keith et al. (1997)
Tropical forest					
Tropical rainforest (global mean)	8.7	15.6	0.56	2,200	Malhi et al. (1999)

^a ANPP is above-ground NPP and NPP includes both above and below ground^b Cited in Scholes and Hall (1996)

net primary production (NPP_{fr}) accounted for 87% of the total BNPP. Therefore, fine root production is the largest single component contributing to NPP for these savannas.

Fine root systems of these savannas are essentially deciduous (D. Bowman, personal communication), with little production during the dry season. This seasonal cycle of root production coincides with rapid growth of C₄ annual grasses (*Sorghum* spp. and *Heteropogon* spp.) of the understorey, leaf flushing of overstorey woody species (Williams et al 1997) and large increases of soil CO₂ efflux (Chen et al. 2002). Grass biomass produced during the wet season can be consumed by fire the following dry season or, if unburnt, is decomposed over subsequent wet seasons with some amount entering the SOC pool.

Using annual incident solar radiation, energy conversion efficiency and energy content of woody biomass, Linder (1985) calculated the potential biomass production for Darwin to be 111 ton DM ha⁻¹ year⁻¹, the highest value of any region in Australia. Using these simple parameters, tropical savannas of Northern Australia should have higher NPP and AGB relative to temperate Australian woodlands, given the high year-round radiation loads and non-limiting temperatures for growth, coupled with high annual rainfall. This potential NPP is well in excess of that measured for these savannas (22.2 ton DM ha⁻¹ year⁻¹) and is an overestimate as it does not consider the seasonal distribution of rainfall and the occurrence of an annual drought, low soil nutrient status and the effects of frequent fires, all of which limit NPP.

Low intensity dry season fires of the mesic savannas of northern Australia are widespread and account for 50–70% of all fires of the Australia continent, consuming up to 23.6 Mt of biomass per annum (Russell-Smith et al. 2002). These fires combust understorey fuels, resulting in significant leaf death of overstorey tree and shrub canopies (up to 80–90% for hot fires, Beringer et al. 2003) and at frequently burnt sites, can result in significant tree mortality (Williams et al 1999). When subjected to an experimental fire regime of annual, late-dry season burning (fire intensity of ~8,000 kW m⁻¹), Williams et al. (1999) reported a 27% decrease in live-tree basal area in open-forest savannas of Kakadu National Park. These measurements were conducted over a 4-year period. A single, high intensity fire (~20,000 kW m⁻¹) resulted in a live stem basal area reduction of 41%. Unburnt plots showed a 3.5% increase in live-stem basal area over the same period. Williams et al. (1999) conducted their study in savanna communities that are floristically and structurally similar to sites used here, although the fire regime of our sites is closer to biannual burning as opposed to the annual treatment imposed by Williams et al. (1999). Fire also had significant impacts on the survivorship of large (>30 cm DBH) trees and we conclude that fire would limit AGB and productivity in these savannas. A further limit to production is due to termite damage and hollowing of tree boles, a common occurrence in the dominant tree species of these savannas (Andersen and Lonsdale 1990). As trees age, termite damage can become extensive and is further compounded by fire, as flames penetrate boles via cavities formed from the action of

Table 5 Ratio of total biomass carbon to NPP (carbon residence time) for a range of ecosystems

Ecosystem	Residence time (years)	Reference
Savanna	5	This study
Savanna (global mean)	3.4	Scholes and Hall (1996)
Savannas (global mean)	4.4	Whittaker and Likens (1973)**
Woodland and shrubland (global mean)	8.6	Whittaker and Likens (1973)**
Tropical rainforest	16	Malhi et al. (1999)
Temperate forest	10	Malhi et al. (1999)

^a Cited from Scholes and Hall (1996)

termites. These dual processes also constrain the production of AGB.

A striking feature of these savannas is the high rate of NPP relative to the biomass and total carbon storage, i.e. the short residence time (Table 5). The mean residence time for biomass carbon in savannas is between 5 and 9 years (Table 5), while the biomass residence time for temperate, boreal and tropical forest biomass is over 10 years (Malhi et al. 1999). Using data given in Scholes and Hall (1996), the average residence time for savanna is 3.4, similar to that estimated in this study (Table 5). Clearly, carbon within the biomass of savannas is quickly turned over and returned to the atmosphere. While savannas have relative low carbon stocks, they have great potential to influence carbon cycling at regional and global scales because of their extensive area, short residence time and concomitant high rate of cycling. This short residence time is attributed to the distinct wet-dry seasons and with frequent atmospheric emission of carbon via biomass burning followed by re-growth the following wet season. Turnover of soil carbon is slower and is of the order of 20 years, similar to soil carbon turnover of tropical forests (Malhi et al. 1999).

Seasonal patterns carbon sink strength

In this study, NEP was positive ($3.8 \text{ ton C ha}^{-1} \text{ year}^{-1}$), indicating that the sites studied are a carbon sink, sequestering approximately $14 \text{ CO}_2 \text{ ha}^{-1} \text{ year}^{-1}$. Using eddy covariance measurements, Miranda et al. (1997) provide seasonal estimates of net carbon exchange from Brazilian cerrado savanna vegetation; extrapolating these data provides an NEP estimate of approximately $3.1 \text{ ton C ha}^{-1} \text{ year}^{-1}$. Cerrado sites used by Miranda et al. (1997) received annual rainfall of 1,550 mm per annum, with a 6–8 month wet season and LAI (1.4–0.62 wet to dry season), similar to sites of the current study and the values of NEP are comparable for these two savannas. These values of NEP also comparable to Sahelian fallow savanna ($0.32 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Hanan et al. 1998), Amazonian rainforest ($1 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Grace et al. 1995 and $5.9 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Malhi et al. 1999), European temperate deciduous forest ($2\text{--}5 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Goulden et al. 1996; Greco and Baldocchi 1996, $5.9 \text{ ton C ha}^{-1} \text{ year}^{-1}$ Malhi et al 1999), eastern North American deciduous forests ($0.7 \text{ to } 3.2 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Curtis et al. 2002) and Siberian Scots pine forests (0.19--

$1.36 \text{ ton C ha}^{-1} \text{ year}^{-1}$, Wirth et al 2002). Given an LAI that ranges from 0.8 to 2.5, comparative studies cited above suggest that an NEP of approximately $3 \text{ ton C ha}^{-1} \text{ year}^{-1}$ as reported for this study is relatively high. It is possible that sink strength is maintained by frequent and re-occurring disturbance and that this savanna ecosystem is in recovery from previous disturbance events, both long-term (cyclonic damage, 25–50 year cycle) and short-term (fire, 1–3 year cycle). From an analyses of tree size class distributions of these coastal open forests of the Darwin region, Wilson and Bowman (1987) and O'Grady et al. (2000) concluded that these forests are dominated by small trees (DBH <20 cm) and are young and actively growing following the major disturbance of Cyclone Tracey in 1974. Consequently, a sink strength in the order of $2\text{--}4 \text{ ton C ha}^{-1} \text{ year}^{-1}$ is possible despite a low LAI (0.6–2.5, dry to wet season), and would represent a maximal value of NEP for these mesic, coastal savannas.

Net ecosystem productivity was negative ($-0.2 \text{ ton C ha}^{-1} \text{ season}^{-1}$) during the dry season (May to October) and was positive ($4 \text{ ton C ha}^{-1} \text{ season}^{-1}$) during the wet season (November–April), indicating seasonal shifts in net carbon exchange with the atmosphere. These seasonal patterns are similar to cerrado vegetation of Brazil, which was a strong sink for carbon during the wet season months (November–April, $0.5\text{--}1.8 \text{ g C m}^2 \text{ day}^{-1}$) but became a source at the height of their dry season (August–September, Miranda et al. 1997). At the Howard Springs and Humpty Doo sites, there is little understorey photosynthesis during the dry season, as the C4 grasses have largely senesced and the evergreen trees are the most significant component of the ecosystem that are actively photosynthesising. Mean daily temperatures are not strongly seasonal and maintenance respiration rates of evergreen trees and shrubs continue over the dry season at rates similar to those of the wet season. Other dry season sources of carbon would include respiration from slowly decomposing grasses and continuing soil CO_2 efflux (microbial plus root respiration), although dry season F_{cs} was 60% lower than wet season rates. However, our data suggest that the dry season reduction in canopy assimilation (overstorey and understorey) is larger than the reduction in ecosystem-scale respiration wet to dry season, and as a result the site becomes a weak carbon source during the dry season months. Eddy covariance measurements of ecosystem-scale CO_2 fluxes confirm these large seasonal changes in carbon exchange at this site, as we observe a dry season decline in canopy-scale

CO₂ flux of 75% relative to wet season rates (Eamus et al. 2001). Eamus et al. (2001) also used these daily CO₂ fluxes measured over the wet-dry seasonal cycle at the Howard Springs site to derive an NEP of 2.8 ton C ha⁻¹ year⁻¹, in reasonable agreement with the estimate provided by this study using a biomass-inventory approach.

Although this study was conducted at savanna sites subjected to burning, our NEP estimate does not specifically include impacts of fire, which represent a non-respiratory carbon loss to the atmosphere (Wirth et al. 2003). A more accurate assessment of savanna carbon sink strength of this region should include some estimate of this loss, which would represent the longer-term carbon sink strength, or the Net Biome Productivity (NBP, after Schulze et al. 2000). For these savannas, net biome production (NBP) can be estimated as NEP minus carbon losses to the atmosphere due to fire. Using data of Russell-Smith et al. (2002), typical fuel loads for these savannas is approximately 4 ton ha⁻¹ (4.6 ton ha⁻¹ this study). Assuming a burning efficiency of 0.72 (ratio of fuel pyrolysed to fuel load within areas over which flames have passed, Russell-Smith et al. 2002) gives an annual mass of fuel burnt of 2.9 ton DM ha⁻¹ year⁻¹ (fuel load multiplied by burning efficiency factor) or approximately 1.5 ton C ha⁻¹ year⁻¹. Assuming an NEP of 3.8 ton C ha⁻¹ year⁻¹, NBP is estimated at 2.3 ton C ha⁻¹ year⁻¹ for this site. This suggests that of the 2–4 ton C ha⁻¹ year⁻¹ sequestered, 40–50% is lost to fire per annum, a significant fraction. This value of NBP is close to the 2.6 ton C ha⁻¹ year⁻¹ woody stem and coarse root increment observed, which suggests that above-ground understorey productivity (wet season grass production and understorey shrub growth) may be close to carbon 'neutral' due to fire (and respiration) losses. Long-term carbon sequestration may therefore be a function of woody growth and inputs to soil carbon pools and fire impacts (Burrows et al. 2002). Burrows et al. (2002) measured a net carbon sink in the grazed, semi-arid savanna woodlands of north eastern Queensland (annual rainfall 450–600 mm) and attributed this sink to reduced fine fuel accumulation due to grazing resulting in a reduced fire frequency coupled with active fire suppression. Long-term (18 year study) woody biomass increment averaged for 52 sites gave a sink strength of 0.53 ton C ha⁻¹ year⁻¹. This compares with 1.6 ton C ha⁻¹ year⁻¹ from this study, although these ecosystems are significant different in terms of rainfall and grazing pressure and our measurements are short-term only. Despite uncertainty inherent in our calculations relating to fire emissions and carbon (e.g. area averaged fuel loads, burning efficiencies), more precise spatial estimates of CO₂ flux and fire emission are clearly required to provide a more precise estimate of net productivity of Australia's tropical savannas.

Conclusions

This study describes a tropical savanna with generally low AGB (32 ton C ha⁻¹) and below-ground biomass (19.3 ton C ha⁻¹). Soil carbon storage was large at 151 ton C ha⁻¹. Carbon flux was highly seasonal with 75% occurring in the wet season, which was dominated by fine root growth (5.7 ton C ha⁻¹ year⁻¹). GPP was 20 ton C year⁻¹, high for an ecosystem with a low LAI (0.8–2.5). Productivity is likely to be constrained by the wet-dry climate, poor soils and constant disturbance from frequent fires. This results in a short residence time (5 year) for carbon stored in savanna biomass.

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References

- AGO-NGGIC (2000) National greenhouse gas inventory 1998. Australian Greenhouse Office, Canberra
- Andersen AN, Lonsdale WM (1990) Herbivory by insects in Australian tropical savannas: a review. *J Biogeogr* 17:433–444
- Andreae MO, Fishman J, Lindesay J (1996) The Southern Tropical Atlantic Region Experiment (STARE): Transport and Atmospheric Chemistry near the Equator-Atlantic (TRACE A) and Southern African Fire-Atmosphere Research Initiative (SAFARI): an introduction. *J Geophys Res* 101:23519
- Attwill PM (1979) Nutrient cycling in a *Eucalypts obliqua* (L'Herit) forest. III. Growth, biomass and net production. *Aust J Bot* 27:439–458
- Beringer J, Hutley LB, Tapper NJ, Coutts A, Kerley A, O'Grady AP (2003) Fire impacts on surface heat, moisture and carbon fluxes from a tropical savanna in north Australia. *Int J Wildland Fire* (in press)
- Bird MI, Veenendaal EM, Moyo C, Lloyd J, Frost P (2000) Effects of fire and soil texture on soil carbon in a sub-humid savanna (Matopos, Zimbabwe). *Geoderma* 94:71–90
- Burrows WH, Henry BK, Black PV, Hoffmann MB, Tait LJ, Anderson ER, Menke N, Danaher T, Carter JO, McKeon GM (2002) Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications *Global Change Biol* 8:769–784
- Calder GJ, Day KJ (1982) Fertility studies on four soils of the northern lateritic uplands, Northern Territory Technical Bulletin No 48. Department of the Northern Territory, Darwin
- Chen X (2002) Carbon balance of a Eucalypt open forest savanna of northern Australia. PhD Thesis, Northern Territory University, Darwin, Northern Territory
- Chen X, Eamus D, Hutley LB (2002) Seasonal patterns of soil carbon dioxide efflux from a wet-dry tropical savanna of northern Australia. *Aust J Bot* 50:43–51
- Chen X, Eamus D, Hutley LB (2003) Seasonal patterns of fine-root productivity and turnover in a tropical savanna of northern Australia. *J Trop Ecol* (in press)
- Christie EK (1978) Ecosystem processes in semi-arid grasslands. I. Primary production and water use of communities possessing

- different photosynthetic pathways. *Aust J Agric Res* 29:773–787
- Cook GD, Heerdegen R (2001) Spatial variation in the duration of the rainy season in monsoonal Australia. *Int J Climatol* 21:1723–1732
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests *Agric For Meteorol* 113:3–19
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1997) The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *J Trop Ecol* 13:697–708
- Eamus D, Prichard H (1998) A cost-benefit analysis of leaves of four Australian savanna species. *Tree Physiol* 18:537–545
- Eamus D, Prior LD (2001) Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies *Adv Ecol Res* 32:113–197
- Eamus D, Myers BA, Duff G, Williams RJ (1999) Seasonal change in photosynthesis of eight savanna tree species. *Tree Physiol* 19:665–671
- Eamus D, O'Grady AP, Hutley LB (2000) Dry season conditions determine wet season water use in the wet-dry tropical savanna of northern Australia *Tree Physiol* 20:1219–1226
- Eamus D, Hutley LB, O'Grady AP (2001) Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiol* 21:977–988
- Eamus D, Chen X, Kelley G, Hutley LB (2002) Root biomass and root fractal analyses of an open Eucalyptus forest in a savanna of north Australia. *Aust J Bot* 50:31–41
- Ewel KC, Cropper WP, Gholz HL (1987) Soil CO₂ evolution in Florida slash pine plantation. I. Changes through time. *Can J For Res* 17:325–329
- Fox ID, Nelder VJ, Wilson GW, Bannink PJ (2001) The vegetation of the Australian tropical savannas. Environmental Protection Agency, Brisbane, Queensland
- Gifford RM (2000a) Carbon contents of above-ground tissues of forest and woodland trees. National Carbon Accounting System, Technical Report No 22. Australian Greenhouse Office, Canberra
- Gifford RM (2000b) Carbon content of woody roots. (Revision 1) National Carbon Accounting System, Technical Report No 7. Australian Greenhouse Office, Canberra
- Goulden ML, Munger JM, Fan SM, Daube BC, Wofsy SC (1996) Exchange of carbon dioxide by a deciduous forest, response to interannual climate variability. *Science* 271:1576–1578
- Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre C, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia: 1992 to 1993. *Science* 270:778–780
- Greco S, Baldocchi DD (1996) Seasonal variation of CO₂ and water vapor exchange rates over a temperate deciduous forest. *Global Change Biol* 2:183–198
- Grierson PF, Adams MA, Attiwill PM (1992) Estimates carbon storage in the above-ground biomass of Victor's forests. *Aust J Bot* 40:631–640
- Hanan NP, Kabat P, Dolman AJ, Elbers JA (1998) Photosynthesis and carbon balance of a Sahelian fallow savanna. *Global Change Biol* 4:523–538
- Haynes BE, Gower ST (1995) Belowground carbon allocation in unfertilized and fertilized red pine plantations in Northern Wisconsin. *Tree Physiol* 15:317–325
- Heanes DL (1984) Determination of total organic-C in soil by an improved chromic acid digestion and spectrophotometric procedure. *Commun Soil Sci Plant Anal* 15:1191–1213
- Hoffmann WA (2002) Direct and indirect effects of fire on radial growth of cerrado savanna trees. *J Trop Ecol* 18:137–142
- House JI, Hall DO (2001) Productivity of tropical grasslands and savannas. In: Roy J, Saugier B, Mooney HA (eds) *Terrestrial global productivity*. Academic Press, San Diego, pp 363–400
- Hutley LB, O'Grady AP, Eamus D (2000) Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. *Funct Ecol* 14:183–194
- Hutley LB, O'Grady AP, Eamus D (2001) Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia. *Oecologia* 126:434–443
- Johnson FL, Risser PG (1974) Biomass, annual net primary production, and dynamics of six mineral elements in a post oak-blackjack oak forest. *Ecology* 55:1246–1258
- Kalpage FSCF (1974) *Tropical soils*. St Martin's, Macmillan, New York, USA
- Keith H, Raison RJ, Jacobsen KL (1997) Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. *Plant Soil* 196:81–99
- Kelley G, Hutley LB, Eamus D, Jolly P (2002) Role of savanna vegetation in soil and groundwater dynamics in a wet-dry tropical climate. In: *Proceedings of the International Association of Hydrogeologists, International Groundwater Conference, 'Balancing The Groundwater Budget'*, Darwin, Northern Territory, Australia, 12–17 May 2002
- Kirschbaum MUF, Eamus D, Gifford RM, Roxburgh SH, Sands PJ (2001) Definitions of some ecological terms commonly used in carbon accounting. Cooperative Research Centre for Carbon Accounting, Canberra, pp 2–5
- Komiyama A, Ogino K, Aksornkoae S, Sabhasri S (1987) Root biomass of a mangrove forest in southern Thailand. I. Estimation by the trench method and the zonal structure of root biomass. *J Trop Ecol* 3:97–108
- Lal R (2002) Soil carbon dynamics in cropland and rangeland. *Environ Pollut* 116:353–362
- Linder S (1985) Potential and actual production in Australian forest stands. In: Landsberg JJ, Parsons W (eds) *Research for forest management*. CSIRO, Division of Forest Research, Canberra, pp 11–35
- Long SP, Jones MB, Roberts MJ (1992) *Primary production of grass ecosystems of the tropics and sub-tropics*. Chapman and Hall, London
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ* 22:15–740
- McDonald NS, McAlpine J (1991) Floods and droughts: the northern climate. In: Haynes CD, Ridpath MG, Williams MAJ (eds) *Monsoonal Australia; landscape, ecology and man in the northern lowland*. Balkema, Rotterdam
- Menaut JC, Cesar A (1979) Structure and primary productivity of Lamto savanna, Ivory Coast. *Ecology* 60:1197–1210
- Miranda AC, Miranda Howard Springs, Lloyd J, Grace J, Francey RJ, McIntyre JA, Meir P, Riggan P, Lockwood R, Brass J (1997) Fluxes of carbon, water and energy over a Brazilian cerrado: an analysis using eddy covariance and stable isotopes *Plant Cell Environ* 20:315–328
- Montgomery RF, Askew GP (1983) Soils of tropical savannas. In: Bourliere F (ed) *Tropical savannas. (Ecosystems of the world, vol 13)* Elsevier, Amsterdam, pp 63–78
- Mott JJ, Williams J, Andrew MH, Gillison AN (1985) Australian savanna ecosystems. In: Tothill JC, Mott JJ (eds) *Ecology and management of the world's savannas*. Australian Academy of Sciences, Canberra, pp 56–82
- Mucha SB (1979) Estimation of tree ages from growth rings of eucalypts in northern Australia. *Aust For* 42:13–16
- Murphy PG, Lugo AE (1995) Dry forests of Central America and the Caribbean. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp 9–34
- Myers BA, Duff GA, Eamus D, Fordyce I, O'Grady AP, Williams RJ (1997) Seasonal variation in water relations of trees of differing leaf phenology in a wet-dry tropical savanna near Darwin, northern Australia. *Aust J Bot* 45:225–240
- O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season, patterns of tree water use in Eucalypt open-forests of Northern Australia. *Tree Physiol* 19:591–597

- O'Grady AP, Chen X, Eamus D, Hutley LB (2000) Composition, leaf area index and standing biomass of Eucalypt open forest near Darwin in the Northern Territory. *Aust J Bot* 48:629–638
- Prior LD, Eamus D, Duff GA (1997a) Seasonal trends in carbon assimilation, stomatal conductance and pre-dawn leaf water potential in *Terminalia ferdinandiana*, a deciduous tree of northern Australia savannas. *Aust J Bot* 45:53–69
- Prior LD, Eamus D, Duff GA (1997b) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet-dry savanna in northern Australia. *Aust J Bot* 45:241–258
- Rochette P, Ellert B, Gregorich EG, Desjardins RL, Pattey E, Lessard R, Johnson BG (1997) Description of a dynamic closed chamber for measuring soil respiration & its comparison with other techniques. *Can J Soil Sci* 77:195–203
- Russell-Smith J, Edwards A, Cook GD (2002) Reliability of biomass burning estimates from savanna fires: biomass burning in northern Australia during the 1999 Biomass Burning and Lightning Experiment-B field campaign. *J Geophys Res* (in press)
- Ryan MG (1991) A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiol* 9:255–266
- Ryan MG, Waring RH (1992) Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology* 73:2100–2108
- San Jose JJ, Montes RA, Farinas MR (1998) Carbon stocks and fluxes in a temporal scaling from a savanna to a semi-deciduous forest. *For Ecol Manage* 105:251–262
- Satoo T, Madgwick HAI (1982) Forest biomass. Nijhoff/Junk, The Hague
- Schmidt S, Stewart GR, Turnbull MH, Erskine PD, Ashwath N (1998) Nitrogen relations of natural and disturbed plant communities in tropical Australia (1998) *Oecologia* 117:95–104
- Scholes RJ, Hall DO (1996) The carbon budget of tropical savannas, woodlands and grasslands. In: Breyer AI, Hall DO, Melillo JM, Ågren GI (eds) *Global change: effects on coniferous forests and grassland*. Wiley, New York, pp 69–100
- Scholes RJ, Kendall J, Justice CO (1996) The quantity of biomass burned in southern Africa. *J Geophys Res* 101:23667–23676
- Schulze E-D, Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science* 289:169–179
- Scurlock JMO, Hall DO (1998) The global carbon sink: a grasslands perspective. *Global Change Biol* 4:229–233
- Setterfield SA, Williams RJ (1996) Patterns of flowering and seed production in *Eucalyptus miniata* and *E. tetrodonta* in a tropical savanna woodland, Northern Australia. *Aust J Bot* 44:107–122
- Smit AL, George E, Groenwold J (2000) Root observations and measurements at (transparent) interfaces with soil. In: Smit AL, Bengough AG, van Noordwijk M, Pellerin S, van de Geijn, SC (eds) *Root methods: a handbook*. Springer, Berlin Heidelberg New York, pp 235–271
- Tiessen H, Feller C, Sampaio EVSB, Garin P (1998) Carbon sequestration and turnover in semiarid savannas and dry forest. *Clim Change* 40:105–117
- Tothill JC, Nix HA, Stanton JP, Russell MJ (1985) Land use and productive potentials of Australian savanna lands. In: Tothill JC, Mott JJ (eds) *Ecology and management of the world's savannas*. Australian Academy of Science, Canberra, pp 125–141
- Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant Soil* 200:71–89
- Werner PA, Murphy PG (2001) Size-specific biomass allocation and water content of above- and below-ground components of three *Eucalyptus* species in a Northern Australia savanna. *Aust J Bot* 49:155–167
- Whitaker RH, Likens GE (1973) Carbon in the biota. In: Woodwell GM, Pecan EV (eds) *AEC Symposium Series 30*, NTIS US Dept of Commerce, Springfield, Va.
- Williams J, Day KJ, Isbell RF, Reddy SJ (1985) Soils and Climate. In: Munchow RC (ed) *Agro-research for the semi-arid tropics: North-West Australia*. University of Queensland Press, Brisbane, pp 31–92
- Williams RJ, Myers BA, Muller MJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a northern Australian tropical savanna. *Ecology* 78:2542–2558
- Williams RJ, Cook GD, Gill AM, Moore PHR (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Aust J Ecol* 24:50–59
- Williams RJ, Griffiths AD, Allan G (2002) Fire regimes and biodiversity in the wet-dry tropical savanna landscapes of northern Australia. In: *Flammable Australia: the fire regimes and biodiversity of a continent*. Bradstock RA, Williams JA, Gill AM (eds) Cambridge University Press, Cambridge, pp 281–304
- Wilson BA, Bowman DMJS (1987) Fire, storm, flood and drought: the vegetation ecology of the Howard Peninsula, Northern Territory, Australia. *Aust J Ecol* 12:165–174
- Wilson BA, Brocklehurst PS, Clark MJ, Dickinson KJM (1990) Vegetation survey of the Northern Territory, Australia, Technical Report No 49. Conservation Commission of the Northern Territory, Darwin
- Wirth C, Czimczik CI, Schulze E-D (2002) Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. *Tellus* 54B:611–630