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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 CO_2 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 t C ha^{-1}, with approximately 84% below-ground and 16% above-ground. Soil organic carbon content (0-1 m) was 151 ± 33 t C ha^{-1}, accounting for about 74% of the total carbon content in the ecosystem. Vegetation biomass was 53 ± 20 t 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 (GPP) was 20.8 t C ha^{-1}, of which 27% occurred in above-ground components and 73% below-ground components. Net primary production (NPP) was 11 t C ha^{-1} y^{-1}, of which 8.0 t C ha^{-1} (73%) was contributed by below-ground net primary production and 3.0 t C ha^{-1} production (27%) by above-ground net primary production. Annual soil carbon efflux was 14.3 t C ha^{-1} y^{-1}. The wet season plays a critical role in controlling carbon flux on a yearly basis. Approximately three-quarters of the carbon flux (above-ground, below-ground and total ecosystem) occurs during the 5-6 months of the wet season. This savanna site is a carbon sink during the wet season, but becomes a source during the dry season. Annual net ecosystem production (NEP) was 3.8 t C ha^{-1} y^{-1}. The loss of carbon due to fire is significant and the long-term sequestration potential (NBP) is approximately 40% of the value for NEP at 1.5 t C ha^{-1} y^{-1}, although there is a degree of uncertainty associated with this estimate.

Key words: CO_2, carbon cycling, wet-dry tropics, carbon source-sink relationships, NEP, NBP

Introduction

Savannas, covering at least 16 million km^2 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). Savanna 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 (Beringer et al. 1995). 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 km^2, which is 12 % of the worlds savannas biome and some of the world's most extensive and intact Eucalypt open-forest is located here. Given the 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 C_4 grasses dominating the understorey (Williams et al. 1997). These savannas have been subjected to minimal anthropogenic disturbance when compared to Eucalypt dominated ecosystems of southern Australia (Tothill at al. 1985). While there is an extensive ecological literature describing savannas of Australia, plus knowledge of ecophysiological processes at leaf (Eamus et al. 1998, 2000), tree (O'Grady et al. 1999, Eamus et al. 1999a, 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 (House and Hall, 2001). Most productivity studies of Australia's tropical savanna have concentrated on the herbaceous layer, with a focus on agricultural potential (eg Mott et al.1985, Williams et al. 1985).

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? We also approximate the impact of fire on the carbon balance of these ecosystems. 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 a) Howard Springs (12°28'S, 131°08'E) , b) Humpty Doo (12°36'S, 131°10'E), c) the Territory Wildlife Park (12°42'S, 131°0'E) and d) 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 leaf area index of these sites typically ranges from 0.6 to 1 with basal areas approximately 8-12 m^2 ha^{-1} (O'Grady et al. 2000), with understorey LAI being far more seasonally dynamic and ranging from 0.2 to 1.5.

The sites used in this study are representative of coastal, mesic savanna vegetation of northern Australia. These sites are frequently burnt and receive annual rainfall in excess of 1200 mm and are dominated by *E. tetrodonta* and *E. miniata* with *Sorghum* spp frequently occurring in the understorey (Wilson 1990). This, and other closely associated *Eucalypt* dominated savanna types also occur in coastal savanna areas of north-western Western Australia to the Gulf of

Carpentaria region of northern Queensland and occupy up to 200 000 km^2 in northern Australia.

In the Darwin region, where the current site were located, *Eucalyptus tetrodonta* and *E. miniata* dominated open-forests are commonly associated with lateritic red and yellow earths (Cole 1986), which tend to have A horizons of well drained, highly weathered sands 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. 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. During this period, greater than 90% of the 1700 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 ^{o}C (July) to 33.1 ^{o}C (October and November). Maximum and minimum temperatures have a range of 7 ^{o}C (wet season) to 11 ^{o}C (dry season) (McDonald and McAlpine 1991).

Measurements and calculations

A. 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 are 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 x 20 m plots were located at each site and biomass components (wood, bark, branch, leaf) were estimated from 48 harvested trees from six dominant tree species (*E. tetrodonta*, *E. miniata*, *E. chlorostachys*, *T. ferdinandiana*, *E. 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 function) relating relationships between tree diameter at the breast height (DBH) and biomass components have been developed for these species at these sites (O'Grady et al. 2000, Chen 2002). Relationships between total tree biomass (W) and DBH were highly significant, with correlation coefficients > 0.93 and confidence can be placed in the use of these functions to estimate AGB. The carbon content of above-ground biomass was assumed to be 50% of dry weight (Gifford 2000a).

Below-ground biomass (BGB) was estimated using the trench method (Komiyama et al. 1987, Eamus et al. 2002). Eight trenches were dug at the Humpty Doo study site, with two mature trees of the same species included at the ends of each trench. Trenches were 3 m × 4 m or 4 m × 5 m, with the depth of 0.6 to 2 m, depending the size of the trees included in the trench (Eamus et al. 2002). A 5 ton excavator with a 300 mm wide bucket was used to excavate soil blocks within each trench. Roots from soil block were extracted manually and sorted into coarse (> 2 mm diameter) and fine (< 2 mm diameter) roots. Root biomass was recorded following oven drying at 70 ^{o}C to a constant weight. The carbon content of below-ground biomass was assumed to be 49 % of dry weight (Gifford 2000b). Fine root biomass, production and turnover was measured using root ingrowth bags (Smit et al. 2000).

Soil carbon stock was estimated using soil organic carbon content and soil bulk density. At each study site, three plots were chosen for soil sampling. Soil samples were collected using an auger at 5, 20, 30, 50, 80 and 100 cm depths and soil organic carbon (SOC) was determined by an improved Walkley-Black wet digestion method (Heanes 1984). Percent SOC values were converted to soil carbon stock (t C ha^{-1}) using a bulk density for each soil layer. Bulk density was determined from pits dug at the Howard Springs site to depth and the profile sampled by taking 3-5 replicate soil samples using 10 cm diameter metal rings of 100 cm^3 volume (A. O'Grady per comm.). Bulk densities ranged from 1.42 at 5 cm depth to 1.7 g cm^{-3} at 1 m.

Table 1 here please

B. Above-ground carbon flux

Above-ground net primary production (ANPP) was estimated by summing annual increments of all components of biomass plus litterfall. AGB included tree and understorey components. Tree growth and productivity was calculated from increments of tree diameter and an allometric regression equation relating tree diameter to above-ground biomass (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 5 randomly located replicate 1 m^2 plots sampled at 3 different locations at the site. Litterfall was measured using 18 litter traps over a two year period (1998 to 2000) at the Wildlife Park site. Traps, with an area of 2463 cm^2 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: 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):

$$R_{lm} = (N_{tot}) (27 \exp(0.07T_a))$$

where N_{tot} (g N m^{-2}) is the total leaf nitrogen content obtained from leaf nitrogen concentration × leaf biomass, and T_a (^{0}C) is the average annual temperature. Leaf nitrogen concentration data was taken from Eamus and Prichard (1998) for both *E. tetrodonta* and *E. miniata*. Wood maintenance respiration (R_{wm}) was calculated using the following equation developed by Ryan and Waring (1992):

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

where V_s (cm^3) 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 the sum of ANPP and above-ground tree respiration.

C. Below-ground carbon flux

Below-ground carbon fluxes were estimated from measures of coarse and fine root production. Fine root production was estimated using ingrowth 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):

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

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 (Keith et al. 1997).

Fine root production (NPP_{fr}) was estimated using ingrowth bags (Smit et al. 2000). A total of 72 ingrowth bags were employed during the study. At the Howard Springs site, soil cores were dug to a depth of 50 cm, with soil collected and divided into two depth zones, 0-25 cm and 25- 50 cm. All roots from soil of each depth zone were carefully removed, and the resulting root-free soil was used to fill ingrowth mesh bags. Bags filled with root-free soil were then inserted into 7 × 50 cm deep holes. Rate of ingrowth of new fine roots (productivity) was determined by sequential re-sampling of the mesh bags over a 1 year period (December 1999 to December 2000).

Soil carbon efflux was measured using a closed chamber technique (Rochette et al. 1997, Chen et al. 2002). A polythene chamber with dimensions of 20 × 21.5 ×12 cm, giving a ground area of 430 cm^2, and an enclosed volume of 5160 cm^3 was used. Inlet and outlet gas lines were connected to a portable infra-red gas analyser (LI-6200, LiCor Inc., Lincoln, Nebraska, USA). Within the chamber, a 12 V fan mixed air to be sampled by the CO_2 analyser. The CO_2 concentration of air entering the IRGA was noted and then scrubbed of CO_2 to approximately 50 $\mu mol\ mol^{-1}$ below ambient concentration and measurement commenced at this within-chamber concentration. The CO_2 soil efflux (F_{cs}) was calculated using the rate of change of CO_2 concentration in the system [CO_2]:

$$F_{cs} = \frac{\partial [CO_2]}{\partial t}\left(\frac{M_w}{M_v}\right)\left(\frac{V}{A}\right),$$

where V is the total volume of the system, A is the area covered by the chamber and M_w and M_v are the molecular weight and volume of CO_2, respectively. Estimates of F_{cs} were made every 4 hours over a 2-3 day period each month for over a 2 year period (September 1998 to January 2001). Monthly mean F_{cs} was calculated from each measurement time, based on 18 rate estimates, being 3 × 1 minute estimates from 6 replicate plots. Further details of these measurements are given by Chen et al. (2002).

D. 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. In addition, Net Biome Production (NBP) is defined as the difference between NEP and non-respiratory carbon losses (L_c) due to events such as fire, storm damage, herbivory (insect plagues) and harvest (Schultze et al. 2000). NBP represents long-term change of carbon storage and productivity in an ecosystem by including losses of carbon due to disturbance (Schulze et al. 2000).

Results

Carbon stocks in tropical savanna of northern Australia

Table 2 here please

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 t C ha^{-1} (range 136 to 286 t 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 soil organic carbon (mean 151.3 t 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 t C ha^{-1} (range 23 to 76.0 t C ha^{-1}). Above-ground woody components accounted for 64% of the total vegetation pool (53 t C ha^{-1}, live plus dead components) with total root carbon at 19 t ha^{-1} or 36 % of the total vegetation pool.

Above-ground carbon flux

Table 3 provides wet and dry season and annual estimates of carbon fluxes between the various carbon pools for the study sites. 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 t C ha^{-1} y^{-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%.

Table 3 here please

Mean annual tree increment was 4.2 ± 0.95 mm y^{-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. During the wet season, mean stem diameter increment was as high as 0.8 mm $month^{-1}$ and in terms of seasonal C flux above-ground, the wet season accounted for approximately 75% and the dry season 25%. Only litterfall was larger in the dry season than in the wet 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 t C ha^{-1} y^{-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 t ha C y^{-1}. Moreover, 81% of the fine root production occurred during the wet season, when over 77% of the annual below ground carbon flux occurred (Table 3).

Ecosystem carbon flux

The total ecosystem carbon flux (GPP) was 20.8 t C ha^{-1} y^{-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.

Carbon budget of a tropical savanna

The carbon balance of these savannas is summarised in Figure 1, using data from Table 3. Integrating all above and below ground fluxes, production indices can be calculated. Net Ecosystem Production (NEP) was calculated by subtracting heterotrophic respiration (R_h) from NPP, which gave a value of 3.8 t C ha^{-1} y^{-1} (Table 3), suggesting that this savanna was a relatively strong carbon sink. Although the ecosystem as a whole sequestered carbon over the entire year, this sequestration was strongly seasonal and was dominated by wet season fluxes.

The ecosystem was a carbon source during the dry season with the vale of -0.2 t C ha^{-1} y^{-1} (Table 3).

Figure 1 here please

Net Biome Production (NBP) was calculated as NEP minus carbon losses due to disturbance, which, for these frequently burnt savannas, equates to losses due to fire. According to data presented by the Australian Greenhouse Gas Inventory (AGO-NGGIC 2000), average fuel load was 4 t ha^{-1} y^{-1} during the period 1994 to 1997 for the Northern Territory. Burning efficiency, the ratio of fuel pyrolised to fuel load within areas over which flames have passed (Russell-Smith et al. 2002), was 0.72 for all savanna fires in Australia. As a result, the annual mass of fuel burnt by fires in the savannas of northern Australia was approximately 2.9 t DM ha^{-1} y^{-1} (fuel load multiplied by burning efficiency factor) or approximately 1.5 t C ha^{-1} y^{-1} (annual mass of fuel burnt multiplied by carbon fraction of biomass), assuming that the carbon fraction of biomass is approximately 0.5 (Edwards et al. 1981). Using an NEP of 3.8 t C ha^{-1} y^{-1}, NBP was estimated at 2.3 t C ha^{-1} y^{-1} (NBP = NEP-Fire losses, 2.3 t C ha^{-1} y^{-1} = 3.8 - 1.5 t C ha^{-1} y^{-1}) for this savanna. Like NEP, NBP was negative in the dry season (-1.7 t C ha^{-1} period^{-1}) becoming positive during the wet season (4.0 t C ha^{-1} period^{-1}). The production efficiency of the savanna (NPP/GPP) was approximately 53% (Table 3), close to the often assumed ratio of NPP/GPP of 0.5. Malhi et al. (1999) obtained similar production efficiencies for tropical (51%), temperate (55%) and boreal (54%) ecosystems.

The mean residence time for carbon for biomass, soil component and the ecosystem as a whole can be calculated by dividing the total carbon stocks (Table 2) by the rates of carbon input (Table 3). Mean carbon residence times for biomass, soil and the ecosystem was 5, 17 and 19 years respectively (Table 3).

Discussion

Carbon stocks in the savannas of northern Australia

Carbon stocks (as opposed to biomass) of the vegetation component in these savannas was 53 t 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 t C ha^{-1}, Tiessen et al. 1998). The value is significantly lower than estimates for tropical forests, where above-ground biomass carbon stocks range from 70 to 179 t C ha^{-1} (Delaney et al. 1997, Malhi et al. 1999). The sites of the present study are closer to values given by Scholes and Hall (1996) for tropical dry forest (74.7 t ha^{-1}) reflecting the significant woody component of these savannas and the seasonality of rainfall. Scholes and Hall (1996) also report 37.4 t ha^{-1} carbon density for woodlands and 11.3 t C ha^{-1} dry savannas.

Below-ground biomass carbon was 19 t 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%) and in arid savannas (30%) (Scholes and Hall 1996). Like the seasonal patterns of ANPP, high below-ground carbon flux relative to above-ground at these sites reflects the pronounced seasonality of rainfall of this climate zone, which has two consequences for root distribution and production. First, there is significant investment of carbon in root systems of the dominant Eucalypt species, via the development of large lignotubers that enable carbon storage and vegetative re-growth following the frequent fire occurrence of these savannas (Williams et al. 1999). These savannas are dominated by evergreen trees which transpire all year (O'Grady et al 1999). Investment in below-ground carbon is evident in the deep root systems of mature Eucalypt trees, which enables extraction of water from the sub-soil (Kelley et al. 2002) during the long dry season, maintaining stand transpiration at a constant rate all year (O'Grady et al 1999). While the root biomass of trees tends to be concentrated in the upper 50 cm of soil (Eamus et al. 2002), roots grow to considerable depth, up to 5 m (Kelley et al. 2002) and we have observed roots to 9 m (A. O'Grady, pers comm.), although the biomass at these depths was small. Secondly, seasonal rainfall results in highly seasonal rates of fine root production and turnover and 80% of the annual fine root production of 7 t ha^{-1} y^{-1} occurs during the wet season. While fine roots are less than 3% of the total root biomass, their rate of production (7 t ha^{-1}) is far higher than coarse root production of 1 t ha^{-1} y^{-1}. Such high wet season root production is likely to provide the bulk of the annual nutrient uptake. Fine root growth is correlated with tree growth, which only occurred during the wet season (Table 3, Item 1).

This dormancy in stem growth occurs despite the maitainence of dry season photosynthetic (and transpiration) rates by tree evergreen species (*E. tetrodonta* and *E. miniata*) during the dry season. Eamus et al. (1999) observed only modest (approximately 10-15%) declines in assimilation rate per unit leaf area for these species during the dry season relative to the wet. Carbon fixed during the dry season is not utilised for shoot growth or significant leaf production and 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 confinement 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 as observed in this study. Hoffmann (2002) also observed strongly seasonal 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 on-set of wet season rains.

Significant investment in root systems also reflects the low nutrient status of the ancient, leached soils of this region, which are characterised by low cation exchange capacity and water holding capacity (Calder and Day 1982). Another factor influencing the ratio of carbon flux between above- and below-ground pools is the frequent occurrence of fire in these savannas. When subject to late-dry season burning, Williams et al. (1999) reported a decrease of 27% of live-tree basal area in open-forest savannas of Kakadu National Park, savanna communities that are floristically and structural similar to sites used in this study. Fire had significant impacts on the survivorship of large (> 30 cm DBH) trees and we conclude that fire would limit above-ground biomass and productivity in these frequently burnt 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 termites. These duel processes constrain the production of above-ground biomass. Thus the high incidence of lignotubers and frequent loss of above-ground biomass due to fire results in an increase in the fraction of total NPP that occurs below-ground.

In woodlands and savannas, soil organic carbon 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 soil organic carbon 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). Soil organic carbon content of savannas generally increases with increasing soil clay content, rainfall, tree cover and decreasing temperature (Scholes and Hall 1996). The soil organic carbon density in these Eucalypt open forest savannas (151 ± 33 t 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 levels of soil organic carbon of these savannas was mainly due to high below-ground carbon allocation and fine root productivity of the wet season.

North Australian savanna productivity

Murphy and Lugo (1995) reported the range of total or ecosystem NPP for tropical dry forests and savanna as 8-21 t DM ha^{-1} y^{-1}, with 6-16 t DM ha^{-1} y^{-1} for ANPP. For total NPP, this is approximately 4-10 t C ha^{-1} y^{-1}, and 3-8 t C ha^{-1} y^{-1} ANPP. At the Howard Springs/Humpty Doo sites, total NPP was at the top of this range, yet ANPP is at the bottom of this range, at 3 t C ha^{-1} y^{-1} (Table 4). This pattern of average to high NPP for these savannas, but low ANPP is also seen in Table 4, with NPP comparable to other savannas and drought-deciduous woodlands, although ANPP is significantly lower (Table 4). This further indicates that savannas of northern Australia have relatively high below-ground carbon allocation (see ratio the of ANPP/NPP, Table 4). In fact BNPP accounted for 70% of NPP, and fine root net primary production (NPP_{fr}) accounting for 87% of the total BNPP. Therefore, fine root production in any given year largely determines ecosystem NPP for these savannas.

This finding concurs with conclusions of Janos et al. (2002), who describe the fine root system of these savanna as essentially deciduous, with little production during the dry season. This seasonal cycle of root production is accompanied by large seasonal changes of soil CO_2 efflux (Chen at al. 2002), with 71% of annual CO_2 efflux occurring in the wet season. The wet season pulse of fine root production also coincides with rapid growth of C_4 annual grasses (*Sorghum* spp and *Heteropogon* spp) of the understorey. This seasonal growth, dominated by the grassy understorey, represents a major seasonal sequestration of carbon in these savannas, although much of this 'grass carbon' can be lost the following dry season to fire or, if unburnt, is decomposed over subsequent wet seasons. This seasonal cycle of grass growth also dominates the seasonal pattern of canopy-scale fluxes of water vapour (Hutley et al. 2000) and CO_2 (Eamus et al. 2001) for this site.

The high NPP_{fr} as observed in this study supports the view that the inherent capacity for productivity of savanna ecosystems is not greatly lower than that of other forest ecosystems (Scholes and Hall 1996). The wet season represents a period of high soil water and nutrient availability. 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 t DM ha^{-1} y^{-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 t DM ha^{-1} y^{-1}) and is an overestimate as it does not consider the seasonal distribution of rainfall, seasonality of available moisture, low soil nutrient status and the effects of frequent fires, all of which limit NPP.

Table 5
here please

A striking feature of these savannas is the high rate of NPP relative to the biomass and total carbon storage, ie the short residence time (Table 5). The mean residence time for biomass carbon in savannas is between 5 - 9 years (Table 5), while the 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 a large 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 highly pulsed productivity and frequent atmospheric emission of carbon via biomass burning. This rapid development of fuel and the frequent occurrence of fires results in a cyclical pattern of carbon flux between the ecosystem and the atmosphere. For savanna patches burnt annually, the residence of carbon stored with the grass biomass would be approximately 1 year. As expected however, the turnover of soil carbon is slower and is the order of 20 years, similar to soil carbon turnover of tropical forest (Malhi et al. 1999).

Seasonal sink strength of tropical savannas of northern Australia

In the present study, NEP was positive (3.8 t C ha^{-1} y^{-1}), indicating that the sites studied are a relatively strong carbon sink, sequestering approximately 14 t CO_2 ha^{-1} y^{-1}. This value of NEP is comparable to Sahelian fallow savanna (0.32 t C ha^{-1} y^{-1}, Hanan et al. 1998), Amazonian rainforest (1 t C ha^{-1} y^{-1}, Grace et al. 1995 and 5.9 t C ha^{-1} y^{-1}, Malhi et al. 1999) and for temperate deciduous forest (2-5 t C ha^{-1} y^{-1}, Goulden et al. 1996, Greco and Baldocchi 1996, 5.9 t C ha^{-1} y^{-1} Malhi et al 1999).

Recently, Eamus et al. (2001) estimated NEP for the Howard Springs site using eddy covariance derived estimates of CO_2 fluxes. The eddy covariance method is a reliable method for estimating NEP (Landsberg and Gower 1997, Steffen et al. 1998) as net carbon balance can be measured by integrating fluxes over diurnal, seasonal and annual cycles (Malhi et al. 1999). Integration of daily fluxes measured at the Howard Springs site provided an annual estimate of NEP at 2.82 t C ha^{-1} y^{-1}, in reasonable agreement with the estimate provided by this study using a biomass-inventory approach. If a carbon content of roots is assumed to be 43% (Gifford 1999), the calculated NEP is 2.8 t ha^{-1} y^{-1} , identical to the value given by the flux measurements. Sensitivity of calculated NEP indicates the dominance of root productivity to ecosystem productivity in this savanna. A comparison of carbon sink strength for terrestrial ecosystems based on eddy flux and forest inventory estimates have lead to conflicting results (Schulze et al. 2000) and it is rare to have two independent studies, conducted at the same site, using differing methodologies, converge to similar values of NEP.

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 and the recurrent impact of fire. Consequently, a sink strength in the order of 2-4 t C ha^{-1} y^{-1} is possible despite a low LAI (0.6-2.5, dry to wet season), and would represent a maximal value of NEP for this savanna type.

Net ecosystem productivity was negative (-0.2 t C ha^{-1} season^{-1}) during the dry season (May to October) and was positive (4 t C ha^{-1} period^{-1}) in the wet season (November to April). This indicates that the savanna ecosystems of northern Australia were both a seasonal carbon source and a seasonal carbon sink. During the dry season, there was no net tree growth and no coarse root growth (zero increment). Fine root production during this period accounted for less than 20% of total annual production. As a consequence, dry season NPP was only 1.9 t ha^{-1} compared to 9.1 t ha^{-1} for the wet season. Mean daily temperatures are not strongly seasonal and maintenance respiration rates continued over the dry season at rates similar to those in the wet. The maintenance of autotrophic respiration (R_a) for the duration of the annual wet-dry cycle, coupled with a strongly seasonal pattern of GPP resulted in this ecosystem becoming a net carbon source during the dry season.

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 and atmospheric water content. This feature has been observed at leaf (Prior et al. 1997a,b, 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). This fact indicates that size and timing of the wet season plays a critical role in controlling the carbon balance of tropical savannas.

True savanna sink strength - Net Biome Productivity

It is likely that this value of NEP presented here overestimates the long-term carbon sink strength, NBP. NBP is used to further describe long-term dynamics of carbon storage of an ecosystem as non-respiratory losses are taken into accounted (Schulze et al. 2000). The temporal scale of NBP is longer than short-term indices of production such as NEP, NPP and GPP and reflects the frequency of longer-term episodic disturbances, which for these savanna ecosystem, is likely to be dominated by carbon losses due to fire and cyclones. Fires of the humid savannas of northern Australia are wide spread 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). Therefore a true assessment of tropical savanna carbon sink strength must include some estimate of this loss, thereby allowing a calculation of NBP.

For estimation of the amount of carbon losses from fire, the following equation was employed:

$$L_c = B_{fl} \times \lambda \times \alpha_c$$

where, L_c is the amount of carbon lost due to fire (t C ha^{-1}), B_{fl} is fuel load, λ is combustion efficiency of fires and α_c is the carbon fraction of the biomass (= 0.5).

Fuel loads do not exceed 10 t ha^{-1} across the tropical savanna because of the effect of frequent fires and decomposition processes (Williams et al. 1999). In Australia, Walker (1981) reported the fuel load of monsoon tall-grass and mid-grass systems of 4 and 1 t ha^{-1}, respectively. Between 1994 to 1997, fuel loads in savannas of the Northern Territory ranged from 3 to 5 t ha^{-1} (Russell-Smith et al. 2001), with a mean of 4 t ha^{-1}. In the present study, grass biomass was typically 2 t ha^{-1} with litterfall and understorey production 1.7 and 0.9 t ha^{-1} y^{-1} respectively, giving a value of approximately 4.6 t ha^{-1} y^{-1}. The combustion efficiency of fuel was assumed to be 0.72 as given by the Australian National Greenhouse Gas Inventory (2000). This gives a carbon loss due to fire of approximately 1.5 t C ha^{-1} y^{-1} if burnt, giving an NBP of 2.3 t C ha^{-1} y^{-1} (Table 8.3). This means that losses due to fire account for only 14% of NPP in this savanna ecosystem. This is similar to the value given by Scholes and Hall (1996) and supports the view that even in annually burned savannas, a small fraction (<20%) of the NPP is consumed by fire (Scholes and Hall 1996). Two-thirds ecosystem NPP occurs below-ground, with roots and lignotubers protected from fire.

To demonstrate the impact of fire on NEP, we can compare emissions of carbon due to burning from the NT as given by Beringer et al. (1995). Using these data, collected during a low fire year (1992), 5% of the total area of the NT was burnt and resulted in an emission from Eucalypt savanna areas of 9 Mt of carbon. Assuming an NEP for this area (53 000 km^{-2}, Beringer et al. 1995) of 3 t C ha^{-1} y^{-1} (this area includes regions of lower rainfall than current site) gives a carbon sink strength of 16 Mt, suggesting 50% of sequestered carbon could be lost to fire. However, average fire years result in burning of between 10-15% of the NT, with fires distributed mostly in humid savanna Eucalypt communities (AGO-NGGI 2000). In the NT, *E. tetrodonta / E. miniata* dominated savanna occupies approximately 130 000 km^{-2} above 15 ^{o}S latitude (Wilson et al. 1990) and assuming an NEP of 3 t ha^{-1} y^{-1} for this area gives a sequestration of approximately 40 Mt C y^{-1}. Simple scaling of the Beringer et al. (1995) estimates for the humid savanna to this larger burnt area of an 'average' year would result in an a loss of carbon due to fire of approximately 20 Mt, again 50% of the carbon sequestered in any year. At a regional scale, extreme fire years could possibly result in no net gain or even a temporary annual net source of carbon for the region. Much of this fire-emitted carbon is lost to the region following fire as there is little or no fixation by savanna vegetation during the mid to late dry season. In addition, atmospheric flow models for northern Australia for the dry season months suggest a mass transport of smoke and fire emissions from northern Australia towards south-east Asia (Tapper 2001), representing a net loss to the region.

There is a deal of uncertainty in these estimates, but they do suggest that the impact of fire may is significant and NBP for the mesic, coastal savannas of northern Australia could range from near 0 to almost 3 t ha^{-1} y^{-1}, depending on fire occurrence and intensity. More precise spatial estimates of CO_2 flux and fire emission are clearly required to estimate the true source/sink strength of Australia's tropical savannas.

Conclusions

Data provided in this paper describes a savanna with generally low above-ground biomass, given a climate of high annual rainfall and temperatures. Above-ground biomass and productivity appears to be constrained by the wet-dry cyclical climate and the resultant fire regime. In other savanna ecosystems, fire can be a stimulatory process, via increased nutrient availability and a release of competition (Hoffmann 2002). However, in these savannas, where fire is frequent and widespread, it ultimately constrains productivity. Ecosystem productivity is dominated by the annual pulse of fine root and grass growth and residence time of carbon is short. Shifts in fire regime, either via climate change and predicted increases in fire occurrence for northern Australia (Cary 2002) or via altered land management, will have profound impacts on carbon sequestration rates of this biome.

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

Component	*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 increment in tree DBH
ΔB_{cr}	coarse root production	Derived from Johnson and Risser 1974, using AGB, ΔB_{ab} and BGB. AGB and BGB were measured using a harvesting method (Satoo and Madgwick 1982) and trench method (Komiyama et al. 1987)
ΔB_{fr}	fine root production	Measured using 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 of Darwin airport and total leaf N content for dominant Eucalypt tree from Eamus and Prichard (1998)
R_{wc}	wood	Derived from Ryan (1991), Keith et al. (1997) using

	construction respiration	woody (branch and stem) production
R_{wm}	wood maintenance respiration	Derived from Ryan and Waring (1992) using an average temperature in Darwin airport and sapwood volume (O'Grady 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)
L_c	carbon loss due to fire	Derived from AGO-NGGIC 1994 using savanna fuel loads of 4.0 t ha^{-1} and combustion efficiency of 0.72

Table 2 Estimated stocks of carbon (t 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.

Parameter	*Range*	*Mean (s.d.)*
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

Table 3 Seasonal and annual C fluxes (t C ha^{-1} $season^{-1}$ or t C ha^{-1} y^{-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
(19) Lc = fuel burnt	1.5	0.0	1.5
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) NBP = (25)-(19)	-1.7	4.0	2.3
(27) NPP/GPP = (23)/(24)	38.8%	57.2%	52.9%
Mean carbon residence time (years)			
(28) Biomass			5
(29) Soil and litter			17
(30) Total ecosystem			19

Table 4 Comparison of ANPP (t C ha^{-1} y^{-1}), NPP (t C ha^{-1} y^{-1}) and ratio of ANPP/NPP for savanna ecosystems, other Australian Eucalypt communities and tropical forests.*

Forest type	*ANPP*	*NPP*	*ANPP /NPP*	*Rainfall (mm)*	*Reference*
Savannas					
Eucalypt open-forest savanna, NT	3.0	11.0	0.27	1750	*This study*
Drought-deciduous woodland	9.7	12.7	0.76		Menaut and Cesar (1979)**
Tropical savanna (global mean)	5			300-	Scholes and Hall (1996)
Drought-deciduous woodland (Sth America)	2.1	4.4	0.48		Scholes and Hall (1996)
Sahelian shrub savanna	2.2			450	Hanan et al. (1998)
Trachypogon savanna (Sth America)	4.6			1300	San Jose and Montes (1989)
Drought-deciduous woodland,	7.5	15.7	0.48		Menaut and Cesar (1979)**
Drought-deciduous woodland,	8.6	13.2	0.65		Menaut and Cesar (1979)**
Drought-deciduous woodland,	6.5	12.3	0.53		Menaut and Cesar (1979)**
Tropical grasslands (Thailand)	7.2	10.0	0.72		Long et al. (1992)**
Tropical grasslands (Australia)	2.3	3.6	0.64		Christie (1978)**
Australian *Eucalyptus* forests					

Eucalypt woodlands, Box-ironbark forest	0.5-2.0			350-500	Grierson et al. (1992)
E. regnans (young)	9			1000	Grierson et al. (1992)
E. regnans (mature)	6.5			1000	"
E. regnans (regenerating)	36				Attiwill (1991)
E. obliqua (45 year old)	14				Attiwill (1979)
E. pauciflora (mature)	12	17	0.71	1200	Keith et al. (1997)
Tropical forest					
Tropical rainforest (global mean)	8.7	15.6	0.56	2200	Malhi et al. (1999)

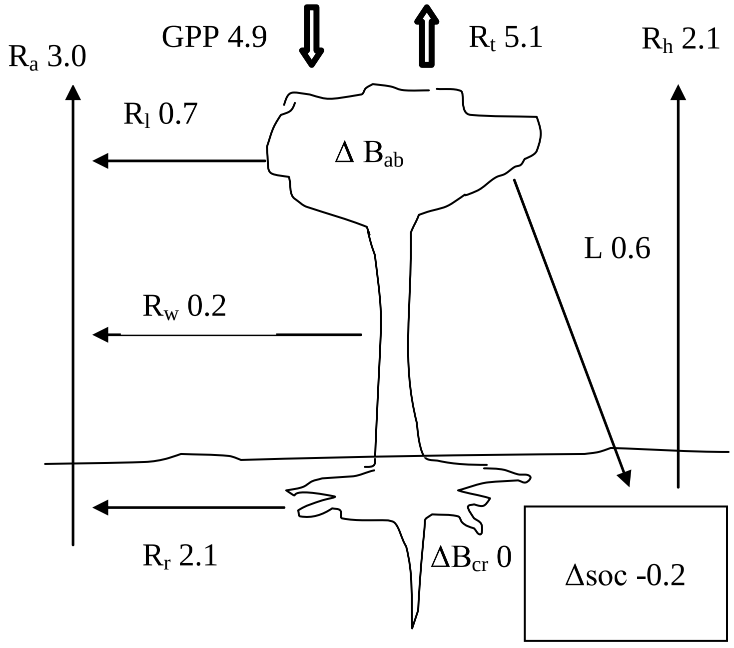
*ANPP is above-ground NPP and NPP includes both above and below ground, **cited in Scholes and Hall (1996).

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

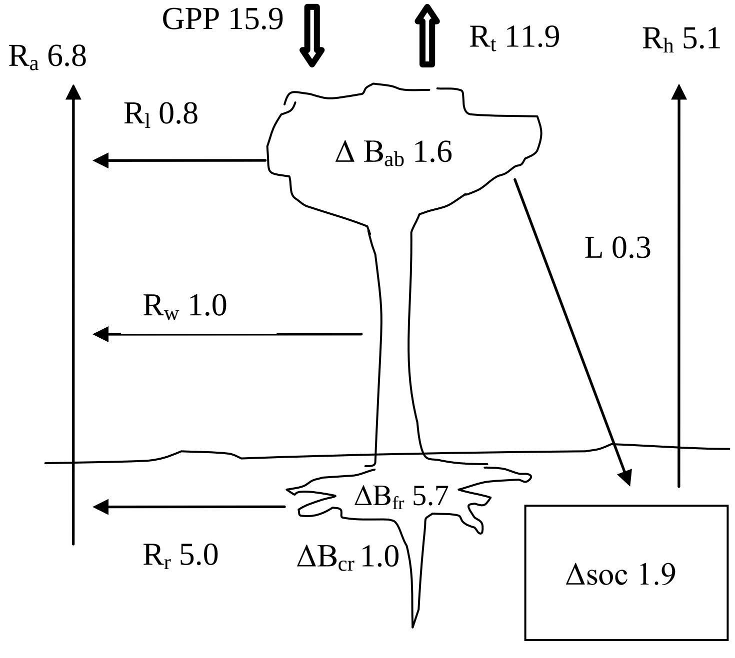
Ecosystem	*Residence time (y)*	*Reference*
Savanna	5	This study
Savanna (global mean)	3.4	Scholes and Hall (1996)
Savannas (global mean)	4.4	Whittaker and Likens (1973)**
Woodland and shrubland (global mean)	8.6	Whittaker and Likens (1973)**
Tropical rainforest	16	Malhi et al. (1999)
Temperate forest	10	Malhi et al. (1999)
Boreal forest	12	Malhi et al. (1999)

** cited from Scholes and Hall (1996).

(a)


GPP 4.9
R_t 5.1
R_a 3.0
R_h 2.1
R_l 0.7
Δ B_{ab}
L 0.6
R_w 0.2
R_r 2.1
ΔB_{cr} 0
Δsoc -0.2

(b)


GPP 15.9
R_t 11.9
R_a 6.8
R_h 5.1
R_l 0.8
Δ B_{ab} 1.6
L 0.3
R_w 1.0
ΔB_{fr} 5.7
R_r 5.0
ΔB_{cr} 1.0
Δsoc 1.9

(c)

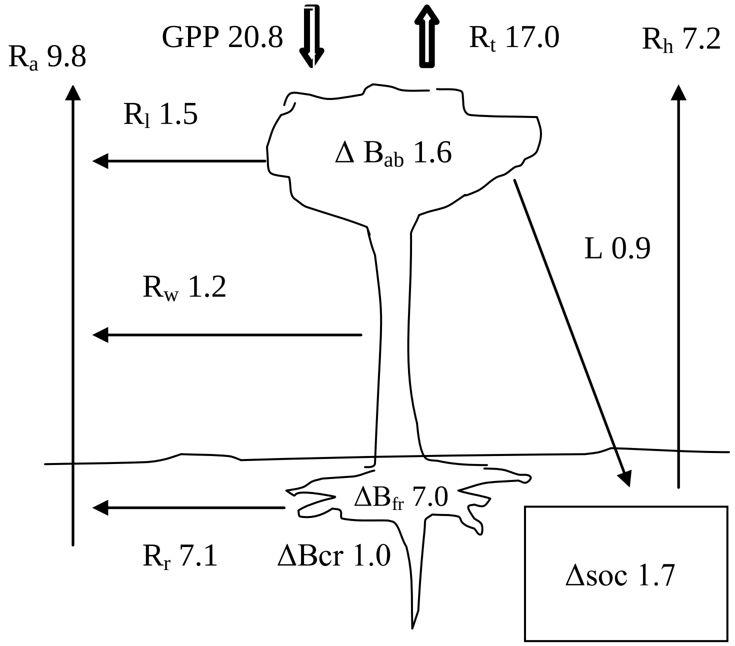


Figure 1 Estimated seasonal and annual carbon flux in the savanna studied. All units are t C ha^{-1} $season^{-1}$ or t C ha^{-1} y^{-1}. (a) dry season; (b) wet season; (c) annual. GPP, gross primary production; R_t, total respiration; R_h, heterotrophic respiration; R_a, autotrophic respiration; R_l, 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; Δsoc, soil organic carbon change.