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Article in *Australian Journal of Botany* · January 2005

DOI: 10.1071/BT04150

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# The estimation of carbon budgets of frequently burnt tree stands in savannas of northern Australia, using allometric analysis and isotopic discrimination

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**Abstract.** The stock, rates of sequestration and allocation of carbon were estimated for trees in 14 0.1-ha plots at Kapalga in Kakadu National Park, Northern Territory, using new allometric relationships of carbon stock to stem cross-sectional area and measured growth rates of trees. Carbon stocks of trees ranged from 12 to 58 t ha<sup>-1</sup>, with sequestration representing ~9% of the total stocks. More than half of the sequestered carbon is allocated to leaves and twigs and ~20% to wood. Only ~25% is retained in the live trees with leaf and twig fall accounting for 80–84% of the total transfers to the environment. An alternative method of calculating sequestration rates from consideration of water use and carbon-isotope discrimination data had a close to 1 : 1 match with estimates from allometric relationships. We developed and applied algorithms to predict the impacts of fire on carbon stocks of live trees. This showed that the reduction in live carbon stocks caused by single fires increased with increasing intensity, but the impact was highly dependent on the tree stand structure.

## Introduction

Savanna burning in Australia accounts for ~3% of the national greenhouse gas emissions (Anon. 2004). There is potential to alter management of Australia's savannas to not only reduce these emissions, but also to increase rates of carbon sequestration (Williams *et al.* 2004). Management of savannas could be included under Article 34 of the Kyoto Protocol, which allows grazing land management as an elective option for meeting specified greenhouse gas emission targets. Tropical savannas cover 12% of the world's land surface and are the world's most extensive grazing land type (Williams *et al.* 2005). However, strategies for the management of savanna lands for greenhouse gas abatement and quantification of emissions and sequestration rates are subject to many uncertainties (Sampson and Scholes 2000; Watson *et al.* 2000; Scholes and Noble 2001; Schulze *et al.* 2002). The major management options in savannas that affect emissions and carbon sequestration are manipulation of grazing and browsing pressure and more direct manipulation of vegetation through altering fire regimes or removal of woody vegetation. Fire management in particular is critical, with frequent burning being one of the dominant features of savannas worldwide.

Because carbon stocks in savanna vegetation have a faster turnover rate than those in soils (Chen *et al.* 2003), and tree stocks dominate the vegetation in most northern Australian savannas, understanding tree dynamics is critical to understanding carbon dynamics of these savannas. Important issues include carbon fluxes in the absence of fire, the impacts of fire on tree survival and the combustion of fuel sourced from trees.

A better understanding of the dynamics of trees will benefit not only estimates of greenhouse gas emissions and CO<sub>2</sub> fluxes, but also vegetation management generally. Fire regimes are key determinants of vegetation structure in tropical savannas. Across many regions of North and South America, Africa and Australia (e.g. Burrows *et al.* 2002; Dyer and Mott 1999; Archer and Stokes 2000), the cover of woody vegetation has increased since Anglo-European settlement, and this is believed to be largely due to changed fire regime. These changes in fire regimes include diminished fire frequency, active exclusion of fires and reduced average fire intensity. In contrast, fire regimes are believed to have become more frequent and of higher intensity following European settlement in much of the high-rainfall belt of Australia's Northern Territory (Russell-Smith *et al.* 1997,

1998). Such an increase in the severity of fire regimes can cause substantial reductions in live biomass of trees (Williams *et al.* 1999).

Various approaches can give inventories of stocks and fluxes relevant to particular scales and questions. Information about regional carbon sources and sinks can be derived from variations in observed atmospheric CO<sub>2</sub> concentrations by inverse modelling with atmospheric tracer transport models (Gurney *et al.* 2002). Greater temporal and spatial resolution from initiatives such as the proposed orbiting carbon observatory (<http://oco.jpl.nasa.gov/>; verified 27 October 2005) will increase the quality of the outputs of such approaches. Micrometeorological methods can provide data at finer temporal and spatial resolutions required to give direct measures of mass and energy exchange of ecosystems (e.g. Williams *et al.* 2004). Such techniques, however, cannot easily discriminate carbon fluxes of trees from those of other components of ecosystems such as grasses and soil biota. This requires estimation of above- and below-ground biomass, turnover and CO<sub>2</sub> efflux (Chen *et al.* 2003).

The estimation of total carbon stocks from allometric relationships that relate biomass to tree stem diameter  $D$  (e.g. Werner and Murphy 2001; Eamus *et al.* 2000; O'Grady *et al.* 2000) requires knowledge of total basal area of trees and their size-class distribution. The requirement for knowledge of the stand structure increases workloads substantially. However, this need can be bypassed when physiological processes scale linearly to the cross-sectional area ( $A$ ) of tree stems, which is equivalent to scaling against  $D^2$ . The ability of this approach to enable scaling from individual trees to whole stands was demonstrated for water use of trees in northern Australian savannas by Cook *et al.* (2002). Although theoretical considerations indicate that total biomass scales against  $D^{8/3}$  (Enquist *et al.* 1998; Enquist and Niklas 2002), leaf mass and gross photosynthesis scale against  $D^2$  or  $A$  (Enquist and Niklas 2002), suggesting that there is potential to estimate carbon fluxes from allometric relationships without knowledge of stand structure.

The aim of this paper is to reduce the uncertainty in quantifying carbon stocks and fluxes of savanna tree stands. We first develop a new approach to the analysis of allometric data and apply it to estimate sequestration rates, carbon allocation and carbon fluxes of tree stands. We check the reliability of the estimates of carbon sequestration by comparison with estimates derived from calculation of water use efficiency of savanna trees and estimated water use of tree stands. Algorithms to estimate the impacts of fires of varying intensity on carbon stocks in live trees are then developed and applied to the same tree stand data to determine the possible outcomes of the observed variations in fire intensity. We conclude with a consideration of the effect of varying fire regimes on carbon fluxes.

## Materials and methods

### Tree-stand data

The algorithms developed in this paper to examine carbon fluxes of savanna trees and to predict the impact of fire were applied to tree-stand data that were collected in 1989–1990 from 14 0.1-ha plots at Kapalga (12°43'S, 132°22'E) in Kakadu National Park, Northern Territory. These plots comprised seven on each of two Kandosol soils (Isbell 1996) differentiated by their depth: shallow (<0.5 m) and deep (>1.2 m). For each plot, the species and diameter at breast height (1.3 m),  $D$  (cm), of each tree with a height greater than 1.3 m was recorded.

The plots contained 41 tree species, with a mean density of 1446 individuals ha<sup>-1</sup> and a mean total basal area at breast height of 10 m<sup>2</sup> ha<sup>-1</sup>. The species for which the allometric methods of estimating carbon flux were derived, and for which growth rates were available comprised 50% of all individuals and 84% of the total basal area on these plots. These species were *Eucalyptus tetrodonta* F.Muell., *E. miniata* Cunn. ex Schauer, *Corymbia porrecta* (S.T.Blake) K.D.Hill & L.A.S.Johnson, *C. bleeseri* (Blakely) K.D.Hill & L.A.S.Johnson, *Erythrophleum chlorostachys* (F.Muell.) Baill. and *Terminalia ferdinandiana* Exell. The allometric relationships and growth rates of *T. ferdinandiana* were applied to the remaining species.

### Determining annual carbon fluxes from allometric relationships

The allometric data were derived from harvests of trees at Howard Springs (12°30'S, 130°45'E), Northern Territory (O'Grady *et al.* 2000). These trees were in a frequently burnt landscape, probably with a fire frequency typical for the region of about one fire every 2 years (Russell-Smith *et al.* 1997). We re-analysed these data by converting them from extant biomass to extant carbon mass by using a carbon proportion of 0.47 for foliage (G. D. Cook, unpubl. data) and 0.49 for all remaining components (Gifford 2000). New allometric relationships were developed to estimate carbon mass as a linear function through the origin, against cross-sectional area  $A$  at breast height.

Annual rates of carbon sequestration were estimated by applying the allometric relationships to the 14 tree stands when first measured and comparing with those calculated after 1 year's growth at the mean growth rates.

Growth rates expressed as annual increments in  $D$  were estimated from records of 453 trees whose  $D$  was first measured in 1990 and then again in 2003. Preliminary analyses revealed no significant effects on variation in growth rate with initial tree size, so simple mean growth rates were estimated.

Twig production was estimated assuming the same biomass as leaf production (Cook 1994). The allometric relationship for root carbon stock was derived similarly by re-analysing the data of Eamus *et al.* (2002) for trees in the greater Darwin area. The allometric relationship for roots was not differentiated by species.

For leaves and twigs that turn over annually, the annual production was calculated as follows:

$$P_c = S_c A_{t+1}, \quad (1)$$

where  $P_c$  is the carbon allocation (kg C year<sup>-1</sup>) to a particular component  $c$  during year  $t$  and  $S_c$  is the slope of the regression of extant carbon mass of component  $c$  against  $A$ . Annual transfers to the environment in the form of litter fall were estimated similarly, but using  $A$  at time  $t$ .

For non-twig wood and non-twig bark that do not turnover annually, the apparent annual production is simply the difference between the carbon mass at time  $t$  and that at time  $t + 1$  year. We called this the apparent production because some of the carbon stock would have been removed by various processes, including fire, termite consumption, decay and shedding. For wood, the gross increase in carbon mass ( $P_w$ )

was calculated taking into account that removed by termites and decay as

$$P_w = (1/(1-h)) \alpha (S_A - (S_l + S_t))(A_{t+1} - A_t), \quad (2)$$

where  $h$  is the proportion of stem hollowing on a cross-sectional area basis,  $\alpha$  is the proportion of total non-leaf and twig above-ground carbon in wood rather than bark and  $S_A$ ,  $S_l$ ,  $S_t$  are the slopes of the regressions of extant carbon mass against  $A$  for the total above-ground, leave and twig components, respectively. We calculated  $\alpha$  from the extant carbon in bark and wood of tree branches. The estimated value of 0.864 was assumed to apply also to tree stems. The value of  $h$  was taken as 0.25 in accordance with estimates that hollows typically comprise half the stem diameter in most eucalypt and bloodwood trees in this region (Fox and Clark 1972).

Bark production could not be estimated directly from allometric relationships of harvested trees, because these take no account of the various processes by which bark is lost to the tree. We therefore estimated the annual production of non-twig, above-ground bark from  $P_w$  by estimating the relative production of bark and wood in several 1-year-old stems for which such losses were negligible, and assuming that this ratio applies to stems of all ages. By this approach, bark production ( $P_b$ ) was found to be 0.584 times wood production (G. D. Cook, unpubl. data). Thus,

$$P_b = 0.584 P_w. \quad (3)$$

Root growth was simply estimated as the stock at time  $t + 1$  year minus the stock at time  $t$ .

The annual rate of carbon sequestration of trees was the sum of the increase in carbon mass of each component. The transfer of carbon to the environment from wood and bark was calculated as the difference between the gross and the apparent production.

#### Determination of annual carbon sequestration of trees from isotopic discrimination

We calculated the mean annual water-use efficiency ( $W$ : mol C assimilated per mol of water transpired) of trees as follows (Farquhar and Richards 1984):

$$W = ((1 - \phi)p_a(1 - p_i/p_a))/1.6\Delta e, \quad (4)$$

where  $\phi$  is the proportion of carbon fixed but later respired,  $p_i/p_a$  is the ratio of the intercellular and atmospheric partial pressures of  $\text{CO}_2$ , and  $\Delta e$  is the difference in the intercellular and atmospheric vapour pressure. We took the value of  $\phi$  to be 0.5 (Chen *et al.* 2003). The mean annual value of  $\Delta e$  (2.69 kPa) was calculated as the reciprocal of the mean of the reciprocals of the morning and afternoon values for each month of the year for *Eucalyptus tetradonta* growing in Darwin from the data of Prior *et al.* (1997). Because we calculated water use efficiency of the whole plant rather than just for the above-ground parts, we made no allowance for the proportion of the total biomass comprising roots, which had been included in the original equation. The ratio  $p_i/p_a$  was calculated from the isotopic discrimination equation of Farquhar *et al.* (1982), assuming negligible difference between total partial pressure of  $\text{CO}_2$  and that of  $^{13}\text{CO}_2$ :

$$\Delta^{13}\text{C}_p = a + (b - a)p_i/p_a, \quad (5)$$

where  $a$  is the discrimination in air associated with differences in the diffusion rates of  $^{13}\text{C}$  and  $^{12}\text{C}$  and has a value of 4.4‰. The discrimination in the carboxylation reaction,  $b$ , is assumed to be 27‰ (Marshall and Monserud 1996). We used a range of values for the isotopic discrimination of plant tissue,  $\Delta^{13}\text{C}_p$ , taken either directly from the literature or calculated from the  $\delta^{13}\text{C}_p$  values (Miller *et al.* 2001 for a rainfall of 1.2 m; Schulze *et al.* 1998; Bowman and

Cook 2002) according to the following formula (Farquhar *et al.* 1982; Beerling and Woodward 1995):

$$\Delta^{13}\text{C}_p = (\delta^{13}\text{C}_a - \delta^{13}\text{C}_p)/(1 + \delta^{13}\text{C}_p/1000). \quad (6)$$

Because Equation 1 strictly applies to just the first product of photosynthesis and does not include fractionations caused by later biochemical processes, the values of  $\Delta^{13}\text{C}_p$  should be adjusted (Marshall and Monserud 1996). Sufficient work has not been carried out to quantify the magnitude of this adjustment for foliar and wood samples of these eucalypts. Nevertheless, since our aim is to determine whether the isotopic discrimination approach gives a similar estimate of carbon sequestration to those from the allometric approach, slight imprecisions will not affect the outcome. Rather, good agreement between the two approaches would support a case for further research to refine the estimates. Accordingly, we used data of Marshall and Monserud (1996) and added 2.13 to the value of  $\Delta^{13}\text{C}_p$ .

For foliar samples, water use efficiency was calculated by using the atmospheric partial pressure of  $\text{CO}_2$  and the atmospheric value of  $\delta^{13}\text{C}_a$  for the year of sampling (Etheridge *et al.* 1996; Francey *et al.* 1999; Trudinger *et al.* 1999). For the 100-mm wood core of Miller *et al.* (2001), an annual increase in stem diameter of ~3 mm was assumed, so the atmospheric values were taken to be the average over the 60 years prior to sampling.

We used an equation relating daily water use to the tree basal area (calculated at breast height) to estimate water use of trees of varying size classes (Cook *et al.* 2002). This equation applies all year for trees in this region. We calculated the annual carbon sequestration of each stand by multiplying the estimated water use by the water use efficiency.

#### Predicting the impact of fire

In 1990, 592 eucalypts and 380 non-eucalypts were tagged and subsequently subjected to fires of varying intensity as part of the Kapalga fire experiment. This experiment has been described in detail elsewhere (Andersen *et al.* 1998, 2003). For each individual, the species and  $D$  were recorded. For 5 years, the intensity of each fire and the survival of each tree stem were noted. The tree-stem survival data were previously analysed by generalised linear models (Williams *et al.* 1999). In the present study, we developed algorithms that could be incorporated into mechanistic models of vegetation dynamics to predict the impact of fires on tree stands. We grouped tree stems into size classes on the basis of the natural logarithm of  $D$  and fires were grouped into classes on the basis of their intensity. For eucalypts, which included the genera *Eucalyptus* and *Corymbia*, the three fire-intensity classes were  $\leq 2 \text{ MW m}^{-1}$ ,  $\leq 6 \text{ MW m}^{-1}$  and  $\leq 20 \text{ MW m}^{-1}$ . Only two fire-intensity classes were used,  $< 3$  and  $\geq 3 \text{ MW m}^{-1}$ , to have sufficient data for the non-eucalypts. The mean intensity faced by trees in each size class was then calculated. The data analysed were thus the probability of stem survival, the size class of each stem and the mean fire intensity of each intensity class for both eucalypts and non-eucalypts.

We developed multivariate regressions separately for trees with values of  $D < 20$  and  $D \geq 20$  cm because previous analyses showed that tree survival increased with increasing values of  $D$  until about this size, and thereafter decreased (Williams *et al.* 1999). Preliminary analyses of the data showed that there were significant main effects of fire intensity on the probability of survival, but no significant main effects of stem size, but there were significant interactions between stem size and fire intensity. Accordingly, we fitted a multivariate regression equation that included terms for fire intensity and the interaction of intensity and stem size and gave a 100% probability of survival in the absence of fire:

$$P = 1 + a \times I + b \times I \times \ln D, \quad (7)$$

where  $P$  is the proportion of stems with a particular diameter,  $D$ , that survive a fire of a particular intensity,  $I$  ( $\text{MW m}^{-1}$ ).

We applied the multivariate equations of stem survival to examine the impact of fire intensity on carbon stocks of live trees in the 14 plots at Kapalga. Three fire intensities were considered: low, which was the mean Byram fire-line intensity for early dry-season fires at Kapalga ( $2.1 \text{ MW m}^{-1}$ ), medium, which was the mean intensity for late dry-season fires ( $7.7 \text{ MW m}^{-1}$ ) and high, which was the maximum fire intensity recorded during the fire experiment ( $15 \text{ MW m}^{-1}$ ) (Williams et al. 2003). Carbon stocks were estimated by applying the allometric relationships developed in this study as previously described.

Results

Carbon budget of live tree stands

A preliminary examination demonstrated that the carbon stocks of all the various subcomponents of the trees showed apparent linear relationships with stem cross-sectional area as shown in Fig. 1 for the total above-ground biomass. Linear regressions through the origin were highly significant, with more than 90% of the variation in carbon stock being explained by stem cross-sectional area in most cases (Table 1). Regression of carbon stocks in leaves, branches and roots showed the lowest  $R^2$  values; however, only for branches of *Erythrophleum chlorostachys* and for roots were the  $R^2$  values less than 0.75.

The coefficients indicate that, for equivalent cross-sectional areas of stems, *Eucalyptus tetrodonta* and *Corymbia bleeseri* had the greatest total carbon stock and *C. porrecta* and *Erythrophleum chlorostachys* the least. *E. chlorostachys* trees have a greater carbon stock in leaves than other species, and together with *Terminalia ferdinandiana* and *C. bleeseri* have the greatest carbon stock in branches. The eucalypts have a greater proportion of their carbon stock as stems than the non-eucalypts, reflecting their position as canopy dominants.

The calculated mean total carbon stock of live trees at Kapalga was  $\sim 23 \text{ t ha}^{-1}$  on shallow soils and  $\sim 43 \text{ t ha}^{-1}$  on deep soils, with an additional  $c. 1$  and  $2 \text{ t ha}^{-1}$  of dead trees, respectively (Table 2). The calculation of the carbon stock in dead trees assumed the same allometric relationships as for

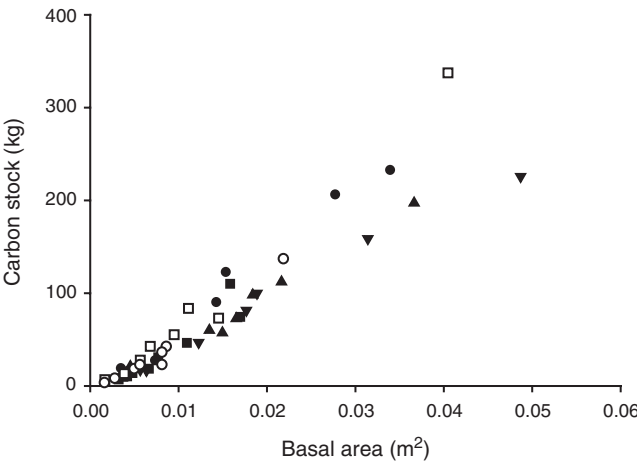


Fig. 1. The relationships between total above-ground carbon stock of trees and the stem cross-sectional area at breast height (1.3 m). (●, *Eucalyptus tetrodonta*; ▲, *E. miniata*; ▼, *Corymbia porrecta*; □, *C. bleeseri*; ■, *Erythrophleum chlorostachys*; ○, *Terminalia ferdinandiana*).

live trees, so would be an overestimate because of gradual decay. Across the 14 plots, carbon stock ranged from  $\sim 12$  to  $58 \text{ t ha}^{-1}$  (Table 2).

The diameter growth rates for each species used to calculate net primary productivity (NPP) were as follows: *E. tetrodonta*,  $0.17 \text{ cm year}^{-1}$ ; *E. miniata*,  $0.24 \text{ cm year}^{-1}$ ; *C. porrecta*,  $0.20 \text{ cm year}^{-1}$ ; *C. bleeseri*,  $0.16 \text{ cm year}^{-1}$ ; *Erythrophleum chlorostachys*,  $0.12 \text{ cm year}^{-1}$ ; and *T. ferdinandiana*,  $0.14 \text{ cm year}^{-1}$ . Total carbon sequestration of the trees, as estimated from allometric data, ranged from  $\sim 1.5$  to  $\sim 5.7 \text{ t ha}^{-1} \text{ year}^{-1}$ , representing  $\sim 9\%$  of the total carbon stocks (Table 2). More than half of the sequestered carbon is allocated to leaves and twigs and  $\sim 20\%$  to wood. Only  $\sim 0.3$ – $1.2 \text{ t ha}^{-1} \text{ year}^{-1}$  or  $\sim 25\%$  of sequestered carbon is retained in the live trees. Leaf and twig fall accounted for 80–84% of the total transfers to the environment, with bark losses contributing a further 10–13% of total transfers.

Table 1. The coefficients relating carbon stock (kg) of subcomponents of various tree species and stem cross-sectional area ( $\text{m}^2$ ) at breast height (1.3 m)

Eute: *Eucalyptus tetrodonta*; Eumi: *E. miniata*; Copo: *Corymbia porrecta*; Cobl: *C. bleeseri*; Erch: *Erythrophleum chlorostachys*; Tefe: *Terminalia ferdinandiana*. Numbers in parentheses are  $R^2$ -values, with  $n = 8$

Fraction	Symbol	Eute	Eumi	Eupo	Eubl	Erch	Tefe
Leaves	$S_l$	122 (0.84)	50 (0.96)	73 (0.85)	49 (0.80)	154 (0.75)	93 (0.89)
Twigs	$S_t$	127	52	76	51	160	97
Bark	$S_b$	341 (0.99)	218 (0.92)	326 (0.98)	347 (0.97)	401 (0.95)	379 (0.92)
Wood	$S_w$	2161 (0.93)	1829 (0.95)	1289 (0.98)	2225 (0.97)	1044 (0.92)	1233 (0.92)
Branches	$S_{br}$	779 (0.85)	375 (0.79)	619 (0.96)	1163 (0.90)	814 (0.62)	935 (0.83)
Stems	$S_s = S_w + S_b$	2502 (0.95)	2047 (0.96)	1616 (0.98)	2573 (0.97)	1445 (0.93)	1612 (0.92)
Total above ground	$S_A = S_s + S_{br} + S_l$	3403 (0.97)	2472 (0.96)	2308 (0.98)	3785 (0.96)	2413 (0.82)	2640 (0.91)
Roots	$S_r$			542 (0.57)			
Total	$S_T = S_r + S_A$	3945	3014	2850	4327	2955	3182

**Table 2.** Carbon budgets and water use of trees in 0.1-ha plots on shallow (<0.5 m) and deep (>1.2 m) soils at Kapalga

Attribute	Shallow soil ( <i>n</i> = 7)		Deep soil ( <i>n</i> = 7)	
	Range	Mean (s.d.)	Range	Mean (s.d.)
Total basal area (m <sup>2</sup> ha <sup>-1</sup> )	3.8–10.9	7.0 (2.4)	9.8–16	13.2 (2.0)
Total C stock (t ha <sup>-1</sup> )				
Live	12.4–35.2	22.9 (7.8)	35.6–57.5	43.5 (6.6)
Dead	0–2.3	0.93 (0.78)	0–5.1	2.1 (1.73)
Estimates of C sequestration and flux by allometric approach (t ha <sup>-1</sup> year <sup>-1</sup> )				
Total sequestration	1.51–2.88	2.12 (0.52)	3.13–5.71	3.91 (0.8)
Leaf and twig	0.93–2.05	1.39 (0.44)	1.73–3.89	2.37 (0.65)
Wood	0.26–0.6	0.41 (0.12)	0.69–1.02	0.87 (0.13)
Bark	0.15–0.35	0.24 (0.07)	0.41–0.6	0.51 (0.07)
Roots	0.05–0.13	0.08 (0.03)	0.13–0.02	0.17 (0.03)
C retention	0.33–0.75	0.5 (0.14)	0.79–1.24	0.99 (0.15)
C transfers to environment				
Total	1.10–2.23	1.62 (0.4)	2.24–4.47	2.91 (0.67)
Leaf & twig	0.90–2.03	1.36 (0.44)	1.69–3.81	2.32 (0.64)
Wood	0.05–0.15	0.10 (0.03)	0.16–0.25	0.21 (0.03)
Bark	0.10–0.25	0.16 (0.05)	0.31–0.43	0.38 (0.05)
Estimates of C sequestration by isotopic discrimination approach				
Water use (10 <sup>6</sup> kg ha <sup>-1</sup> year <sup>-1</sup> )	1.0–2.9	1.9 (0.65)	2.6–4.2	3.5 (0.52)
Total sequestration (t ha <sup>-1</sup> year <sup>-1</sup> )	1.08–3.09	2.01 (0.70)	2.79–4.57	3.77 (0.56)

The water use efficiencies of *E. tetradonta* and *E. miniata* calculated from previously published isotopic-discrimination data ranged from 0.9 to 1.2 g C kg<sup>-1</sup> (Table 3), with a mean of 1.08 g C kg<sup>-1</sup>. Water use on each of the plots at Kapalga ranged from 100–290 mm year<sup>-1</sup> on shallow soils to 260–424 mm year<sup>-1</sup> on deep soils (Table 2). Combining these estimates gave mean sequestration rates of ~2.0 t ha<sup>-1</sup> year<sup>-1</sup> on shallow soils and ~3.8 t ha<sup>-1</sup> year<sup>-1</sup> on deep soils (Table 2). The carbon sequestration estimated for each plot from the isotopic-discrimination data was highly correlated with values estimated from allometric data ( $R = 0.92$ ,  $P < 0.001$ ), with the two series of estimates having close to 1 : 1 correspondence (Fig. 2).

#### Impacts of fire on live trees

For both eucalypts and non-eucalypts, the interactive effects of fire intensity and stem size were described well by

the multivariate linear models. For small trees ( $D < 20$  cm) the probability of stem survival increased with increasing size according to the following equations for eucalypts (Eqn 8) and non-eucalypts (Eqn 9):

$$P = 1 - 0.098 \times I + 0.037 \times I \times \ln D \text{ adj } R^2 = 0.88; \quad (8)$$

$$P = 1 - 0.079 \times I + 0.023 \times I \times \ln D \text{ adj } R^2 = 0.90. \quad (9)$$

In contrast to small stems, the proportion of large stems surviving fires decreased with increasing stem size. For large trees including eucalypts and non-eucalypts, the proportion of stems of a size  $D$  surviving a fire of intensity  $I$  was predicted by:

$$P = 1.0 + 0.029 \times I - 0.01 \times I \times \ln D \text{ adj } R^2 = 0.96. \quad (10)$$

In combining these equations to give the proportion of trees of all size classes surviving fires, we set the boundaries

**Table 3.** Water use efficiency (W) calculated from reported values of  $\Delta^{13}C_p$  and  $\delta^{13}C_p$  for foliar and wood samples of *Eucalyptus tetradonta* (Eute) and *E. miniata* (Eumi) trees

The values of atmospheric  $\delta^{13}C_a$  and partial pressure of carbon dioxide  $P_a$  are for the period that the sampling represents

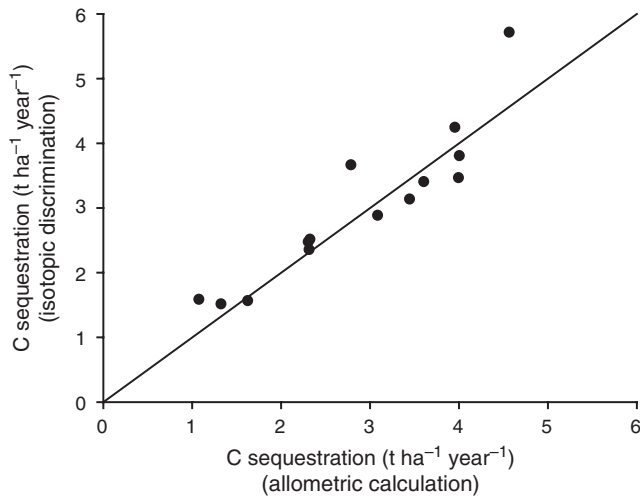
Species	Sampling date	$\Delta^{13}C_p$ (‰)	$\delta^{13}C_p$ (‰)	$\delta^{13}C_a$ (‰) <sup>D</sup>	$P_a$ (ppm) <sup>D</sup>	W (g kg <sup>-1</sup> )
Eumi/Eute (foliar) <sup>A</sup>	1996	20.5	-28.7	-7.858	362	1.09
Eumi/Eute (wood) <sup>A</sup>	1936–96	19.2	-26.7	-7.129	327	1.13
Eumi (foliar) <sup>B</sup>	1993	19.4	-26.7	-7.785	358	1.20
Eute (foliar) <sup>C</sup>	1999	22.1	-29.3	-7.9135	367	0.90

<sup>A</sup>Miller *et al.* (2001).

<sup>B</sup>Schulze *et al.* (1998).

<sup>C</sup>Bowman and Cook (2002).

<sup>D</sup>Etheridge *et al.* (1996), Francey *et al.* (1999) and Trudinger *et al.* (1999).



**Fig. 2.** A comparison of carbon sequestration of trees in 14 savanna plots at Kapalga as estimated by calculation from allometric relationships of carbon stock and tree size and by calculation from estimated water use efficiency from isotopic discrimination and stand water use. The line represents 1 : 1 correspondence.

to survival at 0 and 1, and took the lowest survival calculated from the equations for small trees and large trees. The distinction between the proportion of eucalypt and non-eucalypt stems surviving fires becomes greater with higher fire intensities (Fig. 3).

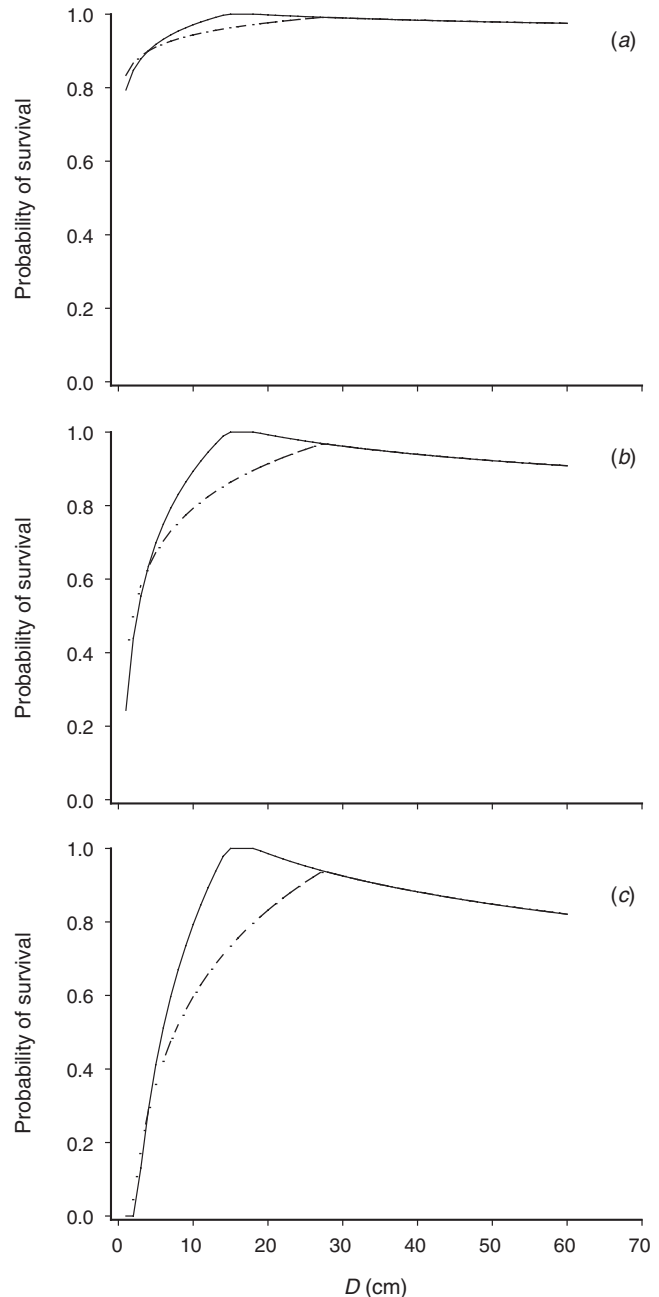
#### *Predicted impacts of fires on live carbon stocks in trees*

Across the seven plots on both the shallow and deep soils at Kapalga, the predicted decline in live carbon stock caused by a single fire increased from ~2 to 25% of total stocks as the intensity increased from 2.1 to 15 MW m<sup>-1</sup> (Table 4). Variation in the proportionate decline in carbon stocks of live trees under low-intensity fires increased with an increasing percentage of the initial carbon stock in trees of  $\leq 20$  cm  $D$ , with the relationship accounting for 74% of the variation in declines (Fig. 4). Under the extremely high-intensity fire, decline decreased with an increasing proportion of initial stocks in trees with 25 cm  $< D \leq 35$  cm. This relationship accounted for 59% of the decline (Fig. 5). Other indices of size distribution of the tree stands were poorly correlated with the predicted impacts of fires.

## **Discussion**

### *The utility of allometric scaling against cross-sectional area*

Our analyses showed that total carbon stock of the tree species examined and that of each subcomponent scales satisfactorily against  $A$  or  $D^2$  (Table 1). Although the successful application of these scaling functions is in apparent breach of general models of allometric scaling (West *et al.* 1997), reconciliation



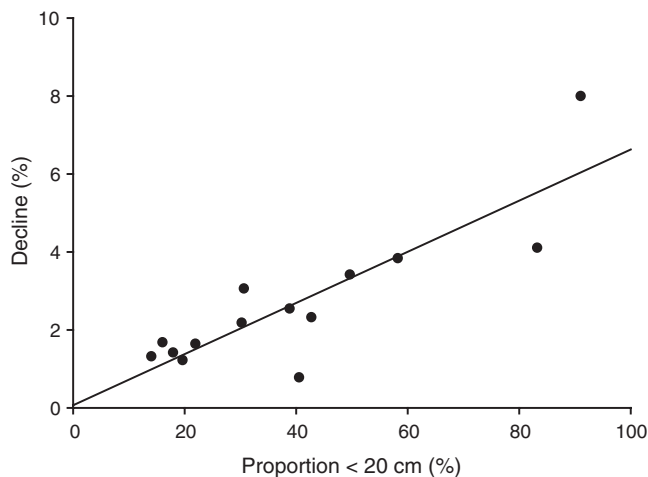
**Fig. 3.** The effect of stem diameter ( $D$ ) on the predicted proportion of eucalypts (solid lines) and non-eucalypts (dotted lines) surviving fires with intensities of (a) 2.1, (b) 7.7 and (c) 15 MW m<sup>-1</sup>, respectively.

may lie in failures of the assumption of constant stem density (Enquist and Niklas 2002), owing to extensive hollowing and branch drop by these savanna trees (Fox and Clark 1972). Regardless, the linear scaling of carbon stocks of whole trees and their subcomponents against  $A$  (Table 1) gives a pragmatic solution, which greatly simplifies comparisons among subcomponents and species and allows total stocks

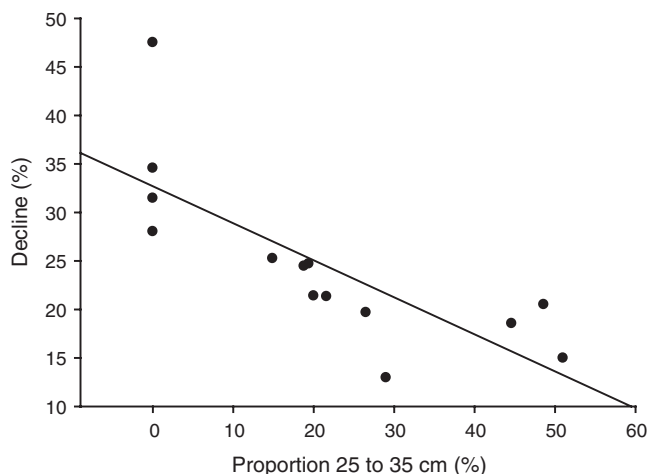
**Table 4.** The simulated impact of fire intensity on carbon stocks of live trees across seven 0.1-ha plots on shallow (<0.5 m) and deep (>1.2 m) soils at Kapalga

Numbers in parentheses represent standard deviations across four replicates and seven plots

Fire intensity (MW m <sup>-1</sup> )	Decline in C stock (t ha <sup>-1</sup> )		Decline in C stock (%)	
	Shallow soil	Deep soil	Shallow soil	Deep soil
2.1	0.56 (0.02)	0.94 (0.03)	2.4	2.1
7.7	2.98 (0.1)	4.25 (0.07)	13.0	9.7
15	5.71 (0.11)	10.77 (0.26)	25	25



**Fig. 4.** The relationship between the proportion of total biomass of trees represented by trees with a diameter at breast height of <20 cm and the predicted decline in carbon stock after a low-intensity fire (2.1 MW m<sup>-1</sup>).



**Fig. 5.** The relationship between the proportion of total biomass of trees represented by trees with diameters at breast height of >25 cm but <35 cm and the predicted decline in carbon stock after a very high-intensity fire (15 MW m<sup>-1</sup>).

to be estimated without knowledge of stand structure apart from total basal area which is easily measured by Bitterlich techniques (Bonham 1989).

The scaling of water use with basal area or  $D^2$  (Cook *et al.* 2002) leads to the conclusion that water availability will limit the total basal area of tree stands regardless of their size structure. Given this, if maximising total extant carbon stocks in trees were a management objective driven by greenhouse abatement concerns, then a choice of allometric scaling of carbon stock against  $D^{8/3}$  (Enquist *et al.* 1998) would lead to a recommendation for management regimes that favoured stands comprising mainly larger trees. In contrast, an assumption of linear scaling against  $A$  or  $D^2$  indicates that carbon stocks could be maximised by simply aiming for maximum sustainable basal area regardless of size structure of the tree population. Given the complexities of managing savanna lands (Dyer *et al.* 2001), the more simple the management recommendation the more likely it is to be adopted regardless of subtle departures from theory.

#### *Carbon sequestration and allocation in the absence of fire*

Our two approaches to estimating the carbon sequestration of tree stands at Kapalga corresponded surprisingly well (Table 1). Although Farquhar *et al.* (1982) described as fortuitous the close match between value of water use efficiency of wheat estimated from isotopic discrimination and that directly measured, we interpret the near 1:1 match between the two techniques for estimating carbon sequestration of the savanna trees (Fig. 2) as giving considerable evidence that both approaches are providing reliable estimates. Therefore, the choice of technique to estimate carbon sequestration can be based simply on pragmatic considerations.

The isotopic-discrimination approach to estimating carbon sequestration has the advantage that much of the required data are already available for many sites, as demonstrated in the analyses presented here. These analyses, however, give no information on retention of carbon in extant trees, nor on the transfers to the wider ecosystem through such processes as litterfall and herbivory.

The transfers of carbon to the environment can only be estimated by an allometric approach to the estimation of sequestration. These transfers help create fertile patches that cause trees to have a major impact on landscape function (Ludwig *et al.* 1999; Cook and Dawes-Gromadzki 2005). With only ~25% of annual sequestration being retained in the trees, the annual transfer of carbon to the environment from trees at Kapalga is of greater magnitude than the production of grass (Cook 1994). While unburnt, tree litter will provide important resources for soil and litter biota and contribute to the maintenance of soil physical and chemical properties. Macroinvertebrates such as termites consume a substantial



proportion of this carbon, not only through consumption of wood and bark in live trees but also of leaf and twig litter (T. Dawes-Gromadzki, pers. comm.). Thus, the trees have a major role in the food chain. The leaf and twig litter also contribute substantially to the fuel load during fires, with tree litter typically comprising more than 50% of fine fuels at Kapalga (Cook 1994). Because of relatively rapid decay and consumption of the litter and a high fire frequency, the fuel load is unlikely to accumulate beyond several years (Cook 2003).

#### *Impacts of fire on carbon stocks*

Since fire intensity is driven in large part by the fine fuel load (Cheney and Sullivan 1997), the substantial contribution of tree litter to the fuel load will feed back into the dynamics of tree populations. The analysis of tree responses presented here indicates that greater fire intensity will cause greater declines in live-tree carbon stock, but that effect can show considerable variation. This will depend on the both stochastic variation in tree survival and on the size structure of the initial tree population. The curvilinear effect of tree size on the response of stem survival to fire intensity (Fig. 3) means that repeated low-intensity fires would drive a tree stand towards a dominance of trees with stem diameters greater than 10–20 cm. Repeated high-intensity fires would increasingly affect the large trees as well, leading to stand dominated by mid-sized (10–20 cm) trees. The greater sensitivity of small non-eucalypts indicates that they would be more affected by fires than eucalypts, so that a regime of more frequent or more intense fires would drive the system towards greater dominance by eucalypts.

The increasing probability of survival of small tree stems with increasing size is likely to be due to increasing height and increasing bark thickness. Because hollowing by termites affects more than 80% of trees in these savannas (Fox and Clark 1972), it probably drives the increasing likelihood of fire-caused mortality with increasing tree size beyond 15–20-cm diameter at breast height. Thus, although the consumption by termites of wood in live trees represents less than 5% of total transfers of assimilated carbon (Table 2), it has great functional significance for tree populations. Tree species that are more resistant to the impacts of wood-feeding termites may be better able to withstand fires as large trees. Indeed, further investigations of the abilities of large trees to withstand fire may reveal different responses of the eucalypts and non-eucalypts, which are currently lumped in our analyses. For example, *Erythrophleum chlorostachys* is relatively termite-resistant and may be better able to withstand fires as a large tree than *Eucalyptus tetradonta*, which is substantially hollowed. Conversely, the greater fire sensitivity of non-eucalypts than eucalypts as small trees could also apply to large trees.

Our analyses show that the 42% decline in tree basal area because of a single high-intensity wildfire (Williams

*et al.* 1999) was a result of not only the high intensity of that fire, but also of the particular size structure of the tree population in the affected plots. In particular, it was probably the dominance of large trees and a relative paucity of highly fire-tolerant, mid-sized trees that allowed such a substantial decline. The application of the survival algorithm to data from other plots indicated that a fire of similar intensity in plots with different size structures would probably have produced varying declines in live biomass. Thus, the impact of a very intense fire on carbon stocks of trees decreases with an increasing proportion of biomass in the relatively fire-tolerant size class of 25–35 cm, whereas the impact of a low-intensity fire increases with an increasing proportion of biomass in small trees with  $D < 20$  cm (Figs 4, 5).

Under low-intensity fires with a frequency of one in 2 years, the annualised loss of live trees on the deep soil would be  $\sim 0.5 \text{ t ha}^{-1}$ . Subtracting this from the mean annual carbon retention would leave the annual accumulation rate of  $\sim 0.5 \text{ t ha}^{-1}$ . Although this figure is half that estimated for whole-system net biome productivity (NBP) of  $-1 \text{ t C ha}^{-1} \text{ year}^{-1}$  for these savannas (Williams *et al.* 2004), it is of the correct order of magnitude for the contribution of trees to NBP. It may be that the analysis of Williams *et al.* (2004) overestimated NBP of the region's savannas because it was based on extrapolating micrometeorological data from a site disturbed by cyclone Tracy in 1974 and thus may have been accumulating biomass more rapidly than other more mature savannas.

The question remains when and under what circumstances the carbon sink will saturate. Cook *et al.* (2002) suggested that water availability will set the ultimate limit on tree populations. The impacts of occasional drought death need to be taken into account in estimating long-term NBP values. The net carbon sink observed in northern Australian savannas (Williams *et al.* 2004) may be a response to previous episodes of drought, storms, and severe fires that reduced populations to well below carrying capacity (Williams and Douglas 1995; Fensham and Holman 1999; Williams *et al.* 1999).

#### **Conclusions**

Allometric scaling of carbon stocks against stem cross-sectional area successfully simplified comparisons of stocks among subcomponents of individual trees, and among species. It allows estimation of carbon stocks when only the total basal area is known. Estimation of rates of carbon sequestration and of the allocation of carbon to each subcomponent does require stand-structure information. We estimated that tree stands at Kapalga in Kakadu National Park retain only  $\sim 25\%$  of sequestered carbon in the extant trees. The carbon sequestration rates estimated from allometric considerations were of similar magnitude to those estimated from isotopic discrimination during photosynthesis. This gives confidence that both approaches give reliable estimates. With mean sequestration rates of  $\sim 2\text{--}4 \text{ t C ha}^{-1} \text{ year}^{-1}$  on

shallow and deep soils, respectively, the transfer of carbon to the environment through various processes, including litterfall and herbivory, represent a substantial contribution to ecosystem processes. Fire can have substantial impacts on carbon stocks in trees, but this varies with stand structure. Simple indices of stand structure can predict the likely impact of fire intensity. Under a regime of biennial low-intensity fires, carbon stocks in trees may increase by  $\sim 0.5 \text{ t ha}^{-1} \text{ year}^{-1}$ , but the limits to this increase remain to be seen.

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Manuscript received 17 September 2004, accepted 17 January 2005