

Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna

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ABSTRACT

We measured stem CO₂ efflux and leaf gas exchange in a tropical savanna ecosystem in northern Australia, and assessed the impact of fire on these processes. Gas exchange of mature leaves that flushed after a fire showed only slight differences from that of mature leaves on unburned trees. Expanding leaves typically showed net losses of CO₂ to the atmosphere in both burned and unburned trees, even under saturating irradiance. Fire caused stem CO₂ efflux to decline in overstorey trees, when measured 8 weeks post-fire. This decline was thought to have resulted from reduced availability of C substrate for respiration, due to reduced canopy photosynthesis caused by leaf scorching, and to priority allocation of fixed C towards reconstruction of a new canopy. At the ecosystem scale, we estimated the annual above-ground woody-tissue CO₂ efflux to be 275 g C m⁻² ground area year⁻¹ in a non-fire year, or approximately 13% of the annual gross primary production.

We contrasted the canopy physiology of two co-dominant overstorey tree species, one of which has a smooth bark on its branches capable of photosynthetic re-fixation (*Eucalyptus miniata*), and the other of which has a thick, rough bark incapable of re-fixation (*Eucalyptus tetradonta*). *Eucalyptus miniata* supported a larger branch sapwood cross-sectional area in the crown per unit subtending leaf area, and had higher leaf stomatal conductance and photosynthesis than *E. tetradonta*. Re-fixation by photosynthetic bark reduces the C cost of delivering water to evaporative sites in leaves, because it reduces the net C cost of constructing and maintaining sapwood. We suggest that re-fixation allowed leaves of *E. miniata* to photosynthesize at higher rates than those of *E. tetradonta*, while the two invested similar amounts of C in the maintenance of branch sapwood.

Key-words: *Eucalyptus*; re-fixation; stem respiration.

INTRODUCTION

Tropical savannas, loosely defined as vegetation communities that possess a discontinuous tree canopy layer overly-

ing a continuous grassy layer, are one of the world's most extensive biomes. They occur in Australia, Africa, South America, India and south-east Asia in wet-dry tropical regions where temperatures are high throughout the year and summer rains are followed regularly by a winter dry season (Huntley & Walker 1982). In Australia, tropical savannas cover approximately one-fourth of the continental land surface, occurring in north-west Western Australia, the northern half of the Northern Territory and northern Queensland (Mott *et al.* 1985).

Frequent dry-season fires are a prominent feature of Australian tropical savannas. For example, in a given year, the area burned in the eucalyptus-dominated open-forest savannas of the top end of the Northern Territory is about half the total area occupied by these communities (Beringer, Packham & Tapper 1995; Russell-Smith, Ryan & Durieu 1997; Edwards *et al.* 2003). These fires are typically surface fires that consume the grassy fuel layer, but do not burn in the crowns of the overstorey trees. However, the foliage of the overstorey trees is often scorched, causing leaf senescence; the amount of scorching can range from very little to comprehensive, depending on fuel load and fire weather conditions (Williams, Gill & Moore 1998). The eucalyptus-dominated overstorey flora of these savannas is well adapted to surviving these frequent fire events. Even so, fires that occur late in the dry season, which tend to be the most intense, can result in significant mortality, mostly in the smallest and largest diameter classes of canopy-dominant species (Williams *et al.* 1999). Despite the frequency and extent of dry-season fires in the tropical savannas of northern Australia, little is known about the impact of such disturbance on the physiological functioning of the overstorey trees.

Autotrophic respiration typically consumes about half the C fixed by plants through photosynthesis (Gifford 1994). In trees, respiration associated with woody tissues comprises a significant fraction of autotrophic respiration. For example, in a beech forest in France, it was estimated that the annual CO₂ efflux from above-ground woody tissues consumed 26% of the annual gross primary production (GPP) (Damesin *et al.* 2002). On the other hand, in a pine forest in the USA, the CO₂ efflux from above-ground woody tissues was estimated to have consumed only 6% of the GPP (Law, Ryan & Anthoni 1999); these results suggest that woody-tissue CO₂ efflux can be a variable, and

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potentially very important, component of ecosystem C balance.

Woody tissues that are covered in a smooth outer bark often possess a green, chlorophyllous layer of photosynthetic tissue just beneath the bark surface. This photosynthetic layer re-fixes respired CO₂ (Benecke 1985; Sprugel & Benecke 1991; Cernusak & Marshall 2000; Pfanz & Aschan 2000; Pfanz *et al.* 2002). This process has been termed *re-fixation* (Sprugel & Benecke 1991), and it uses sunlight that penetrates the bark cortex and internally produced CO₂ as substrate for photosynthesis (Cernusak *et al.* 2001).

The overstorey of the open-forest savannas that occur north of the 1200 mm year⁻¹ rainfall isohyet in northern Australia is dominated by two eucalyptus species, *Eucalyptus miniata* Cunn. ex Schauer and *Eucalyptus tetradonta* Muell. (Brooker & Kleinig 2004). These two species differ in the bark morphology of their branches. The outer bark on the branches of *E. miniata* is smooth and creamy white in appearance, in sharp contrast to the bark on the lower stem, which is dark brown, thick, fibrous and fire resistant. On the branches, just beneath the outermost layer of the creamy-white bark, there is a green, chlorophyllous layer of photosynthetic tissue. In contrast to the branches of *E. miniata*, those of *E. tetradonta* are covered in thick, fibrous bark that has no chlorophyllous layer.

Woody-tissue CO₂ efflux rates have not been reported for any native vegetation community on the Australian continent, although measurements were made in an exotic pine plantation in south-eastern Australia (Ryan *et al.* 1996). In addition, the response of woody-tissue CO₂ efflux to fire in savanna communities is unknown. Thus, we had three objectives in the present study: (1) to examine the role of above-ground, woody-tissue CO₂ efflux in the C balance of a tropical savanna ecosystem in northern Australia; (2) to examine how woody-tissue CO₂ efflux and leaf gas exchange respond to fire in overstorey trees; and (3) to investigate the magnitude by which re-fixation reduces CO₂ efflux from woody tissues in a savanna tree species that has a smooth bark on its branches.

MATERIALS AND METHODS

Study site

Our study site was located 35 km south-east of Darwin, Northern Territory, Australia in the Howard River catchment (12°29.7'S, 131°09.0'E) at an elevation of 38 m. This site has been described recently in detail (Hutley, O'Grady & Eamus 2000; O'Grady *et al.* 2000), and will be described briefly here. The monsoonal climate of northern Australia is characterized by distinct wet and dry seasons. The mean annual rainfall at the Darwin Airport is approximately 1700 mm, nearly all of which falls between November and March (Fig. 1). The mean daily maximum temperature varies between 30.5 and 33.2 °C, while the mean daily minimum temperature varies between 19.3 and 25.3 °C (Fig. 1). The vegetation at the site is an open-forest savanna, with

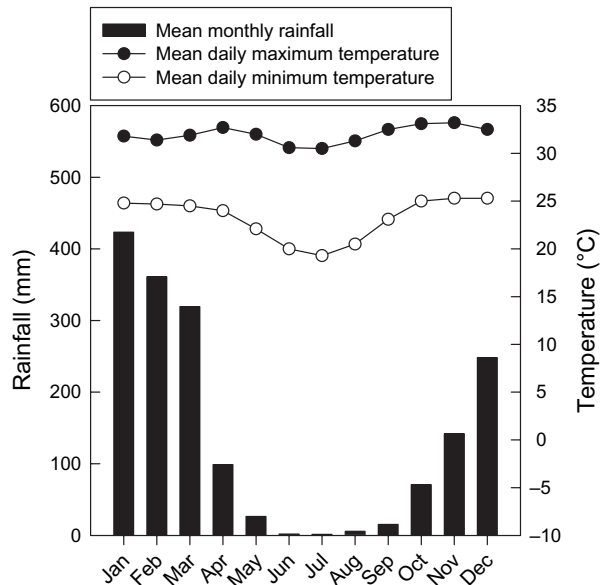


Figure 1. Mean monthly rainfall and average daily values of maximum and minimum temperatures observed at Darwin Airport, 1941–2004 (source: Australian Bureau of Meteorology, http://www.bom.gov.au/climate/averages/tables/cw_014015.shtml).

an overstorey dominated by evergreen eucalypts. Although several species occur in the overstorey, two species dominate and make up nearly 80% of the standing biomass, *E. miniata* and *E. tetradonta* (O'Grady *et al.* 2000). Other overstorey tree species include *Erythrophleum chlorostachys* Muell., *Corymbia polysciada* (Muell.) Hill & Johnson, *Corymbia bleeseri* (Blakely) Hill & Johnson, *Corymbia porrecta* (Blake) Hill & Johnson and *Terminalia ferdinandiana* Exell. The overstorey leaf-area index varies between approximately 1.0 in the wet season and 0.6 in the dry season (O'Grady *et al.* 2000). The tree density is approximately 750 stems ha⁻¹, the overstorey basal area is 8–10 m² ha⁻¹, the total standing biomass is approximately 55 Mg ha⁻¹ and the canopy height is approximately 15 m (O'Grady *et al.* 2000). The understorey vegetation consists of a seasonally continuous cover of annual and perennial grasses, along with semi-deciduous and deciduous small trees and shrubs. The grass community is dominated by annual *Sorghum* spp., which can grow to about 2.5 m in height by the end of the wet season. The grassy layer senesces rapidly with the onset of the dry season in April and May. The understorey leaf-area index ranges between about 1.2 in the wet season and 0.1 in the dry season (Hutley, O'Grady & Eamus 2001). Soils at the site are red earth sands, classified as red Kandosols (Isbell 1996). They are weathered extensively, weakly acidic and generally low in plant-available nutrients. Rounded ferricrete gravel occurs on the soil surface and throughout the soil profile.

Stem CO₂ efflux

The stem CO₂ efflux was initially measured at two locations, each of which was nested within a 3 km² plot. One plot was

to be burned, while the other was to serve as an unburned control. At each location, the stem CO₂ efflux rates were measured on six individuals of each of the following tree species: *E. miniata*, *E. tetradonta*, *E. chlorostachys* and *C. bleeseri*. The trees were selected to be broadly representative of the range of overstorey stem diameters typically found in these savanna woodlands; diameters at 1.4 m height ranged from approximately 10–60 cm on the measured trees. The stem CO₂ efflux measurements commenced on the control plot in June 2004. The treated plot was burned from 31 June to 1 July 2004. The measurements commenced on the burned plot following the fire, but only using trees that suffered some degree of crown scorch.

On 6 August 2004, the control plot was burned by an unplanned fire, despite preventative management. Therefore, a new location was selected for measuring the stem CO₂ efflux in unburned trees. In a testament to the fire-prone nature of the north-Australian savanna landscape, this new location also burned in an unplanned fire in October 2004. However, this fire was of a very low intensity and resulted in minimal scorching of the overstorey canopy (< 5%); we therefore considered that these trees continued to be representatives of unburned trees following this fire event.

Stem CO₂ efflux chambers were constructed from 1 L plastic food-storage containers (Klip It, Sistema Plastics, Auckland, New Zealand). The bottom of each container was cut away, allowing it to be sealed to the surface of a tree stem. A tubing was fitted to one chamber lid, providing an inlet and an outlet, and the seal on the lid was reinforced with closed-cell foam gasket material. The lid could then be sealed to the body of a container mounted on a tree stem by two locking clips. The bodies of the containers were sealed to tree stems with a silicon sealant, and remained in place between stem CO₂ efflux measurements. We checked the chambers for leaks by exhaling near the seals and monitoring the CO₂ concentration inside the chambers (Shibistova *et al.* 2002). The chamber volumes were determined following the method of Edwards & Hanson (1996); the mean chamber volume was 793 ± 20 mL (mean ± 1 SD). The mean total system volume including the infrared gas analyser (IRGA) was 958 ± 21 mL (mean ± 1 SD). Each chamber covered an area of 150 cm² of stem surface. Thermocouples were inserted to approximately 1 cm depth in the stem sapwood of the sample trees. The chambers were placed near 1.4-m stem height, and were located randomly with respect to aspect.

The efflux of CO₂ from each stem was measured with a closed-system, portable IRGA (LI-6200, Li-Cor, Lincoln, NE, USA). Soda lime was used to scrub the CO₂ concentration inside the closed system to below the ambient concentration before each measurement. The concentration was then allowed to increase to about 15 μmol mol⁻¹ below the ambient concentration, at which time three successive measurements of the time taken for a 10 μmol mol⁻¹ change in CO₂ concentration were logged. All flow through the IRGA was directed first through a magnesium perchlorate desiccant trap to remove water vapour, thereby disposing of the need for a band-broadening correction (Hooper *et al.*

2002). The CO₂ efflux rate was calculated as recommended by Hooper *et al.* (2002), using their eqn 13.

The stem CO₂ efflux was measured in the original set of control trees on 16–22 June and again on 15–20 July 2004. It was measured in the second set of control trees on 10–21 September and 21–22 October 2004, and on 18 January 2005. The burned trees were measured on 13–19 July, 3–7 September and 19–20 October 2004, and on 17 January 2005. During each measurement period, the stem CO₂ efflux was measured five to seven times on each tree from pre-dawn to late afternoon, in order to cover the full diurnal range of stem temperatures and CO₂ efflux rates. An exception was in the January measurements, when each tree was measured only once near midday. In November 2004, a core was removed from each of the original control trees for the determination of sapwood depth, sapwood volume beneath the CO₂ efflux chamber and sapwood density. Dendrometer bands (Agricultural Electronics Corp., Tucson, AZ, USA) were fitted to each of the trees measured for stem CO₂ efflux in January; the stem growth was recorded over a 9 d period beginning the day after the CO₂ efflux measurements. Of the 48 dendrometer bands installed initially, 14 were found to have seized in the wet-season conditions; these trees were excluded from the analyses of stem growth.

Branch CO₂ efflux

Branch CO₂ efflux rates were measured from detached *E. miniata* and *E. tetradonta* branch sections on 26–29 October 2004. The branches were felled from unburned trees using a 5 m pruning saw, and were returned to the laboratory at the Charles Darwin University, Darwin, Australia where they were cut into sections ranging from 20 to 41 cm length. Branch section diameters ranged from 0.7 to 9.7 cm. The ends of the branch sections were sealed with Parafilm (American National Can, Greenwich, CT, USA) to prevent desiccation of the exposed sapwood and dissolution of CO₂ from the exposed air–sap interface (Teskey & McGuire 2005). The branch sections were wholly enclosed in a 34 L soil respiration chamber for measurements of CO₂ efflux rates. The chamber was darkened during measurements. The branch sections showed no apparent trend in CO₂ efflux rate when measurements were made both on the day of collection and again on the following day. In addition, Cernusak & Marshall (2000) observed previously no difference between branch CO₂ efflux rates measured in the field on intact branches and those measured on the same branch sections after they were excised and returned to the laboratory.

In order to gain insight into the distribution of sapwood in the branches of *E. miniata* and *E. tetradonta*, we made measurements of the ratio of sapwood cross-sectional area to subtending leaf area (i.e. Huber value). The Huber value measurements were made in January 2005; the diameters of sampled branches ranged from 3.5 to 9.6 cm. The sapwood/heartwood boundary of each branch was identified visually based on a distinct colour change between the two.

The leaves were stripped from each branch and the fresh weight (FW) was determined. A subsample was then dried to constant weight at 75 °C to determine the ratio of FW to dry weight (DW). The leaf DWs were converted to leaf areas using site-specific measurements of specific leaf area for *E. miniata* and *E. tetradonta* (Chen 2002); the values were 6.0 and 5.3 m² kg⁻¹, respectively. These values agree well with other published measurements of specific leaf area for these two species in the high rainfall zone of the Northern Territory (Schulze *et al.* 1998; Eamus *et al.* 1999a; Miller 2002; Prior, Eamus & Bowman 2003).

Branch re-fixation

We measured re-fixation in excised *E. miniata* branch sections. Re-fixation was not measured in *E. tetradonta* branches because they are covered in thick, rough bark that has no chlorophyllous layer. For the *E. miniata* branch sections, CO₂ efflux was first measured in the dark in either a 1 L Li-Cor leaf photosynthesis chamber, or in the 34 L soil respiration chamber, depending on the branch diameter. The 1 L chamber could accommodate branch sections up to 3 cm in diameter. After the CO₂ efflux measurements in the dark, the branch sections were placed under an artificial light source at an incident photon flux density (PFD) of approximately 1000 μmol m⁻² s⁻¹. After approximately 2 h of illumination, the CO₂ efflux was measured in the light. The 1 L chamber could be positioned directly under the light source so that the same irradiance was maintained during measurements as experienced before measurements. However, it was not possible to position the 34 L soil respiration chamber directly under the light source, and so the larger branch sections were not illuminated at as high an intensity during the light measurements. This may have resulted in an underestimation of the true capacity for re-fixation in the larger-diameter branch sections. The diameters of the measured branches ranged from 1.5 to 6.0 cm.

Branch temperatures were higher by 4–7 °C during the light measurements compared to those during the dark measurements. To calculate the proportional re-fixation rates, we scaled the dark-respiration measurements to the temperatures experienced during illumination using the Q_{10} value determined for *E. miniata* stems as described later. The proportional re-fixation rate was then calculated as $(F_D - F_L)/F_D$, where F_D is the dark CO₂ efflux rate adjusted to the light temperature, and F_L is the light CO₂ efflux rate.

Leaf gas exchange

Photosynthesis was measured on 12–15 October 2004 on what had been called previously the control plot, which burned approximately 9 weeks earlier on 6 August 2004. This fire resulted in a nearly comprehensive scorch of the overstorey canopy, and measurements were thus made on leaves that flushed subsequent to the fire event. Measurements were also made on unburned trees in an adjacent patch of open-forest savanna. Three trees each of *E. miniata* and *E. tetradonta* were sampled at each location.

On each tree, light-saturated photosynthesis (incident PFD > 1000 μmol m⁻² s⁻¹) was measured on 6–10 mature, fully expanded leaves and on 6–10 expanding leaves. The expanding leaves had one-sided areas of approximately 10–30 cm². The mature leaves had one-sided areas of approximately 50–70 cm². Gas-exchange measurements were made with an LI-6400 portable photosynthesis system (Li-Cor). Canopy access was obtained with a 16 m elevated work platform, and measurements were made on overstorey trees at heights ranging from 8 to 15 m. The flow rate through the LI-6400 leaf chamber was 500 μmol s⁻¹. No attempt was made to control the vapour pressure within the cuvette, which therefore varied depending on the transpiration rate of the sample leaf. The leaves were sealed in the chamber for 3–5 min before gas-exchange data were logged. This was assumed long enough for the leaf temperature to acclimate to conditions within the cuvette, and short enough to avoid a significant alteration of stomatal conductance.

Leaf gas exchange in savanna trees of northern Australia has previously been shown to be sensitive to variation in leaf to air vapour pressure difference (Eamus *et al.* 1999b). To confirm that our results were not biased by sampling one population of trees when the air saturation vapour pressure deficit (VPD) was different than for another population of trees, we performed an analysis of variance (ANOVA) of VPD at the time of sampling with species and treatment taken as independent factors. The variation in VPD at the time of sampling was not significant between species ($P = 0.10$, $n = 98$), treatments ($P = 0.19$, $n = 98$) or for the species by treatment interaction ($P = 0.41$, $n = 98$).

Dark respiration was measured on the leaves from one *E. miniata* and one *E. tetradonta* tree at both the burned and unburned locations. The branches were excised, lowered to the ground and darkened for at least 30 min prior to measurement. Dark-respiration measurements were thus made during daylight hours. For each branch, six to eight mature and six to eight expanding leaves were measured.

Estimating annual stem and branch CO₂ efflux

We scaled instantaneous measurements of stem and branch CO₂ efflux to an annual total by employing the functional model of plant respiration (McCree 1970; Thornley 1970; Wit, Brouwer & Penning de Vries 1970). The functional model partitions respiration into growth and maintenance components:

$$R = g \frac{dM}{dt} + mM \quad (1)$$

In our case, R is the annual stem and branch respiration rate (in grams of C per square metre of ground area per year), g is the growth respiration coefficient (in grams of C respired per gram of C incorporated into new above-ground woody tissue), M is the sapwood biomass in stems and branches (in cubic metres of sapwood per square metre of ground area), t is the time (1 year) and m is the maintenance respiration coefficient (in grams of C respired per cubic metre of sapwood per year).

We determined m for stem respiration using the mature-tissue method (Sprugel & Benecke 1991). This method involves the measurement of the CO_2 efflux from a tissue that is not actively growing, then assuming that the measured CO_2 efflux rate is representative of m under all other environmental and physiological conditions, including while growth is taking place (Amthor 2000). Stem growth in the open-forest savannas of northern Australia is distinctly seasonal, ceasing completely during the dry season (Mucha 1979; Ogden 1981; Chen 2002; Prior, Eamus & Bowman 2004). This pattern has been confirmed at our study site (Chen 2002). Therefore, we used our measurements of stem CO_2 efflux in the second half of July 2004 to define m .

It was recently demonstrated that stem CO_2 efflux rates can at times differ from stem respiratory CO_2 production rates, because of longitudinal fluxes of CO_2 in the transpiration stream, and transient changes in the storage of respired CO_2 within stem segments (McGuire & Teskey 2004). McGuire & Teskey (2004) suggested an improved method for estimating stem respiratory CO_2 production rates, which combines measurements of stem CO_2 efflux with measurements of sap flow and internal stem CO_2 concentrations. In our study, we did not make concurrent measurements of sap flow and internal stem CO_2 concentrations, and therefore could not apply their new method. Thus, in our application of the functional model of plant respiration, we make the assumption that observed stem CO_2 efflux rates were equivalent to stem respiratory CO_2 production rates; we note that this assumption could be a source of bias in our model predictions.

Diurnal variation in stem temperature and stem CO_2 efflux was used to develop temperature response functions for scaling m to an annual total. For each tree during each set of measurement dates, except in January, the stem CO_2 efflux was measured several times from pre-dawn to late afternoon. The following equation was fitted to the data for each tree for each measurement period by non-linear regression:

$$F = F_R Q_{10}^{(T-T_R)/10}, \quad (2)$$

where F is the measured stem CO_2 efflux rate, F_R is the predicted stem CO_2 efflux rate at a reference temperature, Q_{10} is the proportional increase in stem CO_2 efflux with a 10°C increase in stem temperature, T_R is the reference stem temperature and T is the stem temperature at the time of measurement. The T_R was defined as 25°C . Each measured CO_2 efflux rate was then expressed as that rate relative to the fitted value at 25°C for that particular tree (F/F_{25}). The F/F_{25} was then plotted against temperature for the full data set, and Eqn 2 was again fitted by non-linear regression, this time using F/F_{25} in place of F . This procedure allowed us to evaluate the response of CO_2 efflux to variation in stem temperature (i.e. Q_{10}) independently of inter-tree variation in F_{25} .

We scaled m to an annual total for an average year using daily maximum and minimum air temperature data from the Darwin Airport. We found that the daily mid-range air

temperature at the Darwin Airport was a very good predictor of daily mid-range stem temperature at our study site for the days on which measurements were made [$T_m = 1.11A_m - 1.36$ ($R^2 = 0.87$, $P < 0.0001$, $n = 156$), where T_m is the daily mid-range stem temperature, and A_m is the daily mid-range air temperature]. The daily stem temperature amplitude was not significantly different from the daily air temperature amplitude ($P = 0.11$, $n = 156$), and was therefore modelled as $T_a = A_a$ (where T_a is the daily stem temperature amplitude, and A_a is the daily air temperature amplitude). The daily m was calculated as (Ågren & Axelsson 1980)

$$m_d = 86\,400 F_0 I_0(\beta T_a) \exp(\beta T_m), \quad (3)$$

where m_d is the daily m , 86 400 scales from seconds to days, F_0 is the measured CO_2 efflux rate normalized to 0°C in July, I_0 corrects for non-linearity in the temperature response and $\beta = \ln(Q_{10})/10$. The term $I_0(\beta T_a)$ can be approximated as (Ågren & Axelsson 1980)

$$I_0(\beta T_a) = 1 + 0.25(\beta T_a)^2 + 0.016(\beta T_a)^4 + 0.0004(\beta T_a)^6. \quad (4)$$

The daily m was totalled over the annual cycle to estimate the annual m .

The annual m for the branches was estimated in the same way as for the stems. The branch daily mid-range air temperature, the branch daily temperature amplitude and the branch Q_{10} were assumed the same as those for the stems. The branch F_0 was based on the October measurements of the branch CO_2 efflux rates. Although October is near the end of the dry season, we have reason to believe that the branches that we measured were not growing at this time. Firstly, the stem CO_2 efflux in *E. miniata* and *E. tetradonta* did not differ between the July and October measurements (see Results), indicating that growth respiration had not yet started for these stems. Secondly, no bark slippage was apparent in the excised branch sections, which would have indicated cambial cell division. In contrast, bark slippage was easily observed on the branches of these two species in January 2005.

The above-ground M at the stand level was estimated using census data and allometric equations reported previously for the Howard Springs study site (Eamus, O'Grady & Hutley 2000; O'Grady *et al.* 2000; Chen 2002). The stem sapwood basal area and the stem height were predicted from allometric equations relating these properties to diameter at breast height. The stem sapwood volume was calculated as a cylinder with the same dimensions from stem base to the base of the live crown. The branch biomass was predicted using the allometric equations of O'Grady *et al.* (2000). It was assumed that branches < 1 cm in diameter comprised 12%, those 1–4 cm in diameter comprised 23% and those > 4 cm in diameter comprised 65% of the branch biomass, based on data presented by Chen (2002). The branch sapwood volume was predicted from measurements of the ratio of the sapwood volume to the dry mass for the different diameter classes.

The g was assumed to be $0.25 \text{ g C respired g}^{-1} \text{ C}$ incorporated into new woody biomass (Penning de Vries 1975).

The annual increment of above-ground woody biomass, dM/dt , was calculated from allometric equations relating stem and branch biomass to diameter at breast height (O'Grady *et al.* 2000), and assuming an annual diameter at breast height increment of 0.3 cm (Chen 2002; Chen, Hutley & Eamus 2003; Prior *et al.* 2004; Werner 2005). The mass fraction of C in new wood was assumed to be 0.49 (Gifford 2000).

Analysis

We tested for variation among species in the temperature response of stem CO₂ efflux using analysis of covariance (ANCOVA). The $\ln(F/F_{25})$ was analysed to linearize the data and improve the distribution of residuals over the full range of stem temperatures. Variation in F_{25} between treatments and among species was analysed using repeated measures ANOVA, with the following exception: the unburned trees in the July sampling were different from the unburned trees in the subsequent samplings because of the unplanned fire that scorched the initial set of unburned trees. Therefore, the July sampling was not included in the repeated measures ANOVA. For the July sampling date, variation between burned and unburned trees and among species was analysed using ANOVA. Variation in leaf gas exchange between treatments and species was analysed with ANOVA. All statistical analyses were performed in SYSTAT 9.0 (SPSS, Chicago, IL, USA).

RESULTS

Fire conditions

We estimated the fine fuel load at the study site, including grass, leaf litter and woody litter up to 1 cm in diameter, to be $4.3 \pm 0.7 \text{ Mg ha}^{-1}$ (mean ± 1 SD) in September 2004; this estimate was based on oven-dried collections of fine fuels from 15 randomly located 1 m^{-2} plots. The mean scorch height at the location where burned trees were sampled for stem respiration was $12.3 \pm 2.3 \text{ m}$ (mean ± 1 SD). According to the relationship between scorch height and fire line intensity developed for open-forest savannas in northern Australia (Williams *et al.* 1998), this corresponds to a fire line intensity of 2.4 MW m^{-1} . Among the burned trees sampled for stem CO₂ efflux, we estimated visually that their crowns had suffered $66 \pm 27\%$ scorch (mean ± 1 SD; range 20–100%). The burned trees were estimated to have recovered an average of 60 and 100% of the scorched fraction of their crowns after 8 and 12 weeks, respectively. The mean scorch height at the location where the leaf gas exchange was measured 9 weeks post-fire was $14.8 \pm 1.7 \text{ m}$, corresponding to a fire line intensity of 3.6 MW m^{-1} .

Stem CO₂ efflux

Figure 2 shows variation between burned and unburned trees in stem CO₂ efflux rates normalized to 25 °C for each

of the sampled species. In the July sampling, which took place about 2 weeks post-fire, F_{25} did not vary between burned and unburned trees ($P = 0.14$, $n = 48$), or among species ($P = 0.13$, $n = 48$). However, on the subsequent sampling dates, there were significant differences in F_{25} between burned and unburned trees ($P < 0.0001$, $n = 48$), among species ($P = 0.0001$, $n = 48$) and in the treatment by species interaction ($P < 0.0001$, $n = 48$). An examination of Fig. 2 shows that F_{25} was markedly lower in all species for burned than for unburned trees in the September sampling, which took place approximately 8 weeks post-fire. For *C. bleeseri*, the F_{25} for burned trees remained markedly depressed in the October and January samplings. In contrast, the F_{25} of burned *E. miniata* and *E. tetradonta* recovered to values similar to unburned trees in the October and January samplings. The F_{25} of *E. chlorostachys* was similar between burned and unburned trees in October, but slightly higher for unburned trees in January (Fig. 2).

For the unburned trees that were sampled in June and July only (because of scorching in August by the unplanned fire), a paired *t*-test suggested that F_{25} decreased from June to July ($P = 0.01$, $n = 18$). Therefore, the July measurements were used to define m in the functional model. Cores were extracted from these trees to estimate the sapwood volume beneath the respiration chambers. The sapwood depth ranged from 1.2 to 3.0 cm. The July F_{25} values for these trees, expressed as micromoles of CO₂ per metre squared per second, were significantly correlated with estimates of sapwood volume beneath the respiration chambers ($r = 0.47$, $P = 0.02$, $n = 24$). The mean F_{25} on a surface-area basis was $1.02 \pm 0.07 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (mean ± 1 SE), and the mean F_{25} on a sapwood-volume basis was $64.2 \pm 3.9 \mu\text{mol CO}_2 \text{ m}^{-3} \text{ sapwood s}^{-1}$. These F_{25} values did not vary among species, whether expressed on a surface area ($P = 0.63$, $n = 24$) or a sapwood volume ($P = 0.33$, $n = 24$) basis. They were not also correlated with stem diameter, either when expressed on a surface area ($P = 0.38$, $n = 24$) or a sapwood volume ($P = 0.24$, $n = 24$) basis. The sapwood density varied significantly among species ($P = 0.002$, $n = 24$). Mean values were 0.81, 0.94, 0.89 and 0.89 g cm^{-3} for *C. bleeseri*, *E. chlorostachys*, *E. miniata* and *E. tetradonta*, respectively.

The stem CO₂ efflux rates measured in January were significantly correlated with the stem diameter increments measured over the following 9 d ($r = 0.69$, $P < 0.0001$, $n = 34$). When CO₂ efflux rates were scaled to the 9 d period and plotted against stem diameter growth, expressed in the same units as CO₂ efflux, the equation relating the two was $F = 0.25G + 1.3$ ($R^2 = 0.48$, $P = 0.0001$, $n = 34$), where F is the stem CO₂ efflux (in micromoles of CO₂ per metre squared per second) and G is growth (in micromoles of C per metre squared per second). The SE of the slope was 0.04, and that of the intercept was 0.31. This analysis can be interpreted in the context of Eqn 1, such that the slope gives an estimate of g and the intercept gives an estimate of mM , the maintenance respiration rate. Thus, we estimate a value for g as $0.25 \pm 0.04 \text{ g C respired g}^{-1}$ of C incorpo-

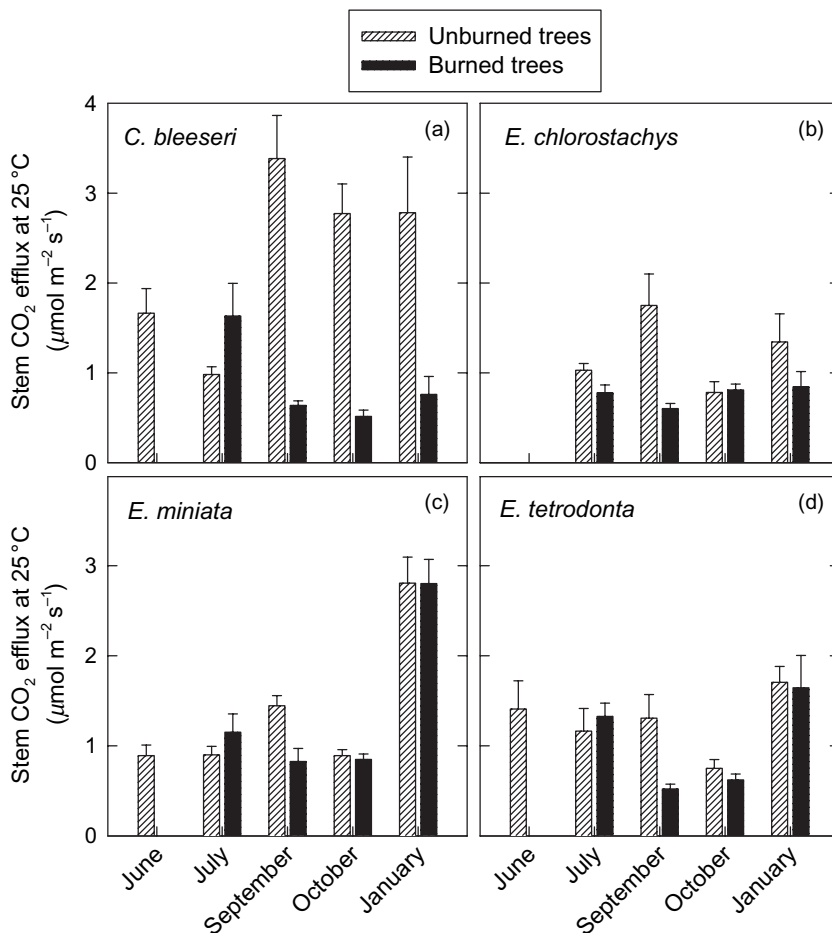


Figure 2. Stem CO₂ efflux separated by species (a–d) and normalized to 25 °C for burned and unburned trees. The July sampling took place approximately 2 weeks post-fire. Error bars represent 1 SE.

rated into new stem tissue. This estimate matches exactly the value of 0.25 suggested by Penning de Vries (1975) for generic wood. The estimated mean stem temperature over the 9 d period was 30.6 °C. Using this value and a Q_{10} of 1.92 calculated for all species, the intercept of the regression equation scales to an F_{25} of 0.92 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; this estimate of maintenance CO₂ efflux is close to that estimated from the July stem CO₂ efflux measurements (1.02 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 25 °C). The diameter growth increments over the 9 d measurement period did not vary significantly between treatments ($P = 0.11$, $n = 48$), but did vary among species ($P = 0.003$, $n = 48$). The mean 9 d increment for unburned trees was 0.29 ± 0.04 mm (mean \pm 1 SE), whereas that for burned trees was 0.18 ± 0.04 mm (mean \pm 1 SE).

The temperature response of the stem CO₂ efflux varied among species (Fig. 3). ANCOVA indicated variation among species in the rate of increase of $\ln(F/F_{25})$ with increasing stem temperature ($P < 0.0001$, $n = 1018$; Fig. 3); however, there was no variation in temperature response between burned and unburned trees ($P = 0.65$, $n = 1018$). The fitted Q_{10} values for the different species were 1.67, 2.32, 1.67 and 1.92 for *C. bleeseri*, *E. chlorostachys*, *E. miniata* and *E. tetradonta*, respectively. The Q_{10} fitted to the entire data set combined was 1.92.

Branch CO₂ efflux

The branch CO₂ efflux rates ranged from 0.4 to 2.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when expressed on a surface-area basis (Fig. 4a); the measurement temperature was 24 °C. ANCOVA indicated that these rates increased with increasing branch diameter for both *E. miniata* and *E. tetradonta* ($P < 0.0001$, $n = 60$), and that there was a significant difference between species in CO₂ efflux rate at a given diameter ($P = 0.02$, $n = 60$).

The trend of CO₂ efflux rate with diameter was reversed when the branch CO₂ efflux rates were expressed on a sapwood-volume basis, rather than on a surface-area basis (Fig. 4b). The values ranged from 908 to 124 $\mu\text{mol CO}_2 \text{ m}^{-3}$ sapwood s^{-1} , and decreased exponentially with increasing branch diameter (Fig. 4b). The difference between species was less apparent when respiration rates were expressed per unit sapwood volume, and collapsed completely for branches larger than 4 cm in diameter (Fig. 4b).

The *E. miniata* branches had a larger sapwood cross-sectional area than the *E. tetradonta* branches of the same diameter for branch diameters larger than about 4 cm (Fig. 5a). This was not simply the result of a thicker bark in *E. tetradonta*, as the difference was still apparent if the

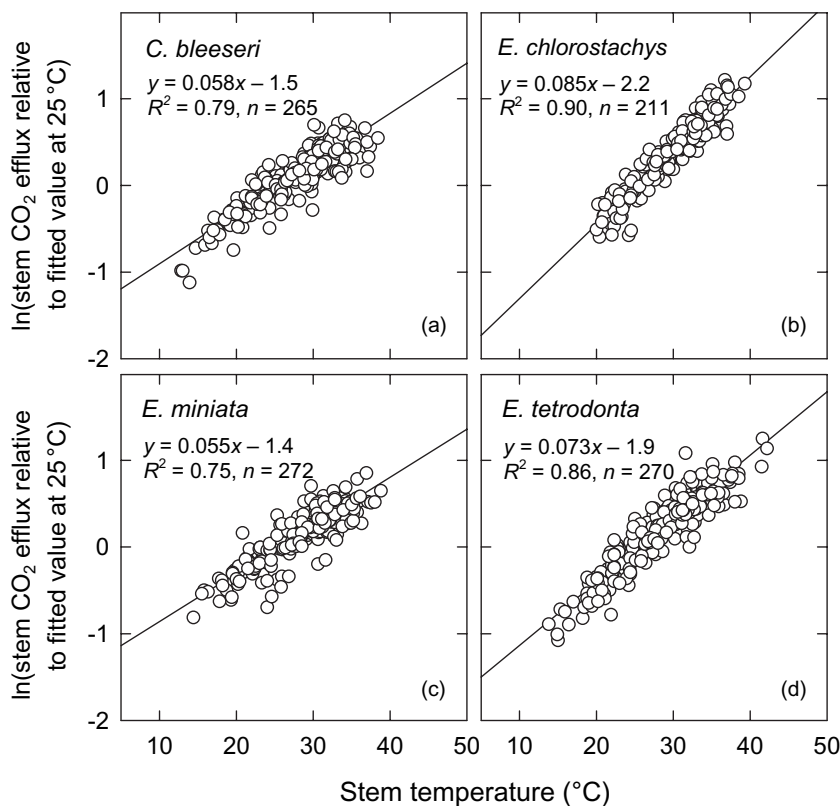


Figure 3. Temperature response of stem CO₂ efflux for each species (a–d). The ln of CO₂ efflux rate relative to the value at 25 °C is plotted against stem temperature. Analysis of covariance indicated variation in the temperature response among species, as seen by the different slopes of the regression lines.

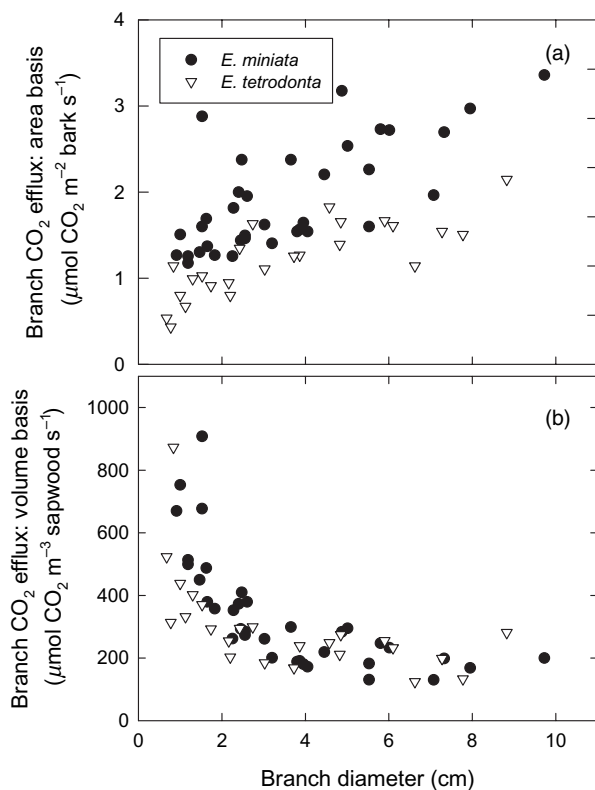


Figure 4. Branch CO₂ efflux for *Eucalyptus miniata* and *Eucalyptus tetradonta* branches expressed on a surface-area basis (a) and on a sapwood-volume basis (b). Measurements were made in the laboratory on excised branch sections at 24 °C. Branches were harvested from unburned trees in October 2005.

values of sapwood cross-sectional area were plotted against the diameter under bark, rather than over bark (Fig. 5b). In addition, the ratio of branch sapwood cross-sectional area to subtending leaf area was larger in *E. miniata* than in *E. tetradonta* ($P = 0.002$, $n = 11$). The mean value for *E. miniata* was $2.25 \pm 0.08 \text{ cm}^2 \text{ sapwood m}^{-2} \text{ leaf area}$ (mean ± 1 SE, $n = 5$), whereas the mean value for *E. tetradonta* was $1.76 \pm 0.09 \text{ cm}^2 \text{ sapwood m}^{-2} \text{ leaf area}$ (mean ± 1 SE, $n = 6$).

Branch re-fixation

The CO₂ efflux rates of *E. miniata* branches measured in the light were lower than those measured in the dark in all cases, despite branch temperatures being 4–7 °C higher during the light measurements. The mean difference was $0.70 \pm 0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (mean ± 1 SE, $n = 10$). The mean proportional re-fixation rate, calculated after adjusting the dark CO₂ efflux rates to the light temperatures, was 0.55 ± 0.04 (mean ± 1 SE, $n = 10$). This indicates that an average of 55% of the dark CO₂ efflux was re-fixed by photosynthetic bark at an irradiance of approximately $1000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

Leaf gas exchange

The relationship between stomatal conductance and photosynthesis under light-saturated conditions for expanding and mature foliage of *E. miniata* and *E. tetradonta* is shown in Fig. 6. The data are combined for both burned and

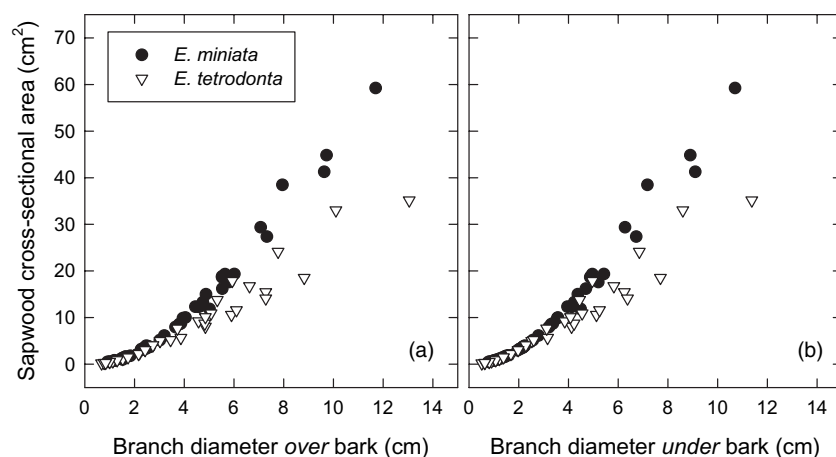


Figure 5. The relationship between sapwood cross-sectional area and branch diameter for *Eucalyptus miniata* and *Eucalyptus tetradonta* branches. Data are plotted against branch diameter, measured both over the bark (a), and under the bark (b) to remove variation in the relationship associated with bark thickness.

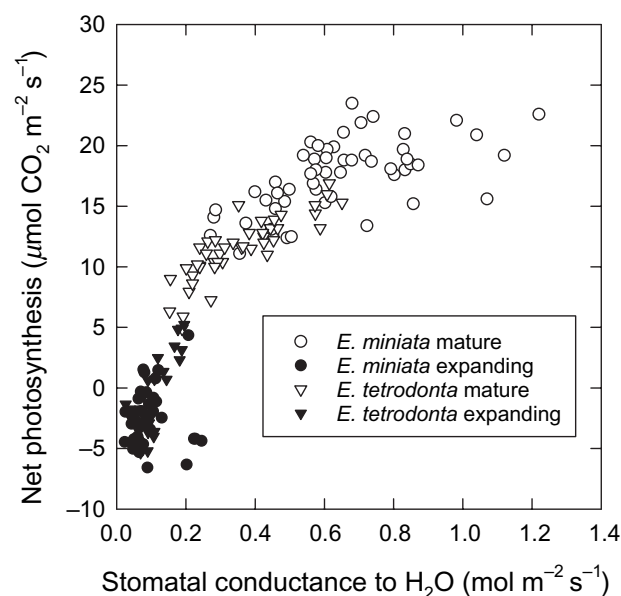


Figure 6. The relationship between photosynthesis and stomatal conductance in *Eucalyptus miniata* and *Eucalyptus tetradonta* leaves under light-saturated conditions (photon flux density > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Data are shown for both mature and expanding leaves, and include both burned and unburned trees.

unburned trees. Expanding foliage typically showed net C losses to the atmosphere, although incident PFD exceeded 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Interestingly, the trajectory of the relationship between stomatal conductance and photosynthesis appeared to be similar between expanding and mature foliage. Thus, in addition to having very low or negative net photosynthesis rates, the expanding foliage also typically had lower stomatal conductance than the mature foliage. Leaf dark respiration tended to be higher in expanding foliage than in mature foliage (Table 1).

The light-saturated stomatal conductance of mature foliage differed between species ($P < 0.0001$, $n = 98$) and between burned and unburned trees ($P = 0.009$, $n = 98$), as shown in Fig. 7a. The interaction between species and treatment was close to being significant ($P = 0.06$, $n = 98$). In contrast, the light-saturated photosynthesis of mature foliage differed between species ($P < 0.0001$, $n = 98$), but not between burned and unburned trees ($P = 0.91$, $n = 98$), as shown in Fig. 7b. The difference between species was pronounced, with mature *E. miniata* foliage having a mean photosynthetic rate of $17.5 \pm 0.4 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (mean ± 1 SE, $n = 54$), as compared to a mean rate of $11.5 \pm 0.4 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (mean ± 1 SE, $n = 44$) for *E. tetradonta*. The ratio of intercellular to ambient CO_2 concentrations (c_i/c_a) also differed between species ($P = 0.0008$,

Table 1. Dark respiration rates of foliage from both burned and unburned trees of *Eucalyptus miniata* and *Eucalyptus tetradonta*

Tree	Species	Treatment	Mature foliage			Expanding foliage		
			T_{leaf} ($^{\circ}\text{C}$)	Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R_{30} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	T_{leaf} ($^{\circ}\text{C}$)	Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R_{30} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
EM1	<i>E. miniata</i>	Not burned	35.4 (0.8)	4.8 (0.8)	3.3 (0.7)	36.6 (0.2)	6.4 (1.2)	4.0 (0.7)
EM4	<i>E. miniata</i>	Burned	38.8 (0.3)	6.3 (1.1)	3.4 (0.6)	38.9 (0.1)	6.1 (0.8)	3.3 (0.5)
ET1	<i>E. tetradonta</i>	Not burned	34.8 (0.2)	3.1 (0.7)	2.3 (0.5)	35.5 (0.2)	6.2 (1.0)	4.3 (0.7)
ET4	<i>E. tetradonta</i>	Burned	39.5 (0.3)	6.3 (0.4)	3.3 (0.2)	38.8 (0.5)	9.7 (1.6)	5.3 (1.0)

Measurements were made during daylight hours on foliage of detached branches that had been darkened for at least 30 min. Predicted R_{30} is also presented to allow comparison among rates measured at different T_{leaf} . Observed rates were scaled to R_{30} by assuming a Q_{10} value of 2. Values in parentheses are 1 SD.

T_{leaf} , leaf temperature; R_{30} , respiration rates at 30 $^{\circ}\text{C}$; EM1, *E. miniata* tree one; EM4, *E. miniata* trees four; ET1, *E. tetradonta* tree one; ET4, *E. tetradonta* trees four; Q_{10} , proportional increase in stem CO_2 efflux with a 10 $^{\circ}\text{C}$ increase in stem temperature.

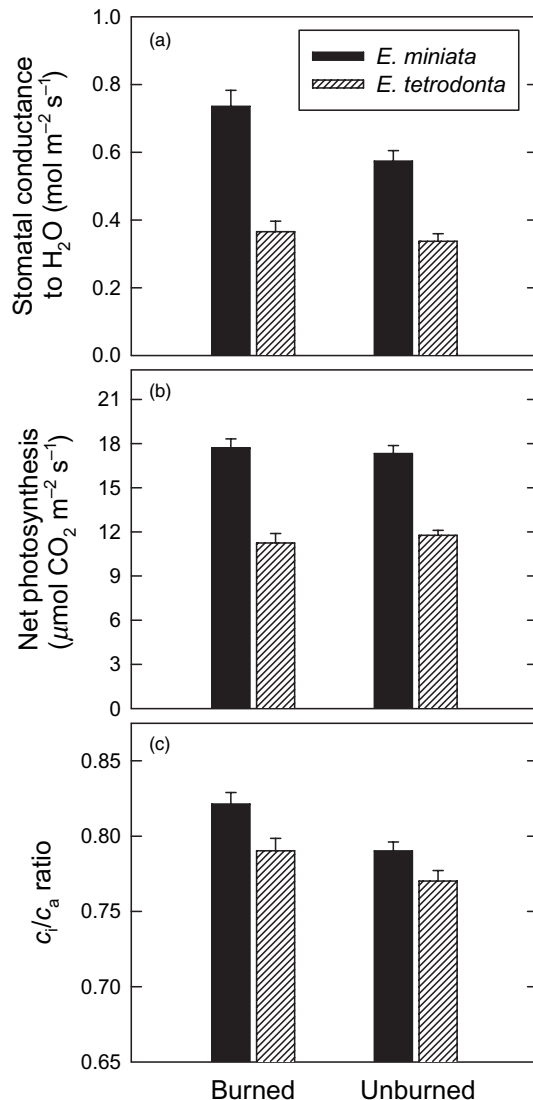


Figure 7. Mean values for stomatal conductance (a), photosynthesis (b) and c_i/c_a ratio (c) of mature (fully expanded) foliage from burned and unburned trees of *Eucalyptus miniata* and *Eucalyptus tetradonta* under light-saturated conditions (photon flux density > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Measurements were made in October, approximately 9 weeks post-fire, at canopy heights ranging from 8 to 15 m. Error bars represent 1 SE.

$n = 98$) and between burned and unburned trees ($P = 0.0008$, $n = 98$), as shown in Fig. 7c.

Estimated annual stem and branch CO_2 efflux

We estimated the above-ground sapwood density at our study site, M in Eqn 1, to be $0.0032 \text{ m}^3 \text{ sapwood m}^{-2} \text{ ground area}$. Stem sapwood accounted for 58% of the total above-ground sapwood, and branch sapwood for 42%. The above-ground wood production, dM/dt in Eqn 1, was estimated to be $121 \text{ g C m}^{-2} \text{ ground area year}^{-1}$, based on the assumed diameter at a breast height increment of 0.3 cm year^{-1} . The m used in the scaling exercise for stems was $64 \mu\text{mol}$

$\text{CO}_2 \text{ m}^{-3} \text{ sapwood s}^{-1}$ at 25°C . Our estimate for branches, weighted by the assumed distribution of branch diameter classes, was $270 \mu\text{mol CO}_2 \text{ m}^{-3} \text{ sapwood s}^{-1}$ at 25°C . The g was taken as 0.25 for both stems and branches. Combining these estimates of M , dM/dt , m and g with temperature response functions and predicted stem and branch temperatures resulted in an estimate for total above-ground woody-tissue respiration of $297 \text{ g C m}^{-2} \text{ ground area year}^{-1}$. This estimate is for a climatically average year in the absence of fire. Maintenance respiration, mM in Eqn 1, made up 89.8% of the estimated annual total, whereas growth respiration, gdM/dt in Eqn 1, made up 10.2%. Branch respiration accounted for 72.0% of the total woody-tissue respiration, whereas stem respiration accounted for 28.0%.

We estimated the annual re-fixation for the overstorey tree species that have smooth bark on their branches (*E. miniata*, *C. bleeseri* and *C. polysciada*). To do this, we assumed a proportional re-fixation rate of 0.55, based on the re-fixation measurements in *E. miniata*, for 10 h d^{-1} . We estimated that 50% of dark CO_2 efflux would have occurred during these daylight hours because of diel temperature variation. Combining these two estimates yields a daily proportional re-fixation rate of 0.275. Scaling this to an annual re-fixation total resulted in an estimate of $21.9 \text{ g C m}^{-2} \text{ ground area year}^{-1}$. Subtracting re-fixation from the estimate of annual above-ground wood respiration gives the net CO_2 efflux from above-ground woody tissues, which we estimate to be $275 \text{ g C m}^{-2} \text{ ground area year}^{-1}$ for a tropical savanna ecosystem in northern Australia.

DISCUSSION

Stem and branch CO_2 efflux

In the context of the functional model of plant respiration, as defined in Eqn 1, the respiration rates measured in non-growing tissues represent mM . Because stem growth ceases during the dry season in the open-forest savannas of northern Australia (Mucha 1979; Ogden 1981; Chen 2002; Prior *et al.* 2004), which was also confirmed at our study site (Chen 2002), stem CO_2 efflux measurements made at this time should provide an estimate of maintenance CO_2 efflux rates. In the peak of the dry season in late July 2004, we observed a mean stem CO_2 efflux rate of $1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when normalized to a stem temperature of 25°C ; this rate did not vary significantly among species. A similar mean rate was observed at the same study site in late July 2002 (Tame 2002); the mean rate normalized to 25°C at that time was also $1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *E. miniata*, *E. tetradonta* and *E. chlorostachys*. These values also agree well with our estimate of maintenance CO_2 efflux during the growing season in January 2005, based on a regression analysis between stem growth and stem CO_2 efflux ($0.92 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 25°C). When expressed on a sapwood-volume basis, the mean stem CO_2 efflux rate that we observed in July 2004 was $64.2 \mu\text{mol CO}_2 \text{ m}^{-3} \text{ sapwood s}^{-1}$.

These estimates of stem maintenance CO₂ efflux can be compared to rates reported for other tropical vegetation at 25 °C. A rate of 0.65 μmol CO₂ m⁻² s⁻¹ (45 μmol CO₂ m⁻³ sapwood s⁻¹) was reported for two tree species in a tropical wet forest in Costa Rica (Ryan *et al.* 1994). Rates ranging from 1 to 3 μmol CO₂ m⁻² s⁻¹ were reported for several tree species with stem diameters between 10 and 60 cm in a tropical forest in Cameroon (Meir & Grace 2002), and values of 0.37 and 0.25 μmol CO₂ m⁻² s⁻¹ were reported for two Sahelian shrub species in West Africa (Levy & Jarvis 1998). For temperate tree species, stem maintenance CO₂ efflux rates have been reported that are both higher and lower than the values we observed (Sprugel & Benecke 1991; Ryan *et al.* 1995; Edwards & Hanson 1996; Carey, Callaway & DeLucia 1997; Maier, Zarnoch & Dougherty 1998; Stockfors & Linder 1998; Bosc, De Grandcourt & Loustau 2003).

The branch CO₂ efflux rates that we measured in October 2004 were higher on average than the stem CO₂ efflux rates measured at the same time (Figs 2 & 4). The maintenance CO₂ efflux rate that we calculated for branches from these measurements was about 1.5 times higher than that measured for stems on a surface-area basis, and about four times higher on a sapwood-volume basis, when averaged across branch diameters. This is consistent with observations on other species, in which branches have been shown to have higher maintenance CO₂ efflux rates than stems (Sprugel 1990; Ryan *et al.* 1996; Maier *et al.* 1998; Ceschia *et al.* 2002; Damesin *et al.* 2002; Bosc *et al.* 2003; Wieser & Bahn 2004). These higher rates have been at least partially accounted for on the basis of higher tissue N concentrations and live-cell fractions in branches than in stems (Maier *et al.* 1998; Ceschia *et al.* 2002; Bosc *et al.* 2003; Wieser & Bahn 2004).

We observed variation among species in the response of stem CO₂ efflux to variation in sapwood temperature (Fig. 3). It is not possible to tell from measurements of stem CO₂ efflux and stem temperature alone whether these differences represent variation in the temperature responses of respiratory CO₂ production, or variation in other factors that can influence the diffusion of CO₂ out of the stem. For example, variation in the diffusive resistance of the bark could cause variation in the amount of time elapsed between a change in respiration rate and an observed change in stem CO₂ efflux (Ryan *et al.* 1995). In addition, there may be differences among species in the way that stem CO₂ efflux is affected by movement of the transpiration stream (Negisi 1972; Martin, Teskey & Dougherty 1994; Levy *et al.* 1999; Teskey & McGuire 2002; McGuire & Teskey 2004). In spite of these complications, variation in stem temperature still explained at least 70% of the variation in F/F_{25} when the species were analysed individually, and 74% of the variation when they were analysed collectively.

We estimated the annual stem and branch CO₂ efflux in a tropical savanna ecosystem in northern Australia to be 275 g C m⁻² year⁻¹ in a year without fire. The annual GPP at the study site was estimated at 2080 g C m⁻² year⁻¹ in a year

without fire based on an inventory approach (Chen *et al.* 2003), and 1700–1900 g C m⁻² year⁻¹ in years with fire based on eddy-covariance measurements (Beringer *et al.*, unpublished results). Taking the GPP estimate for a year without fire, our estimate of woody-tissue CO₂ efflux (also for a year without fire) is equivalent to 13.2% of GPP. In a tropical wet forest in Costa Rica, above-ground woody-tissue CO₂ efflux was estimated to be between 8 and 13% of GPP (Ryan *et al.* 1994), and in a tropical forest in Cameroon, it was estimated to be 10% of GPP (Meir & Grace 2002). Estimates of above-ground woody-tissue CO₂ efflux as a percentage of GPP in temperate forests range from 6% for a pine forest (Law *et al.* 1999) to 24% for a beech forest (Damesin *et al.* 2002), with several other estimates falling in between these two (Ryan & Waring 1992; Lloyd *et al.* 2002; Maier *et al.* 2004; Zha *et al.* 2004). We estimated that maintenance CO₂ efflux accounted for 90% of the total above-ground woody-tissue CO₂ efflux. This is a higher percentage of total CO₂ efflux assigned to the maintenance component than in previous reports on woody-tissue CO₂ efflux, although reasonably close to estimates of 80% in the Cameroon tropical forest (Meir & Grace 2002) and 85% for pine trees in the Great Basin Desert, USA (Carey *et al.* 1997). Although our estimate of 90% is high, it is perhaps not unexpected, given that the mean annual air temperature at our study site is ~28 °C.

Our estimate for above-ground woody tissue CO₂ efflux of 275 g C m⁻² ground area year⁻¹ is more than twofold larger than that reported previously by Chen *et al.* (2003) for the same study site of 120 g C m⁻² ground area year⁻¹. The estimate of Chen *et al.* (2003) was based on CO₂ efflux rates reported by Ryan & Waring (1992) for north-American conifers, and thus did not include site-specific measurements of stem or branch respiration. The main reason that our estimate is much larger than that of Chen *et al.* (2003) is because we included a different coefficient for maintenance CO₂ efflux for branches as compared to stems, with the former being about four times larger than the latter on a sapwood-volume basis.

Responses of stem and leaf gas exchange to fire

We did not observe large differences in leaf gas exchange between mature (fully expanded) leaves that flushed following a fire event and similar leaves on unburned trees (Fig. 7), although stomatal conductance and c_i/c_a ratio were slightly higher in the former than in the latter. The increase in c_i/c_a ratio indicates a decreased stomatal limitation on photosynthesis in the mature foliage of the burned trees. This higher stomatal conductance in the burned trees may be linked to the availability of soil moisture in the burned versus unburned patches of open-forest savanna. Soil moisture is progressively depleted over the course of the dry season in these savanna communities (Cook *et al.* 1998). When a fire scorches a large fraction of the overstorey canopy, evapotranspiration is reduced greatly (Beringer *et al.* 2003). The canopy then takes 2–3 months to return to pre-fire canopy cover values (Bowman 2003). After this

recovery period, one would expect the soil moisture availability to be higher than in a contiguous patch of unburned savanna, because of the decreased evapotranspiration during the interval for which the scorched canopy was inactive.

By far, the most significant effect on the overstorey canopy of a fire event would be the reduction in functional leaf area caused by the senescence of scorched leaves. Over the weeks and months following a fire, new foliage emerges; however, this foliage is not immediately photosynthetically competent (Fig. 6). Thus, the overstorey trees must not only expend C resources in reconstructing new foliage, but additionally suffer a reduction in net assimilation rate during the reconstruction phase. We can make an initial estimate of the C cost of reconstructing the canopy after a fire by applying the following simplifying assumptions: the canopy scorch is 0.5 m^2 of foliage m^{-2} ground area (corresponding to about 80% of dry season canopy cover), the specific leaf area is $5.5 \text{ m}^2 \text{ kg}^{-1}$, the C mass fraction of new foliage is 0.5 and the g is 0.25. Under these conditions, the C cost of replacing scorched foliage would be 57 g C m^{-2} ground area. The reduction in assimilation incurred during the reconstruction phase, when emerging foliage is not fully photosynthetically competent, is more difficult to quantify. However, ongoing eddy-covariance measurements at the study site (Beringer *et al.* unpublished results) should prove helpful in this regard. The very low to negative net photosynthesis rates and coordinated behaviour between photosynthesis and stomatal conductance that we observed in expanding *E. miniata* and *E. tetradonta* foliage are similar to observations of expanding *Corymbia gummifera* foliage following a fire in south-eastern Australia (Choinski, Ralph & Eamus 2003).

We observed significant reductions in stem CO_2 efflux rates in all four studied tree species in the September sampling, both in comparison to unburned trees and in comparison to measurements of the same trees in the July sampling (Fig. 2). The September sampling took place approximately 8 weeks following the fire event, which scorched 66% of the canopy of the sampled trees, on average. We suggest that this reduction in stem CO_2 efflux was caused by a decrease in the amount of photosynthate available to serve as respiratory C substrate. This would have been caused by the reduction in net assimilation rate of the canopy, because of leaf scorching, and priority allocation of fixed C towards the reconstruction of a new canopy. Reduced stem CO_2 efflux rates in response to reduced C substrate availability have been observed previously when substrate availability was altered experimentally, either by girdling stems (Edwards & McLaughlin 1978; Martin *et al.* 1994; Lavigne, Little & Riding 2004), or by decreasing canopy photosynthesis by reducing the concentration of CO_2 in the canopy air space from 1.4 times ambient to ambient (Edwards, Tschaplinski & Norby 2002). In addition, daily stem CO_2 efflux was observed to be related linearly to daily GPP in a Scots pine stand in Finland (Zha *et al.* 2004).

It has been well recognized in recent reviews that the functional model of plant respiration, as we have described

it in Eqn 1, represents an oversimplification of the respiratory process (Amthor 2000; Cannell & Thornley 2000; Thornley & Cannell 2000; Saxe *et al.* 2001). A primary weakness of Eqn 1 is that it sets maintenance respiration at a fixed cost that is uncoupled from C substrate supply (Thornley & Cannell 2000). In the present study, this weakness is highlighted, in so far as Eqn 1 does not provide us with a means of incorporating into our annual respiratory budget the impact of fire on stem CO_2 efflux during the dry season, when stems are not actively growing. This is because m in Eqn 1 is a constant. Other models have been formulated that would presumably allow for a more realistic representation of respiration in a tissue that is not growing actively, but that has a variable C substrate supply (Dewar 2000; Thornley & Cannell 2000). However, the parameterization of such a model is beyond the scope of this study.

Of the four tree species studied, *C. bleeseri* appeared to suffer the largest reduction in stem CO_2 efflux rate as a result of burning. *Corymbia bleeseri* differs from the other three studied tree species in that it does not have a thick protective bark at the base of its stem. Thus, the reduction in stem respiration rate could have been caused by an exposure of the cambial tissues to elevated temperatures during the fire event, or may have resulted from an insufficient availability of carbohydrate reserves for sustaining respiration following the scorching of the crown. In either case, it would appear that *C. bleeseri* is not as well adapted to coping with frequent fire as the other three studied species. This may go some way towards explaining its relatively low abundance in these open-forest savanna communities (O'Grady *et al.* 2000).

Comparisons between *E. miniata* and *E. tetradonta*

In the mesic tropical savannas of the top end of northern Australia, *E. miniata* and *E. tetradonta* dominate the overstorey canopy in terms of abundance and biomass (O'Grady *et al.* 2000). Therefore, analyses of their canopy physiology can contribute to an understanding of ecosystem C flux and its variation in response to seasonality and disturbance. We observed significantly higher stomatal conductance, photosynthesis and c_i/c_a ratio in mature *E. miniata* leaves compared to mature *E. tetradonta* leaves (Fig. 7). The higher c_i/c_a ratio in *E. miniata* indicates a lesser stomatal limitation on photosynthesis in this species compared to *E. tetradonta*. These observations are consistent with the results obtained previously, with regard to variation between the two species in photosynthesis (Eamus *et al.* 1999b), and C isotope discrimination (Schulze *et al.* 1998; Miller, Williams & Farquhar 2001), which provides a time-integrated estimate of c_i/c_a (Farquhar, O'Leary & Berry 1982). We also observed that *E. miniata* branches have a larger sapwood cross-sectional area at a given branch diameter than *E. tetradonta* branches, when branch diameter is larger than about 4 cm (Fig. 5). Furthermore, we observed that *E. miniata* branches have ratios of cross-sectional sapwood area to

subtending leaf area (Huber values) that are on average 1.3 times those observed for *E. tetradonta* branches. This observation is consistent with Huber value measurements in saplings of *E. miniata* and *E. tetradonta* (Prior & Eamus 2000). The above considerations led us to suggest that the differences in leaf gas exchange between *E. miniata* and *E. tetradonta* result from differences in hydraulic architecture. Specifically, we suggest that *E. miniata* branches have a larger volume of sapwood in the canopy supporting a given amount of leaf area compared to *E. tetradonta* branches.

Whereas *E. miniata* branches had similar CO₂ efflux rates to *E. tetradonta* branches when expressed per unit sapwood volume, the rates per unit surface area were higher (Fig. 4a & b). These rates were measured in the dark and did not take into account the photosynthetic re-fixation in the bark of *E. miniata* branches. We estimated a mean proportional re-fixation rate in *E. miniata* branches at an irradiance of 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ of 0.55. This rate is in good agreement with the mean value measured on the branches of *Pinus monticola* of 0.55 at similar irradiance (Cernusak & Marshall 2000), and with an estimate of 0.50 for *Betula pendula* during daylight hours (Matyssek *et al.* 2002). As a first approximation, we estimated that re-fixation reduced CO₂ efflux from *E. miniata* branches by 27.5% on a diel basis. Thus, when re-fixation is taken into account, CO₂ efflux on a surface-area basis should be lower for *E. miniata* than for *E. tetradonta* branches during daylight conditions, and only slightly higher on a diel basis. Therefore, the capacity of *E. miniata* bark for re-fixation reduces significantly the respiratory C cost of maintaining the larger volume of branch sapwood in *E. miniata* relative to *E. tetradonta*. Our calculations suggest that re-fixation allows *E. miniata* branches to maintain roughly 1.3 times the volume of sapwood that *E. tetradonta* can maintain at the same net respiratory C cost. This savings is approximately equal to the difference observed in the ratio of sapwood area to subtending leaf area between branches of the two species.

At the ecosystem level, we estimate that re-fixation reduced above-ground woody-tissue CO₂ efflux by 7.4%. This value can be compared to an estimated reduction in woody-tissue CO₂ efflux because of re-fixation of 11.1% in a Sahelian shrub ecosystem (Levy & Jarvis 1998). Thus, re-fixation is likely to be only a small fraction of ecosystem-level C flux. However, the data presented here suggest that re-fixation by photosynthetic bark plays a significant role in influencing plant form and function, and this could have an additional impact on ecosystem C balance. Re-fixation reduces the C cost of constructing and maintaining sapwood. As a result, the C cost of delivering water to the evaporative sites in leaves is reduced. We suggest that re-fixation in *E. miniata* branches allowed *E. miniata* foliage to operate at significantly higher photosynthetic rates than *E. tetradonta* foliage, while the C cost of maintaining branch sapwood was similar between the two species. The higher leaf-level photosynthetic rates in *E. miniata* compared with those in *E. tetradonta* provide a possible mech-

anism for explaining observations of faster stem diameter growth in the former compared to the latter (Werner 2005).

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