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# Composition, leaf area index and standing biomass of eucalypt open forests near Darwin in the Northern Territory, Australia

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**Abstract.** Savanna communities dominate the wet–dry tropical regions of the world and are an important community type in monsoonal northern Australia. As such they have a significant impact on the water and carbon balance of this region. Above the 1200-mm isohyet, savanna's are dominated by *Eucalyptus miniata*–*E. tetradonta* open forests. We have described in detail the composition and structure as well as seasonal patterns of leaf area index and above-ground biomass in the *E. miniata*–*E. tetradonta* open forests of the Gunn Point region near Darwin in the Northern Territory of Australia. In all, 29 tree species from four phenological guilds were recorded in these forests. Stand structure suggests that the forests were still recovering from the impacts of cyclone Tracy and subsequent frequent fires. *Eucalyptus miniata* and *E. tetradonta* were significant contributors to overstorey leaf area index and standing biomass (>70%), and both leaf area index and biomass were strongly correlated to basal area. Leaf area index was at a maximum (about 1.0) at the end of the wet season and declined over the dry season by about 30–40%. There were proportionally greater changes in the understorey reflecting the greater contribution of deciduous and semi-deciduous species in this strata. Standing biomass was about 55 t ha<sup>-1</sup>. Detailed descriptions of leaf area index and biomass are important inputs into the development of a water and carbon balance for the savanna's of northern Australia.

## Introduction

Savanna communities dominate the wet–dry tropical regions of the world and are characterised by a discontinuous tree canopy layer with a seasonal understorey of grasses (Andersen *et al.* 1998). In the Northern Territory, savanna's occur across a large rainfall gradient ranging from more than 2000 mm per year at Melville Island in the north to about 500 mm per year near Newcastle Waters in the south. Most (>90%) of the annual rainfall occurs during the wet season which extends from October through to April, and water availability is thought to be one of the main determinants of savanna composition and structure (Williams *et al.* 1996).

Vegetation above the 1200-mm isohyet is dominated by the *Eucalyptus miniata*–*E. tetradonta* open forests (*sensu* Specht 1981; Wilson *et al.* 1990; Williams *et al.* 1997), and these forests form the matrix within which other important vegetation communities occur including monsoon rainforests, melaleuca forests, woodlands and wetlands. Despite their importance to the tourism and pastoral industries, as well as their conservation significance, there have been few studies that have described in detail the structure, composition and biomass of the eucalypt open forests of the Northern Territory (but see for example, Bowman 1986; Bowman and Minchin 1987; Wilson and Bowman 1987). However,

detailed studies on forest biomass and productivity are available elsewhere in Australia (Attiwill 1962, 1966; McColl 1966; Holland 1969; Ashton 1975; Briggs 1977; Westman and Rogers 1977; Bevege 1978).

Descriptions of forest structure are important for a number of reasons including habitat description (Taylor *et al.* 1984) and as inputs into models dealing with land–atmosphere interactions (Li and Avisar 1994; Avisar 1995). The structure and composition of the northern Australian savanna's are governed principally by water availability and plant available nutrients (Williams *et al.* 1996), although fire plays an important role (Andersen *et al.* 1998). Indeed, fire is a dominant feature of savanna's worldwide (Andersen *et al.* 1998) and the impact of fire on the structure and composition of the northern Australian savanna's has been the topic of much research and discussion (e.g. Fensham 1990; Lonsdale and Braithwaite 1991; Setterfield 1997; Andersen *et al.* 1998).

The world's forests are a sink for atmospheric CO<sub>2</sub> (Eamus and Jarvis 1989). Covering more than 25% of the continental Australian landmass, Australia's tropical savanna's are an undescribed component of the Australian carbon cycle. Carbon and water fluxes above savanna's are being studied in the *E. miniata*–*E. tetradonta* open forests near Darwin in the Northern Territory. O'Grady *et al.* (1999) showed that spatial

heterogeneity in forest structure is a major determinant of stand water use and identified a need for detailed descriptions of forest structure in both space and time. Such descriptions are vital for extrapolating CO<sub>2</sub> and water use estimates across catchments, as interactions between the forest and atmosphere are complex and non-linear (Avisar 1995).

As part of Kyoto agreement, Australia requires an inventory of carbon stocks for all major ecosystems, this paper contributes to this requirement. The paper also describes the species composition, spatial and temporal patterns of leaf area index (LAI) and biomass within the *E. miniata*–*E. tetradonta* open-forests near Darwin in the Northern Territory.

## Methods

### Site description

The LAI surveys were carried out in the *E. miniata*–*E. tetradonta* open forests near Howard Springs about 35 km east–south-east of Darwin (12°30'S, 130°45'E) in the Northern Territory of Australia. Biomass harvesting was carried out at Humpty Doo about 10 km south of the Howard Springs site. Vegetation at both sites was characterised by an open canopy (less than 50% cover) of evergreen eucalypt trees with a mean canopy height of about 15 m, LAI was typically low (about 1.0) and mean basal area was 8–10 m<sup>2</sup> ha<sup>-1</sup>. The understorey consisted of semi-deciduous and deciduous small trees and a seasonally continuous cover of annual and, to a lesser extent, perennial grasses. Species composition at both sites was similar to that described by Williams *et al.* (1997), and soils were highly weathered sandy-clay laterites. Groundwater levels vary from 1 to 15 m below the soil surface (Pidsley *et al.* 1994). The climate of the region has been described in detail (Taylor and Tulloch 1985), but can be briefly described as monsoonal with a wet season from October to March during which 95% of the annual rainfall occurs (mean 1700 mm), followed by a prolonged dry season characterised by little or no rainfall.

### Validation of the Adelaide technique for estimation of leaf area index

The 'Adelaide technique' described by Andrew *et al.* (1979) was used to estimate the leaf area of individual trees. The technique involved selecting representative leaf units (modules) for each species and counting the number of units on each tree. Reference modules for each species were then collected and the leaf area of each module determined with a Delta T leaf area meter (Delta-T Devices, Cambridge, UK). This method of leaf area estimation was chosen over other methods (principally light interception methods for example the DEMON or Li-Cor Plant Canopy analyser) because the Adelaide technique provides information of the leaf area of individual trees. Although this is possible by using some light interception techniques it is difficult in forest environments.

To test the suitability of the Adelaide technique, LAI was estimated in five randomly selected plots of 78 m<sup>2</sup> (circular plot, radius 5 m). Module counts and DBH (diameter at 1.3 m) were recorded for each tree, and all trees in the plot were then harvested for total leaf fresh weight and total above-ground biomass (fresh weight). Random subsamples of leaves from each species were collected and the leaf area of the tree estimated by developing leaf area to leaf weight relationships. Leaf area predicted from leaf weight was regressed against leaf area predicted by using the Adelaide technique in order to assess the utility of the technique for estimating LAI of plots. Allometric relationships were developed relating DBH and leaf area.

### Temporal variability in LAI in *E. miniata*–*E. tetradonta* open forest

Seasonal changes in LAI were monitored at five locations (main, rn20734, rn21047, rn29422, rn5880) within the Howard Springs region at four times of the year corresponding to the wet, early dry, mid-dry and

late dry/early wet periods for two complete seasonal cycles. At each location, two sites of about 1 ha were randomly selected. Within each site, tree species, leaf area, and DBH were determined in each of three randomly selected 20 × 20-m plots. Trees were assigned to one of the following three size classes: Height Class 1, trees >1.5 m ≤ 2 m; Height Class 2, trees >2 m ≤ 7 m; Height Class 3, trees >7 m. These size classes were chosen as being representative of the understorey, mid-storey and canopy height classes. Locations with a year-round access were chosen.

Leaf area index data were analysed by a four-factor analysis of variance, the four factors being year (fixed), season (fixed), location (random) and site (random, nested in location, season and year). Seven outliers were identified in the data and were removed and replaced with the overall mean of the data set to stabilise variances and restore normality to the data. These outliers consisted of six plots at one location (rn29422, August 1995) that were severely burnt by fire before sampling resulting in 100% crown damage and another plot that recorded unusually high LAI (seven standard deviations away from the mean) and severely skewed data set. The high leaf area at this plot was attributed to the presence of an unusually large *E. tetradonta* (DBH 32.5 cm, leaf area 534 m<sup>2</sup>) and an unusually large *Erythrophloeum chlorostachys* (DBH 25.1 cm, leaf area 438 m<sup>2</sup>) occurring in the plot. Although such trees occur in the savanna's of northern Australia and are important contributors to the biomass of the region, their occurrence skewed the data set so severely that the data could not be analysed parametrically with them present.

The main contributors to stand structure were determined by the method of conspecific dominance (Cintron and Novelli 1984).

$$\text{Conspecific dominance} = \frac{\text{basal area (m}^2 \text{ ha}^{-1}\text{)}/\text{total basal area (m}^2 \text{ ha}^{-1}\text{)}}{(1)}$$

Conspecific dominance was calculated from a wet-season data set (January 1996), as species dominance would not be expected to change greatly over the study period. Dominance was calculated for each plot and the data sets were pooled, dominance values were then calculated as the mean dominance for each species. The DBH distributions of the seven dominant species were also calculated for January 1996 and December 1996. Wet-season data sets were chosen to ensure that deciduous species that are difficult to identify during the dry season, were fully represented.

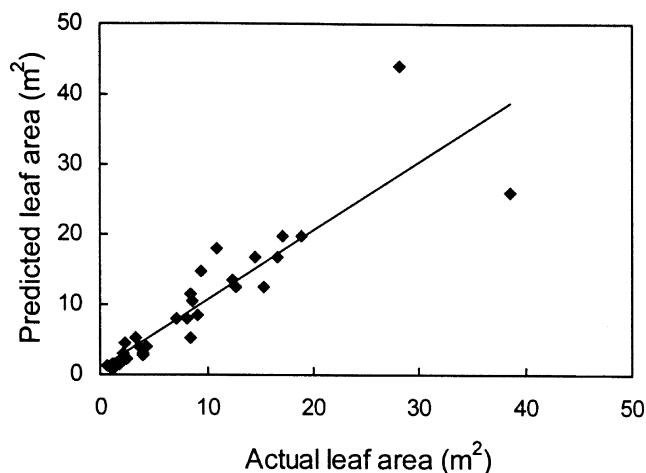
Species diversity ( $D_s$ ) (Simpson 1949) for the *E. miniata*–*E. tetradonta* open forests was calculated as

$$D_s = 1 - \frac{\sum_{j=1}^s N_j(N_j - 1)}{N(N - 1)} \quad (2)$$

where  $N$  is the number of individuals in the sample,  $N_j$  is the number of individuals of species  $j$  and  $s$  is the total number of species. Species diversity was calculated from the January 1996 data set. Importance values, a measure of a species' contribution to the community, were calculated for each of the main species as the sum of relative basal area, relative density and relative frequency (Curtis and McIntosh 1951).

### Estimation of above-ground biomass

Eight trees of six species identified above as being important contributors to standing biomass, were harvested for the calculation of allometric relationships relating DBH and biomass. Trees were sampled over a range of DBH and heights. After a tree was felled, the leaves were stripped and trees were surveyed for total height, height to the lowest live branch, DBH, diameter at the base and diameter at the lowest live branch. The main stem was then cut into 1-m sections, weighed, and a disk (5 cm thick) was cut from each end of the section, for determination of bark thickness, bark weight, wood weight and the ratio of fresh to dry weight for wood and bark. This ratio was then used to calculate total dry weight. Branches were removed and separated into three size classes on



**Fig. 1.** Relationship for leaf area predicted by using the 'Adelaide technique' and leaf area predicted from fresh leaf weight. There was a strong linear relationship of the form  $y = 0.98x + 0.92$ ,  $r^2 = 0.80$  (species pooled).

the basis of the diameter at the base of the branch: Size Class 1, diameter <1 cm; Size Class 2, diameter 1–4 cm; and Size Class 3, diameter >4 cm. After weighing subsamples from each branch class were retained for dry weight determination.

Spatial patterns of above-ground biomass were examined from the January 1996 LAI survey data. Again, the wet-season data set was chosen to incorporate deciduous components that are difficult to identify during the dry season. The above-ground biomass of each tree was estimated by using the community allometric equation formulated above and the biomass ( $\text{t ha}^{-1}$ ) was calculated for each plot. Data were analysed by a two-factor analysis of variance, with factors location (fixed) and site (random, nested in location).

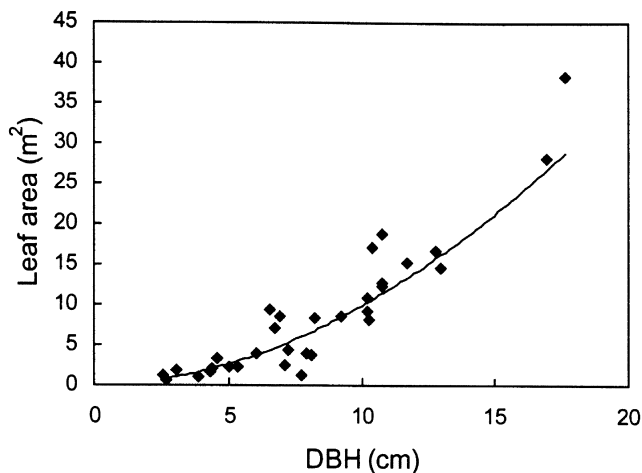
## Results

### Validation of the Adelaide technique for leaf area estimation

Thirty trees across five species were harvested to validate the Adelaide technique. Species harvested were *E. miniata*, *E. tetradonta*, *E. clavigera*, *Erythrophloeum chlorostachys* and *Terminalia ferdinandiana*. Leaf area, estimated by the Adelaide technique, was regressed against leaf area estimated from leaf weight obtained by harvesting. A strong linear correlation ( $r^2 = 0.8$ , slope = 0.98) was found (Fig. 1). Although there was variability on estimates for individual trees, the slope of the line (close to 1) suggests that the technique is particularly useful for predicting the LAI of plots. Allometric relationships, relating DBH (diameter at 1.3 m) to leaf area (species pooled) are shown in Fig. 2. The relationship between DBH ( $x$ ) and leaf area ( $y$ ) was best described by a second-order polynomial  $y = 0.1238x^2 - 0.3159x + 1.5457$ ,  $r^2 = 0.87$ .

### Species composition

A total of 29 tree species from 14 families were recorded during the surveys of LAI. Species diversity was low (0.23). Main contributors to basal area are shown in Table 1; importance scores were calculated for these species and are also shown in Table 1. *Eucalyptus miniata* was the dominant contributor to basal area



**Fig. 2.** Allometric relationships developed from harvesting show the relationship between diameter at 1.3 m (DBH) and leaf area ( $y = 0.12x^2 + 0.32x + 1.55$ ,  $r^2 = 0.87$ ) for 30 harvested trees.

followed by *E. tetradonta*; the two species combined contributing more than 70% of the total basal area of these forests. A summary of tree density (stems  $\text{ha}^{-1}$ ) and basal area ( $\text{m}^2 \text{ha}^{-1}$ ) for the seven dominant species is shown in Table 1.

The distribution of DBH for main species identified above is shown in Fig. 3. Data for locations, sites and plots were pooled, so that counts represent the total number of stems within the sampling period. DBH ranged between 1 and 50 cm for most eucalypt species, with most stems less than 15 cm, suggesting a young forest structure. The range of DBH for *T. ferdinandiana* was smaller with the largest number of stems occurring in the 0–4.9-cm range and no individuals larger than 20 cm.

### Temporal variability in LAI of *E. miniata*–*E. tetradonta* open forests

Leaf area index varied with season ( $F = 9.683$ , d.f. = 3, 40,  $P < 0.01$ ), location ( $F = 6.396$ , d.f. = 4, 40,  $P < 0.01$ ) and site ( $F = 1.908$ , d.f. = 40, 160,  $P < 0.01$ ). There was also a year  $\times$  season interaction ( $F = 15.606$ , d.f. = 3, 40,  $P < 0.01$ ). Post-hoc comparison of means by Tukey's test was inconclusive, although LAI was largest at the end of the wet season (overall wet season mean  $0.88 \pm 0.41$ ) and lowest in the dry season (overall dry season mean  $0.49 \pm 0.20$ ). Leaf area index increased at the end of the dry season during the build-up period and continued to increase over the course of the wet season. Leaf area index was dominated by trees taller than 7.0 m, trees in the mid- and understorey contributed, on average, less than 10% of total overstorey LAI (Fig. 4). However, seasonal changes in the lower height classes were proportionally larger in the understorey. Leaf area index in Height Classes 1 and 2 increased by more than 60% from dry to wet seasons, compared with a 40% increase in LAI in Height Class 3, reflecting the larger proportion of deciduous and semi-deciduous species in Height Classes 1 and 2.

**Table 1. Conspecific dominance, importance, density and basal area of dominant eucalypt-open-forest species in northern Australia**

Values represent the mean  $\pm$  s.e. of dominance values calculated for each 20  $\times$  20-m plot during the January 1996 survey

Species	Conspecific dominance	Importance score	Density (stems ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )
<i>Eucalyptus miniata</i>	0.436	99.6	218.1 $\pm$ 26.6	3.84 $\pm$ 0.50
<i>Eucalyptus tetradonta</i>	0.328	78.6	175.8 $\pm$ 17.9	2.95 $\pm$ 0.44
<i>Erythrophloeum chlorostachys</i>	0.136	25.9	68.8 $\pm$ 10.2	1.16 $\pm$ 0.29
<i>Eucalyptus clavigera</i>	0.117	12.5	54.5 $\pm$ 6.6	0.91 $\pm$ 0.25
<i>Eucalyptus bleeseri</i>	0.112	7.9	50.0 $\pm$ 14.4	1.16 $\pm$ 0.10
<i>Eucalyptus porrecta</i>	0.096	17.4	53.6 $\pm$ 11.7	0.70 $\pm$ 0.23
<i>Terminalia ferdinandiana</i>	0.045	38.3	131.2 $\pm$ 18.8	0.36 $\pm$ 0.07

Leaf area index varied significantly between locations and within locations (site to site) and varied from less than 0.2 to greater than 2.0 throughout the sampling period. Leaf area index was largest at locations in the catchment where basal area was largest. Mean LAI and basal area (seasons and years pooled) for each location are shown in Table 2. The relationship between LAI and basal area at each sampling period is shown in Fig. 5. There were strong relationships between LAI and basal area for the wet season sampling times, but the relationships were more variable at the end of the wet and during the late dry and build-up periods. The considerable variability in the July 1997 sampling time can be attributed to widespread fires at that time.

#### *Breakdown of above-ground biomass in the E. miniata–E. tetradonta open forests*

Biomass was strongly related to DBH for each species and the power function  $y = ax^b$  was used to describe the relationship between the above-ground biomass component ( $y$ ) and DBH ( $x$ ). A community relationship was also generated with species grouped. The relationships for each species and components are given in Table 3. Stem and branch components dominated above-ground biomass, followed by bark and then leaf.

There were no significant differences in above-ground biomass (t ha<sup>-1</sup>) between locations or sites within the *E. miniata–E. tetradonta* open forests, and above-ground biomass was strongly correlated to basal area (m<sup>2</sup> ha<sup>-1</sup>, Fig. 6). Average above-ground biomass for the *E. miniata–E. tetradonta* open forests was 55.9  $\pm$  4.11 t ha<sup>-1</sup>, a breakdown of biomass at each location is shown in Table 4. The seven dominant species (Table 1) combined contributed about 98% of the standing biomass of these forests. A breakdown of the contribution of these seven dominants to overall forest biomass is shown in Table 5.

## Discussion

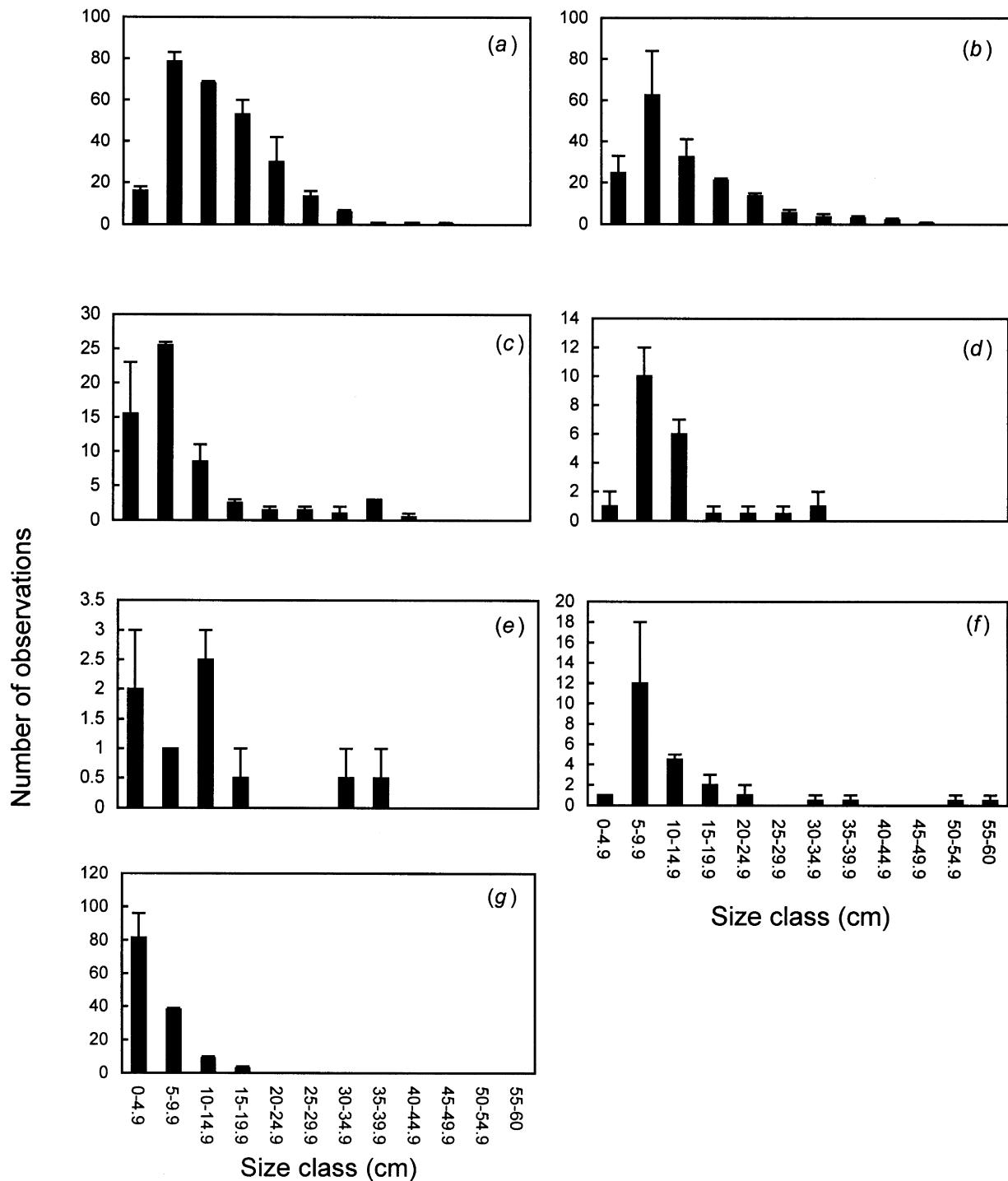
### *Stand structure and composition*

The total number of woody species recorded in this survey was lower than the number observed by Williams *et al.*

(1997, 49 species) at a site nearby and may reflect the impact of fire on the landscape. The study of Williams *et al.* (1997) was conducted in an area excluded from fire for about 20 years (Fensham 1990), and forest structure was quite different (e.g. increased LAI and basal area; grass-dominated understorey absent; O'Grady, pers. obs.). Fire, however, is a widespread and frequent occurrence in the northern Australian savanna's. Therefore, the site of Williams *et al.* (1997) maybe somewhat unrepresentative of this forest type. Lonsdale and Braithwaite (1991) and Williams *et al.* (1999) both reported that even a single unplanned late season fire in Kakadu significantly reduced the number of species present and that deciduous taxa were more sensitive to the effects of fire than evergreen taxa.

Size class distributions were skewed towards smaller trees suggesting a young forest structure (Fig. 3). Wilson and Bowman (1987) found that most eucalypts occurred in size classes <15.0 cm DBH at a site within the same catchment area (Howards peninsula), and noted an absence of trees in the 15–25-cm DBH size class and low numbers in the 25–35-cm DBH size classes, which they attributed to the effects of cyclone Tracy in 1974. Stocker (1976) recorded significant tree fall in the area immediately after the 1974 cyclone. The results presented here indicate that the forests may still be recovering from cyclone Tracy, as indicated by the recruitment of trees into some of these larger size classes. Data for Kakadu (c. 150 km east of Darwin) show peaks in the size class distribution between 15 and 25 cm for most canopy tree species (Werner 1986; Lonsdale and Braithwaite 1991).

Disturbances such as cyclones and fire contribute to the large variability in the basal area of these forests. Tree basal area has been cited as being a useful parameter with which to scale tree water use in natural systems where the accurate determination of LAI is difficult (Hatton *et al.* 1995; Calder 1996). In such systems, careful consideration must be given to the placement and size of measurement plots so that scaled estimates of stand water use and carbon fixation incorporate the natural variability within these forest types.

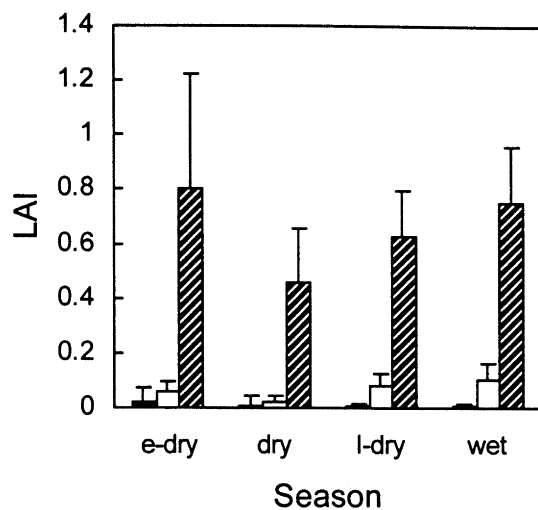


**Fig. 3.** Size-class (diameter at 1.3 m) distributions for each of the dominant species of the *Eucalyptus miniata*–*E. tetradonta* open forests. (a) *Eucalyptus miniata*, (b) *E. tetradonta*, (c) *Erythrophloeum chlorostachys*, (d) *Eucalyptus clavigera*, (e) *E. bleeseri*, (f) *E. porrecta*, (g) *Terminalia ferdinandiana*. Data represent the mean number of observations of two sampling periods: January 1996 and December 1996.

#### Leaf area index

There were significant seasonal shifts in the LAI of the *E. miniata*–*E. tetradonta* open forests. Leaf area index increased from a minimum (towards the end of the dry

season) to a maximum (at the end of the wet season). The late dry–early wet season (October–November) is a time of considerable leaf flushing in these forests (Williams *et al.* 1997). Leaf area index increased in response to decreasing vapour



**Fig. 4.** Seasonal patterns of leaf area index (LAI) in *Eucalyptus miniata*–*E. tetradonta* open forests showing the overall contribution of each stratum of trees, during each of the seasons. Data represent the mean (bars indicate s.e.) for each height class (years pooled): ■, trees 1.5–2 m; □, trees >2–7 m; ▨, trees >7 m.

pressure deficits (Duff *et al.* 1997), initial rainfall events (Myers *et al.* 1998) and changes in the internal water status of individual trees (Williams *et al.* 1997).

Canopy species, principally *E. miniata* and *E. tetradonta*, were the dominant contributors to LAI. Despite the fact that these are evergreen species (Williams *et al.* 1997), LAI of this size class decreased during the dry season by up to 40%. The magnitude of this decline was surprising, given that Williams *et al.* (1997) reported only small seasonal shifts in canopy fullness for these two eucalypts. This suggests that canopy fullness may not be an appropriate correlate of LAI, or as mentioned above, the site of Williams *et al.* 1997 is not truly representative of the *E. miniata*–*E. tetradonta* open forests of the region, as it had been excluded from fire for more than 20 years. Dry season fires of varying intensities (not recorded) were common throughout the Howard Springs catchment. Fires, even fires of low intensity, would have impact on the canopy through effects such as leaf scorch (Williams *et al.* 1999).

There were larger shifts in LAI in the lower- and mid-stratum trees than in the uppermost stratum, reflecting the increased contribution of deciduous species to the standing biomass of these height classes. Prior *et al.* (1997) also noted that *E. tetradonta* saplings were likely to develop water stress during the dry season resulting in leaf loss and even death of the shoot, further contributing to the decline in LAI of these size classes over the dry season.

There was considerable spatial variability in LAI within the *E. miniata*–*E. tetradonta* open forests. Leaf area index was, however, strongly correlated to basal area (Fig. 5). Wilson and Bowman (1987) noted that ‘the eucalypt forests are spatially variable with complex transitions that

**Table 2.** Overall mean basal area ( $\pm$  s.e.) and leaf area index (LAI) ( $\pm$  s.e.) for each of the locations within the Gunn Point region

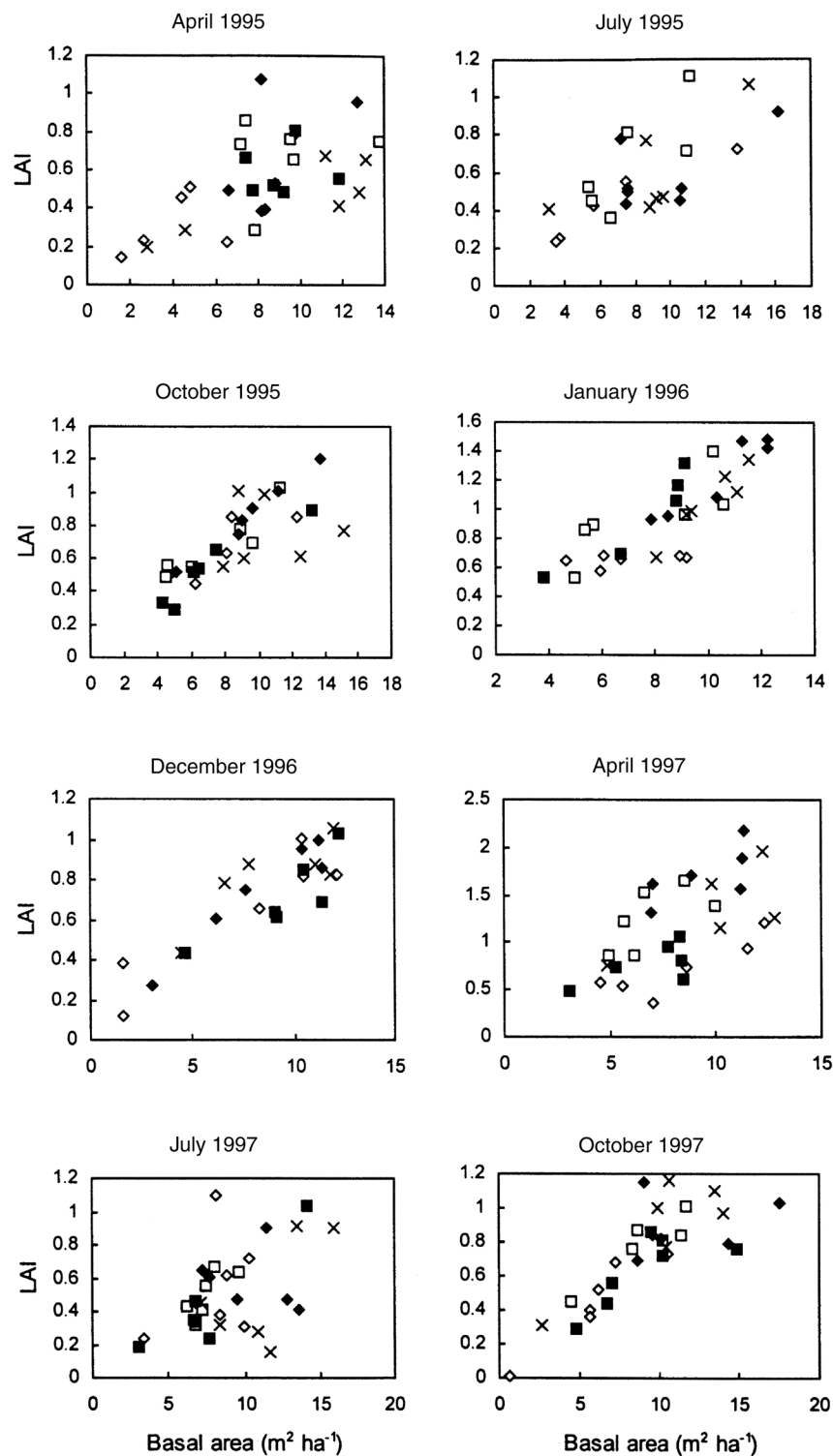
Location	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	LAI
main	9.97 $\pm$ 0.97	0.95 $\pm$ 0.19
rn20734	8.01 $\pm$ 0.87	0.78 $\pm$ 0.11
rn21047	9.92 $\pm$ 0.79	0.79 $\pm$ 0.13
rn29422	7.19 $\pm$ 1.38	0.58 $\pm$ 0.12
rn5880	7.00 $\pm$ 1.11	0.56 $\pm$ 0.09

are difficult to map’. The complex spatial patterning within the forests is the result of many contributing influences, including soil characteristics (Fensham and Kirkpatrick 1992; Williams *et al.* 1996), moisture availability (Wilson and Bowman 1987), recruitment (Setterfield 1997) and fire (Williams *et al.* 1999). The strong correlation between LAI and basal area at the plot scale reflects the good correlation between leaf area and DBH (Fig. 2). There was, however, seasonal variability in the relationship (Fig. 5). The relationship was consistently strongest ( $r^2 > 0.8$ ) during the wet season and was weakest during the late wet to dry season. The variability at the end of the wet season may be due to differences in the stage of leaf senescence throughout the catchment because this period is a time of considerable phenological adjustment (Williams *et al.* 1997). Following this, it would have been expected that the dry season relationships would have been more consistent. However, as mentioned above, the dry season is characterised by periods of widespread fires varying in intensity and impacts on LAI.

#### Stand biomass

There were significant relationships between DBH and above-ground biomass for each of the species studied, similar to that reported for other studies (e.g. Stewart *et al.* 1979). Importantly, a single relationship that accounts for six of the species that dominate forest structure was obtained, suggesting that reliable estimates of above-ground biomass for these communities can be obtained with a generic relationship.

Above-ground biomass of these forests is lower than that of eucalypt forests in temperate Australia that ranges from 100 t ha<sup>-1</sup> (Westman and Rogers 1977) to more than 800 t ha<sup>-1</sup> in the *E. regnans* forests of Victoria (Ashton 1976), but is within the range of 20–150 t ha<sup>-1</sup> reported by Whittaker and Woodwell (1971) for woodlands and scrublands. It is important to note that the forest structure is still developing so that these forests may represent a sink for carbon (D. Eamus, L. B. Hutley, and A. P. O'Grady, unpubl. data). However, this is difficult to establish, as data reporting the release of carbon in fire and underground partitioning of carbon is lacking for these forests. The allometric relationships for these forests (Table 5), however, provide reliable estimates of above-ground biomass and are essential for understanding the carbon balance of these forests.

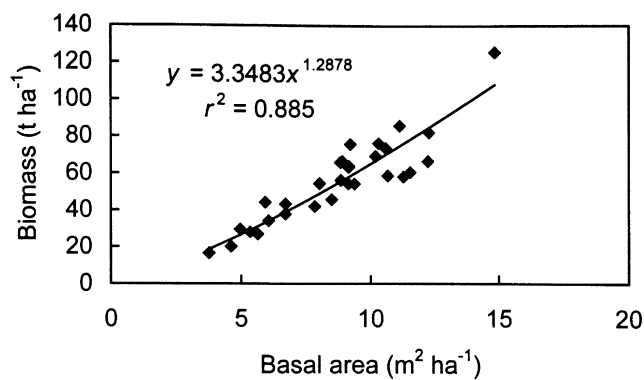


**Fig. 5.** Seasonal relationships between basal area and leaf area index (LAI) for each location studied in *Eucalyptus miniata*-*E. tetradonta* open forests. Different symbols represent different locations: main (◆), rn21047 (×), rn29422 (■), rn20734 (□), m5880 (◇).



**Table 3.** Power relationships ( $y = ax^b$ ) for eucalypt species between DBH (cm) and above-ground biomass (kg) for different tree components and the whole tree (total), and a grouped community relationshipEight trees were harvested for each species. The community relationship combines all species,  $n = 48$ 

Species	Tree component					Total
	Wood	Bark	Stem	Branch	Leaf	
<i>Eucalyptus miniata</i>	$y = 0.08x^{2.44}$ $r^2 = 0.97$	$y = 0.02x^{2.17}$ $r^2 = 0.91$	$y = 0.10x^{2.41}$ $r^2 = 0.97$	$y = 0.002x^{3.18}$ $r^2 = 0.92$	$y = 0.003x^{2.44}$ $r^2 = 0.97$	$y = 0.08x^{2.42}$ $r^2 = 0.91$
<i>E. tetradonta</i>	$y = 0.06x^{2.61}$ $r^2 = 0.95$	$y = 0.04x^{2.15}$ $r^2 = 0.95$	$y = 0.09x^{2.54}$ $r^2 = 0.95$	$y = 0.003x^{3.34}$ $r^2 = 0.93$	$y = 0.001x^{3.03}$ $r^2 = 0.94$	$y = 0.08x^{2.68}$ $r^2 = 0.96$
<i>E. bleeseri</i>	$y = 0.08x^{2.50}$ $r^2 = 0.97$	$y = 0.08x^{2.50}$ $r^2 = 0.97$	$y = 0.09x^{2.50}$ $r^2 = 0.97$	$y = 0.03x^{2.50}$ $r^2 = 0.93$	$y = 0.01x^{1.91}$ $r^2 = 0.80$	$y = 0.14x^{2.50}$ $r^2 = 0.98$
<i>E. porrecta</i>	$y = 0.08x^{2.34}$ $r^2 = 0.99$	$y = 0.02x^{2.34}$ $r^2 = 0.99$	$y = 0.10x^{2.33}$ $r^2 = 0.99$	$y = 0.003x^{3.26}$ $r^2 = 0.96$	$y = 0.007x^{2.21}$ $r^2 = 0.92$	$y = 0.08x^{2.51}$ $r^2 = 0.98$
<i>Terminalia ferdinandiana</i>	$y = 0.04x^{2.59}$ $r^2 = 0.97$	$y = 0.01x^{2.59}$ $r^2 = 0.97$	$y = 0.05x^{2.58}$ $r^2 = 0.97$	$y = 0.0013x^{3.81}$ $r^2 = 0.93$	$y = 0.0073x^{2.32}$ $r^2 = 0.91$	$y = 0.044x^{2.85}$ $r^2 = 0.98$
<i>Erythrophloeum chlorostachys</i>	$y = 0.03x^{2.64}$ $r^2 = 0.97$	$y = 0.01x^{2.58}$ $r^2 = 0.97$	$y = 0.05x^{2.62}$ $r^2 = 0.98$	$y = 0.0002x^{4.52}$ $r^2 = 0.94$	$y = 0.0003x^{3.71}$ $r^2 = 0.94$	$y = 0.021x^{3.12}$ $r^2 = 0.97$
Community	$y = 0.05x^{2.56}$ $r^2 = 0.92$	$y = 0.02x^{2.28}$ $r^2 = 0.93$	$y = 0.07x^{2.51}$ $r^2 = 0.94$	$y = 0.006x^{3.03}$ $r^2 = 0.83$	$y = 0.006x^{2.30}$ $r^2 = 0.94$	$y = 0.08x^{2.60}$ $r^2 = 0.95$

**Fig. 6.** Relationship between basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and above-ground biomass ( $\text{t ha}^{-1}$ ) in the *Eucalyptus miniata*–*E. tetradonta* open forests of northern Australia. Data from January 1996 survey.**Table 4.** Above-ground biomass ( $\text{t ha}^{-1}$ ) at five locations in the *Eucalyptus miniata*–*E. tetradonta* open forestsData are the mean ( $\pm$  s.e.) above-ground biomass of three plots at each site estimated by using the power equation: biomass =  $0.0804 \times (\text{diameter at } 1.3 \text{ m})^{2.5995}$ . Data were calculated from the January 1996 survey

Location	Site	Basal area ( $\text{m}^2 \text{ha}^{-1}$ )	Biomass ( $\text{t ha}^{-1}$ )
main	1	$11.29 \pm 0.57$	$72.0 \pm 7.21$
	2	$9.52 \pm 1.37$	$51.4 \pm 7.58$
rn5880	1	$6.59 \pm 1.37$	$46.6 \pm 16.06$
	2	$7.22 \pm 0.87$	$46.1 \pm 10.14$
rn20734	1	$8.10 \pm 1.60$	$54.0 \pm 12.34$
	2	$7.19 \pm 1.70$	$42.8 \pm 15.31$
rn21047	1	$10.53 \pm 0.63$	$57.8 \pm 1.85$
	2	$9.44 \pm 0.91$	$67.9 \pm 9.26$
rn29422	1	$8.94 \pm 0.10$	$58.7 \pm 3.55$
	2	$8.44 \pm 3.31$	$61.7 \pm 32.82$

**Table 5.** Above-ground biomass ( $\text{t ha}^{-1}$ ) for each of the dominant species of the *E. miniata*–*E. tetradonta* open forests near Darwin

Species	Biomass ( $\text{t ha}^{-1}$ )	Percentage contribution (%)
<i>Eucalyptus miniata</i>	$23.19 \pm 6.10$	41.5
<i>E. tetradonta</i>	$20.08 \pm 6.39$	35.9
<i>Erythrophloeum chlorostachys</i>	$5.47 \pm 2.97$	9.8
<i>Terminalia ferdinandiana</i>	$1.17 \pm 0.56$	2.1
<i>Eucalyptus porrecta</i>	$2.26 \pm 1.74$	4.1
<i>E. bleeseri</i>	$0.93 \pm 1.54$	1.6
<i>E. clavigera</i>	$2.17 \pm 1.55$	3.9
Other species	$0.62 \pm 0.30$	1.1

The nature of the relationship between basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and biomass ( $\text{t ha}^{-1}$ , Fig. 6) demonstrates the potential for the incorporation of remote sensing and GIS technology for scaling biomass estimates in these forests. These relationships are important contributors to the understanding of the relationship between forest biomass and radar backscatter (Foody *et al.* 1997), and the role for remotely sensed data in extrapolating results over larger areas is now well recognised. The biomass reported here, however, does not include below-ground biomass or the seasonally dynamic understorey biomass (grasses), both of which are significant contributors to forest biomass. Further studies are being conducted to quantify the seasonal changes in root and understorey biomass in the context of developing a carbon balance for these forests (X. Chen and D. Eamus, unpubl. data).

## Conclusions

The *E. miniata*–*E. tetradonta* open forests exhibit complex spatial patterning with respect to LAI and biomass. Leaf area index was largest during the wet season and at a minimum by

the mid-dry season, increasing towards the end of the dry season as tree species flush in response to decreasing vapour pressure deficits and initial rainfall events. Leaf area index and above-ground biomass were strongly correlated to basal area, suggesting that LAI and standing biomass can be predicted from existing vegetation data sets that contain information on basal area. Basal area is also recognised as an important parameter for scaling tree water use in forests where accurate estimates of LAI are difficult to obtain. Leaf area index and standing biomass are also important inputs into models of mass and energy exchange between the vegetation and the atmosphere. Recognition of the spatial heterogeneity is important when attempting to scale water and carbon fluxes in the wet–dry tropical forests of northern Australia.

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### References

- Andersen AN, Braithwaite RW, Cook GD, Corbett LK, Williams RJ, Douglas MM, Gill AM, Setterfield SA, Muller WJ (1998) Fire research for conservation management in tropical savanna's: introducing the Kapalga fire experiment. *Australian Journal of Ecology* **23**, 95–110.
- Andrew MH, Noble IR, Lange RT (1979) A non-destructive method for estimating the weight of forage on shrubs. *Australian Rangelands Journal* **1**, 225–231.
- Ashton DH (1975) Studies of litter in *Eucalyptus regnans* forests. *Australian Journal of Botany* **23**, 413–433.
- Ashton DH (1976) Phosphorous in forest ecosystems at Beenak, Victoria. *Journal of Ecology* **64**, 171–186.
- Attiwill PM (1962) Estimating branch dry weight and leaf area from measurements of branch girth in eucalypts. *Forest Science* **8**, 132–141.
- Attiwill PM (1966) A method for relationships between crown weight in eucalyptus and some implications of relationships between crown weight and stem diameter. *Ecology* **47**, 795–804.
- Avisar R (1995) Scaling of land–atmosphere interactions: an atmospheric modelling perspective. *Hydrological Processes* **9**, 679–695.
- Bevege DI (1978) Biomass and nutrient distribution in indigenous forest ecosystems. Queensland Department of Forestry, Technical paper no. 6.
- Bowman DMJS (1986) Stand characteristics, understorey associates and environmental correlates of *Eucalyptus tetrodonta* F.Muell. forests on Gunn Point, northern Australia. *Vegetatio* **65**, 105–113.
- Bowman DMJS, Minchin PR (1987) Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. *Australian Journal of Botany* **35**, 151–169.
- Briggs SV (1977) Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology* **2**, 369–373.
- Calder IR (1996) Water use by forests at the plot and catchment scale. *Commonwealth Forestry Review* **75**, 19–30.
- Cintrón G, Novelli VS (1984) Methods for studying mangrove structure. In 'The mangrove ecosystem: research methods'. Monographs on Oceanographic Methodology. No. 8. (Eds SC Snedaker, JG Snedaker) pp. 91–111. (UNESCO: Paris)
- Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie–forest border region of Wisconsin. *Ecology* **31**, 434–455.
- Duff GA, Myers BA, Williams RJ, Eamus D, O'Grady A, Fordyce IR (1997) Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a northern Australian savanna. *Australian Journal of Botany* **45**, 211–224.
- Eamus D, Jarvis PG (1989) The direct effects of the increase in global atmospheric CO<sub>2</sub> on natural and commercial temperate trees and forests. *Advances in Forest Research* **19**, 1–55.
- Fensham RJ (1990) Interactive effects of fire frequency and site factors in *Eucalyptus* forest near Darwin, northern Australia. *Australian Journal of Ecology* **15**, 255–266.
- Fensham RJ, Kirkpatrick JB (1992) Soil characteristics and tree distribution in the savanna of Melville Island, Northern Territory. *Australian Journal of Botany* **40**, 311–333.
- Footy GM, Green RM, Lucas RM, Curran PJ, Honzak M, Amaral ID (1997) Observations on the relationship between SIR-C radar backscatter and biomass of regenerating tropical forests. *International Journal of Remote Sensing* **18**, 687–694.
- Hatton TJ, Moore SJ, Reece PH (1995) Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiology* **15**, 219–227.
- Holland PG (1969) Weight dynamics of *Eucalyptus* in the mallee vegetation of southeast Australia. *Ecology* **50**, 212–219.
- Li B, Avisar R (1994) The impact of spatial variability of land surface characteristics on land surface heat fluxes. *Journal of Climate* **7**, 527–537.
- Lonsdale WM, Braithwaite RW (1991) Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* **16**, 363–374.
- McColl JG (1966) Accession and decomposition of litter in spotted gum forests. *Australian Forestry* **30**, 191–198.
- Myers BA, Williams RJ, Fordyce IR, Duff GA, Eamus D (1998) Does irrigation affect leaf phenology in deciduous and evergreen trees of the savanna's of northern Australia. *Australian Journal of Ecology* **23**, 329–339.
- O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season: patterns of tree water use in the eucalypt open forests of northern Australia. *Tree Physiology* **19**, 591–597.
- Pidsley D, Kerle E, Williams D, Hatton TJ, Myers BA (1994) Role of transpiration in the recharge/discharge process of an aquifer system underlying open eucalypt forest in the wet–dry north Australian tropics. In 'Proceedings of Water Down 94, Adelaide 21–25 November 1994'. (Institute of Engineers) pp. 491–496.
- Prior LD, Eamus D, Duff GA (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet–dry savanna in northern Australia. *Australian Journal of Botany* **45**, 241–258.
- Setterfield SA (1997) Factors affecting seedling regeneration in a northern Australian tropical savanna. PhD Thesis, Northern Territory University, Darwin.
- Simpson EH (1949) Measurement of diversity. *Nature* **163**, 688.
- Specht RL (1981) Foliage projective cover and standing biomass. In 'Vegetation classification in Australia'. (Eds AN Gillison, DJ Andersen) pp. 10–21. (CSIRO: Canberra)
- Stewart HLT, Flinn DW, Aeberli BC (1979) Above-ground biomass of a mixed eucalypt forest in eastern Victoria. *Australian Journal of Botany* **27**, 725–740.
- Stocker GC (1976) Report on cyclone damage to natural vegetation in the Darwin area after cyclone Tracy 25 December 1974. Department of Primary Industries, Forestry and Timber Bureau. Leaflet 127.

- Taylor JA, Tulloch D (1985) Rainfall in the wet–dry tropics: extreme events at Darwin and similarities between years during the period 1870–1983 inclusive. *Australian Journal of Ecology* **10**, 281–295.
- Taylor JA, Friend GR, Dudzinski ML (1984) Influence of sampling strategy on the relationships between fauna and vegetation structure, plant lifeform and floristics. *Australian Journal of Ecology* **9**, 281–287.
- Westman WE, Rogers RW (1977) Biomass and structure of a subtropical eucalypt forest, North Stradbroke Island. *Australian Journal of Botany* **25**, 171–191.
- Werner PA (1986) Population dynamics and productivity of selected forest trees in Kakadu National Park. Report to the Australian National Parks and Wildlife Service.
- Whittaker RH, Woodwell GM (1971) Measurement of net primary production of forests. In 'Productivity of Forest Ecosystems. Proceedings of the Brussels Symposium 1969'. (Ed. P Duvigneaud) pp. 159–175. (UNESCO: Paris)
- Williams RJ, Duff GA, Bowman DMJS, Cook GD (1996) Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography* **23**, 747–756.
- Williams RJ, Myers BA, Muller MJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a northern Australian tropical savanna. *Ecology* **78**, 2542–2558.
- Williams RJ, Cook GD, Gill AM, Moore PHR (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50–59.
- Wilson BA, Bowman DMJS (1987) Fire, storm, flood and drought: the vegetation ecology of the Howards Peninsula, Northern Territory, Australia. *Australian Journal of Ecology* **12**, 165–174.
- Wilson BA, Brocklehurst PS, Clark MJ, Dickinson KJM (1990) Vegetation survey of the Northern Territory, Australia. Conservation Commission of the Northern Territory, Technical Report No. 49, Darwin.

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