Seasonal changes in photosynthesis of eight savanna tree species

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Summary Seasonal variations in carbon assimilation of eight tree species of a north Australian tropical savanna were examined over two wet seasons and one dry season (18 months). Assimilation rates (A) in the two evergreen species, *Eucalyptus tetrodonta* F. Muell. and *E. miniata* A. Cunn. *ex* Schauer, were high throughout the study although there was a 10--20% decline in the dry season compared with the wet season. The three semi-deciduous species (*Erythrophleum chlorostachys* (F. Muell.) Baillon, *Eucalyptus clavigera* A. Cunn. *ex* Schauer, and *Xanthostemon paradoxus* F. Muell.) showed a 25–75% decline in A in the dry season compared with the wet season, and the deciduous species (*Terminalia ferdinandiana* Excell, *Planchonia careya* (F. Muell.) Kunth, and *Cochlospermum fraseri* Planchon) were leafless for several months in the dry season. Generally, the ratio of intercellular CO_2 concentration to ambient CO_2 concentration (C_i:C_a) was larger in the wet season than in the dry season, indicating a smaller stomatal limitation of photosynthesis in the wet season compared with the dry season.

In all species, the C_i:C_a ratio and A were essentially independent of leaf-to-air vapor pressure difference (LAVPD) during the wet season, but both parameters generally declined with increasing LAVPD in the dry season. The slope of the positive correlation between A and transpiration rate (E) was less in the wet season than in the dry season. There was no evidence that high E inhibited A. Instantaneous transpiration efficiency was lowest in the wet season and highest during the dry season. Nitrogen-use efficiency (NUE) was higher in the wet season than in the dry season because the decline in A in the dry season was proportionally larger than the decline in foliar nitrogen content. In the wet season, evergreen species exhibited higher NUE than semi-deciduous and deciduous species. In all species, A was linearly correlated with specific leaf area (SLA) and foliar N content. Foliar N content increased with increasing SLA. All species showed a decline in midday leaf water potential as the dry season progressed. Dry season midday water potentials were lowest in semi-deciduous species and highest in the deciduous species, with evergreen species exhibiting intermediate values.

Keywords: assimilation, Cochlospermum fraseri, Erythrophleum chlorostachys, Eucalyptus clavigera, Eucalyptus miniata, Eucalyptus tetrodonta, nitrogen, phenology, Planchonia careya, savannas, Terminalia ferdinandiana, transpiration, Xanthostemon paradoxus.

Introduction

Savannas, which consist of an open canopy of trees overlying a closed canopy of grass, are a significant global biome, equal in area to that of tropical forests (Andreae 1991). Savannas occupy approximately 25% of the Australian continent. The high net primary productivity of savannas (Long et al. 1989) coupled with the extensive area that they occupy imply that they contribute significantly to global carbon cycling. Before this contribution can be accurately incorporated into global estimates of carbon budgets, a detailed understanding of the seasonality of savanna photosynthesis is required. Savannas, along with seasonally dry forests, experience a wet–dry climate, with distinct seasonality of rainfall. Although the presence of a grass understory and a low tree leaf area index serve to distinguish savannas from seasonally dry forests, useful comparisons of the ecophysiology of the two systems can be made.

Four phenological guilds are represented in trees and tall shrubs of north Australian savannas (evergreen, brevi-deciduous, semi-deciduous and deciduous), with approximately equal numbers of species in each guild (Williams et al. 1997). The species composition of Australian savannas differs significantly from that of Indian and African savannas, which comprise mainly deciduous species (Chidumayo 1990, Yadava 1990), and of the Llanos savannas of South America, which are dominated by evergreens (Sarmiento et al. 1985). Seasonally dry forests of Costa Rica are dominated by deciduous or semi-deciduous species (Borchert 1994).

In tropical Australian savannas, about 90% of the annual precipitation occurs during November to March inclusive. Seasonal variations in rainfall, soil water content and evaporative demand have significant impacts on stomatal conductance (Eamus and Cole 1997, Prior et al. 1997a, 1997b), predawn leaf water potential (Myers et al. 1997), phenology (Williams et al. 1997) and tree responses to CO_2 enrichment (Goodfellow et al. 1997). However, the impacts of seasonality of water availability and evaporative demand on patterns of gas exchange, the ratio of intercellular CO_2 concentration to ambient CO_2 concentration (C_i:C_a), water-use efficiency (WUE) and nitrogen-use efficiency (NUE) of mature savanna trees differing in phenology remain largely unknown. In the Cerrado (Neotropical savanna), it has been shown that deciduous species have higher assimilation rates than evergreen species in the wet season (Neotropical savanna, Prado and de Moraes

1997). Franco (1998) showed that there were large seasonal changes in assimilation rate between wet and dry seasons for an evergreen species of the Cerrado, but no phenological comparisons were made.

Based on the Cerrado studies, we tested three hypotheses: (1) rates of photosynthesis are larger in the wet season than the dry season; (2) different phenological guilds show different seasonal patterns of change of photosynthesis; and (3) relationships between photosynthetic rate, SLA and foliar N concentration are the same for all phenological guilds.

Materials and methods

Study site and species

The study was conducted at Solar Village (12°37′ S, 131°10′ E), 35 km southeast of Darwin, Australia. Vegetation is open forest (*sensu* Specht 1981) dominated by *Eucalyptus tetrodonta* F. Muell. and *E. miniata* A. Cunn. *ex* Schauer with sub-canopy dominants mostly comprising *Erythrophleum chlorostachys* (F. Muell.) Baillon, *Xanthostemon paradoxus* F. Muell. and *Terminalia ferdinandiana* Excell. Perennial and some annual grasses (*Sorghum*, *Chrysopogon* and *Ericahne* spp.) are present in the understory. Rainfall is about 1600 mm per annum, 90% of which falls between December and March inclusive (wet season). Mean maximum and minimum temperatures are 31.8 and 24.8 °C, respectively, in the wet season and 30.5 and 20.0 °C, respectively, in the dry season. Seasonal variations in microclimate, water relations and phenology have been described by Duff et al. (1997), Myers et al. (1997) and Williams et al. (1997).

Eight species were chosen to represent the dominant (in terms of standing biomass) evergreen, semi-deciduous and deciduous species and to complement the studies of Myers et al. (1997), Prior et al. (1997*a*, 1997*b*) and Williams et al. (1997). Three deciduous species (*Planchonia careya* (F. Muell.) Kunth, *Terminalia ferdinandiana*, and *Cochlospermum fraseri* Planchon), three semi-deciduous species (*Erythrophleum chlorostachys*, *Xanthostemon paradoxus*, and *Eucalyptus clavigera* A. Cunn. *ex* Schauer) and two evergreen species (*Eucalytpus tetrodonta*, and *E. miniata*) were chosen. The eight species represent more than 90% of standing biomass and more than 90% of tree canopy leaf area. The trees were between 4 and 7 m tall. Scaffolding was used to access the upper canopies.

Assimilation and transpiration

Light-saturated assimilation was measured with an LI-6200 portable photosynthesis unit (Li-Cor, Inc., Lincoln, NE). Three fully expanded healthy leaves from the upper canopy of each of seven trees were measured in the morning (between 0900 h and 1200 h) or afternoon (1400 h to 1530 h) under light-saturating conditions (PAR > 1000 μmol m^{-2} s^{-1}) in October (end of dry season), late March (end of wet season), May (early dry season), July (mid-dry season), October (end of dry season), and early February (mid-wet season). Transpiration rate was determined on the same leaves as those used for determination of assimilation rate, with the Li-Cor LI-6200 system. Instanta-

neous transpiration efficiency (ITE) was calculated as the ratio of assimilation rate (*A*) to transpiration rate (*E*).

Midday leaf water potential was measured on the same trees that were used in the assimilation study, with a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). A minimum of three leaves per tree were measured. These leaves were then stored in a sealed plastic bag in the dark overnight for determination of total foliar Kjeldahl nitrogen (TKN) by a micro-Kjeldahl procedure. Samples of 0.2 g were digested in concentrated sulfuric acid and subjected to quantitative flow injection analysis (QuickChem method 13-107-06-2-D; Lachat Instruments, Milwaukee, WI). Nitrogen-use efficiency was calculated as the ratio of assimilation (expressed either on a leaf area or a leaf dry weight basis) to TKN.

The area of fresh leaves was measured with a Delta-T Devices leaf area meter (Cambridge, U.K.). Leaves were then dried at 70 °C to constant weight. Five leaves from each of seven trees of each species were sampled at the same time as leaves were harvested for determination of *A*. Specific leaf area (SLA) was determined in mid-January, from the ratio of leaf area to dry weight.

Statistical analyses

Statistical analyses were performed with Systat software (SYSTAT, Inc., Evanston, IL). Comparisons of means between species and times were made by analysis of variance (ANOVA). Bartlett's test of homogeneity of group variances was performed. The significance of the effects of season and species were assessed and comparisons between pairs of means were made using Tukey's pairwise comparisons. Linear regressions were fitted with either SigmaPlot (Jandel Scientific Software, San Rafael, CA) or Microsoft Excel (Microsoft Corp., Redmond, WA).

Results

Photosynthetic rates (*A*) of the two evergreen species varied between 10 and 16 μmol m^{-2} s^{-1} over the 18-month period (Figure 1). A 10--20% decline in *A* was observed between the maximum values in the wet season and the minimum values in the dry season. In contrast, the semi-deciduous species showed a 25--75% decline in *A* between the peak wet and dry season values (10--12 versus 2--8 μmol m^{-2} s^{-1}). Because deciduous trees were leafless for 3 or 4 months of the year, *A* declined 100% between wet and dry seasons (Figure 1).

In most cases (81% of comparisons), *A* was higher in the morning than in the afternoon (Figures 1 and 2). The three exceptions were *Eucalyptus miniata*, *Erythrophleum chlorostachys* and *Eucalyptus clavigera* in the wet season, when *A* remained unchanged or increased in the afternoon compared with the morning.

The afternoon decline in *A* was generally associated with a decline in C_i:C_a ratio (Figure 2). *Eucalyptus tetrodonta*, *Terminalia ferdinandiana*, *Cochlospermum fraserii* and *Planchonia careya* showed an afternoon decline in *A* and C_i:C_a ratio in both seasons, whereas *Eucalyptus clavigera*, *Erythrophleum chlorostachys* and *Xanthostemon paradoxus* showed an afternoon
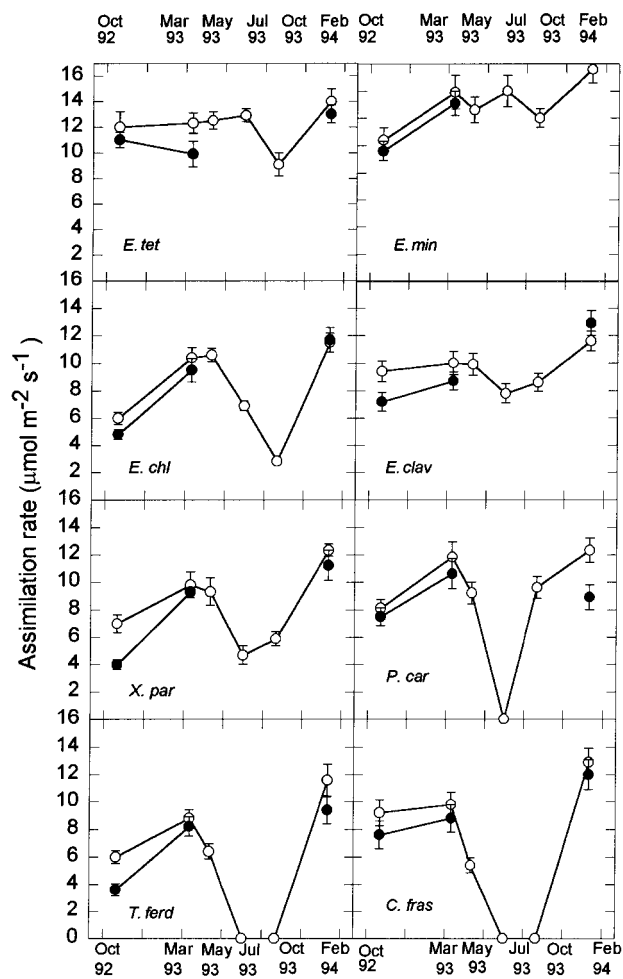
Figure 1. Assimilation rate of eight species of savanna tree measured six times during the year in the morning (○), and three times during the year in the afternoon (●). Cloud cover prevented light saturation being attained during the other three afternoon measurements.

Figure 2. Assimilation rate of eight species of savanna tree as a function of the average C_i:C_a ratio measured during either the morning or afternoon of the wet season (●), or dry season (○).

decline in A and the C_i:C_a ratio only in the dry season (Figure 2). In contrast, *Eucalyptus miniata* showed a decrease in A in the afternoon, but an increase in the C_i:C_a ratio in the dry season (Figure 2). Similarly, but in the wet season, *Xanthostemon* showed an afternoon decrease in A and an increased C_i:C_a ratio (Figure 2).

During the wet season, A in all species was essentially independent of leaf-to-air vapor pressure difference (LAVPD) ($P = 0.77$) (Figure 3a), whereas the C_i:C_a ratio showed a small but significant ($P < 0.01$) increase with increasing LAVPD (Figure 3c). In contrast, in the dry season, there were significant declines in both A and C_i:C_a ratio with increasing LAVPD ($P < 0.001$ for both parameters) (Figures 3b and 3d).

In all species, A increased linearly ($r^2 = 0.4$) with increasing foliar N concentration and with increasing SLA ($r^2 = 0.9$) (Figures 4a and 4c). Consequently, when A was expressed on a leaf dry weight basis, it was higher in the deciduous species than in the evergreen species (Table 1). Foliar N concentration also increased with increasing SLA ($r^2 = 0.3$) (Figure 4b).
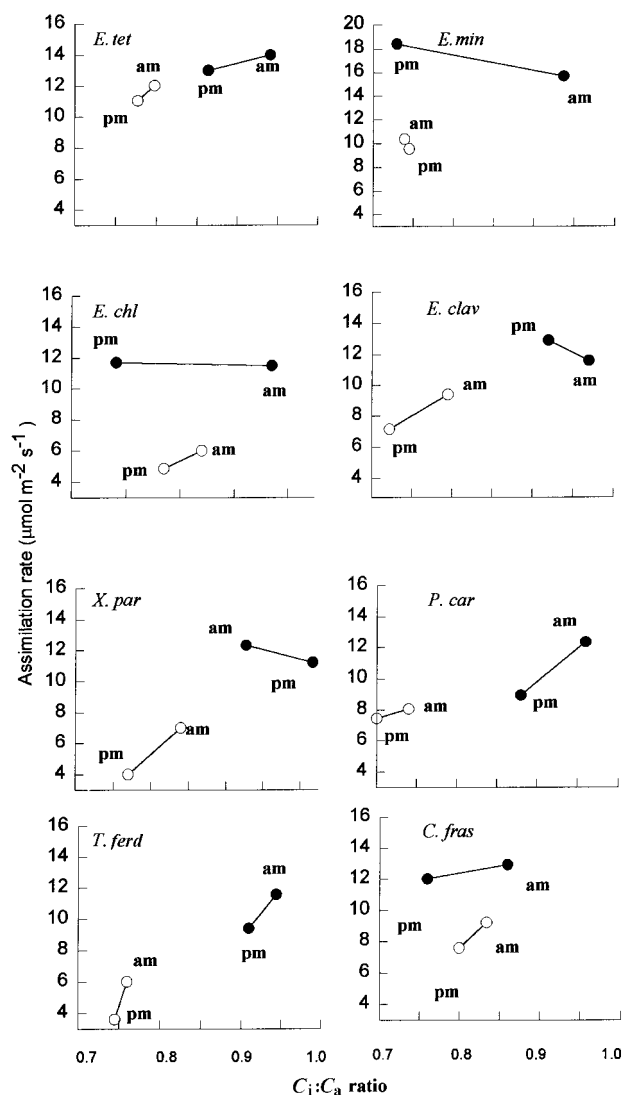
Instantaneous transpiration efficiency (ITE) was at a minimum in the wet season (March) and in October, which in this particular year was after the start of significant rainfall (about 100 mm). In the dry season (May–August), when soil water content was declining, ITE was 50–100% higher than in the wet season (Figure 5). Morning values of ITE were consistently higher than afternoon values ($P < 0.05$) for all eight species examined (data not shown), but there were no clear differences in ITE among evergreen, semi-deciduous and deciduous species.

Nitrogen-use efficiency (NUE) generally declined between wet and dry seasons (Table 1). Evergreen species showed a higher NUE than semi-deciduous species, which exhibited a higher NUE than deciduous species (Table 1).

Midday water potential was highest in the wet season and lowest in the dry season in all species (data not shown). The
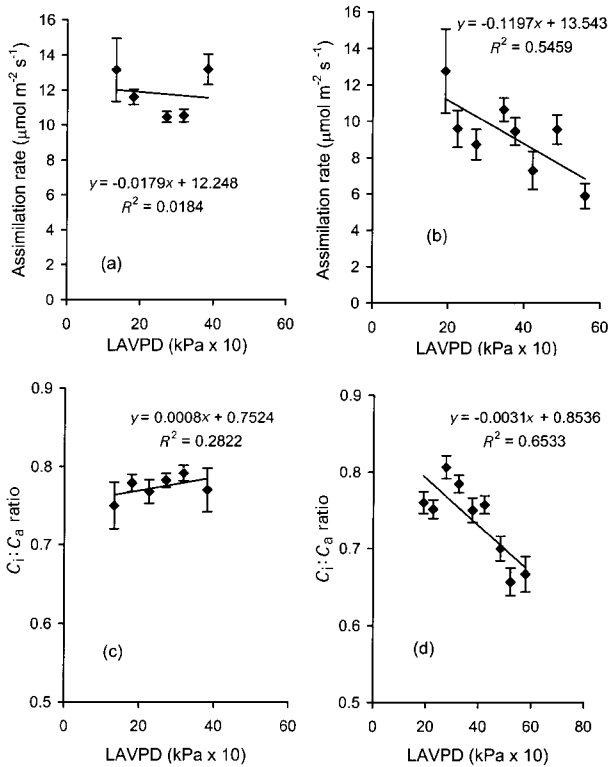
Figure 3. (a) Assimilation rate of eight species of savanna trees as a function of leaf-to-air vapor pressure difference (LAVPD) during the wet season; (b) C_i:C_a ratio as a function of LAVPD during the wet season; (c) assimilation rate of eight species of savanna trees as a function of LAVPD during the dry season; and (d) C_i:C_a ratio as a function LAVPD for eight savanna tree species during the dry season.
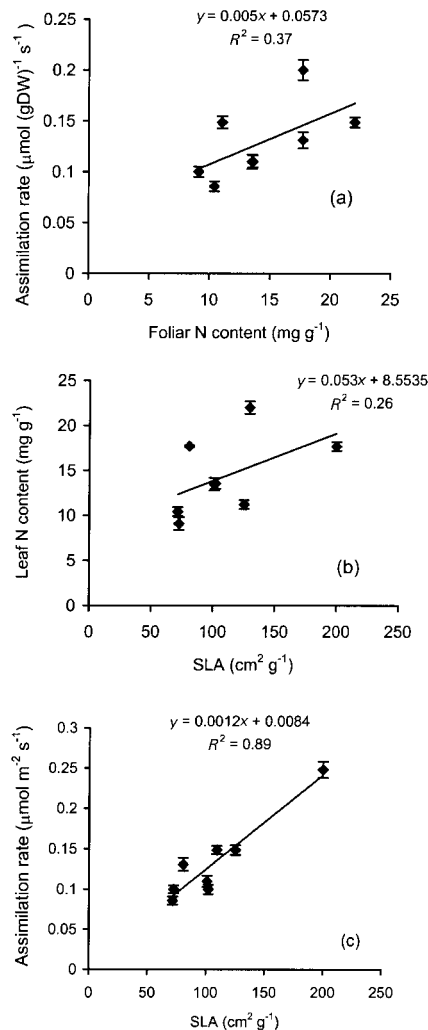

Figure 4. Assimilation rate of eight savanna tree species as a function of (a) foliar N concentration and (c) specific leaf area (SLA); and (b) leaf N concentration as a function of SLA of eight savanna tree species.

lowest water potentials (−3.0 to −4.0 MPa) were found late in the dry season in the semi-deciduous species. The highest water potentials were observed in deciduous species and the evergreen species exhibited intermediate values.

Discussion and conclusions

Phenological comparisons of assimilation rate

On a leaf area basis, deciduous species had lower photosynthetic rates than evergreen species (cf. Medina 1984, Sarmiento et al. 1985, Goldstein et al. 1989, Eamus and Prichard 1998). However, because deciduous species have thinner leaves than evergreen species (i.e., SLA is smaller; Sobrado 1991, Medina and Francisco 1994, Reich et al. 1995, Prado and de Moraes 1997, Eamus and Prichard 1998) and a larger investment in leaf nitrogen (N) (Medina and Francisco 1994, Prado and de Moraes 1997, Eamus and Prichard 1998), when photosynthetic rate was expressed per unit leaf dry weight, deciduous species had higher photosynthetic rates than evergreen species (Table 1) (cf. Prado and de Moraes 1997). Linear relationships among leaf N concentration and A_{max} and SLA were observed (Figure 4) (cf. Evans 1989, Reich et al. 1991, 1994, 1995). Although photosynthetic nitrogen-use efficiency (PNUE) has been observed to increase with SLA

(Poorter and Evans 1998), we found that evergreen species had a smaller SLA and larger PNUE than either semi-deciduous or deciduous species. In a study of PNUE of deciduous and evergreen species in southern Wisconsin, USA, the slope of the relationship between photosynthesis and foliar N content was larger in broad-leaved deciduous species than in needle-leaved evergreen species (Reich et al. 1991), indicating that species with long leaf life spans and low SLA tend to have lower A_{max} per unit leaf N (lower PNUE). The relationship between photosynthesis and foliar N content differed among deciduous, broadleaf and evergreen coniferous species. Reich et al. (1995) explained a similar finding on the basis that conifers were adapted to nutrient-depleted soils whereas deciduous species were adapted to nutrient-rich soils. In the present study, evergreen and deciduous species co-occur and do not occupy locations obviously differing in nutrient availability. Other studies have shown that potential PNUE of deciduous species can be higher (Sobrado 1991) or lower (Medina and Francisco

Table 1. Mean (± SE) values of nitrogen-use efficiency (NUE) and assimilation rate (*A*), expressed on a leaf dry weight basis, for evergreen, semi-deciduous and deciduous species of north Australian savannas. Means within a column followed by a different letter are significantly different ($P < 0.05$).

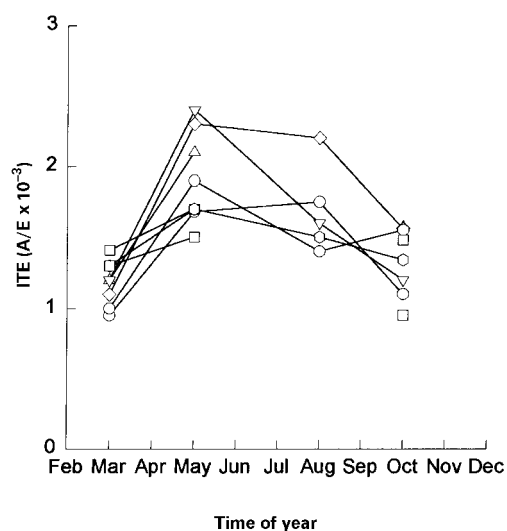|	NUE (μmol CO_2 g_{DW}^{-1} s^{-1} (g N)$^{-1}$)		*A* (μmol CO_2 g_{DW}^{-1} s^{-1})
	Wet season	Dry season	Wet season
Evergreen	21.2 ± 6.4 a	19.0 ± 5.8 a	0.116 a
Semi-deciduous	8.7 ± 1.0 b	4.9 ± 2.0 b	0.128 b
Deciduous	7.3 ± 1.4 b	n/a	0.160 c

Figure 5. Instantaneous transpiration efficiency (ITE; the ratio of assimilation rate to transpiration rate) was calculated four times during the year. Measurements were made during the morning and each point within a single time of measurement represents the mean of all data for one species.

1994) than that of evergreen species. It is probable that local conditions (soil nutrient and water availability; microclimate) are more important determinants of PNUE than phenology.

Seasonal patterns of assimilation

Photosynthetic rates of mature trees of the two evergreen species showed little seasonal variation (10–20%), even though midday foliar water potentials declined to about −2.25 MPa in the dry season. In contrast, Prior et al. (1997*a*) showed that, for *Eucalyptus tetrodonta* saplings growing in the field, A_{max} declined by 50% between wet and dry seasons. This larger decline in A_{max} in saplings than in mature trees was associated with a large decline (to −2.25 MPa) in predawn leaf water potential (and hence presumably an even larger decline in midday water potential). The difference in seasonal response of assimilation and (inferred) midday water potential between saplings (Prior et al. 1997*a*) and mature trees presumably reflects the different rooting depths of saplings and large trees. In a study of three *Acacia* species and a eucalypt species on a mesic site on Melville Island, in the NT of Australia, a small impact of seasonality on assimilation rates of mature trees was observed in the morning (Eamus and Cole 1997),

whereas large effects of seasonality on assimilation rates were measured in the afternoon, when LAVPDs were large and differences in foliar leaf water potentials between wet and dry seasons were maximal.

Two of the three semi-deciduous species (*Erythrophleum chlorostachys, Xanthostemon paradoxus*) exhibited larger declines (about 60–75%) in assimilation rate during the dry season than the two evergreen species. The third species (*Eucalyptus clavigera*) exhibited a 30% decline between wet and dry seasons. However, in all cases, a positive carbon balance was probably maintained throughout the year. In contrast, the three deciduous species showed a 100% loss of photosynthetic activity for at least two months of the year when trees must have exhibited a negative carbon balance because of stem, branch and root respiration in the absence of leaves. Thus, estimates of carbon fluxes to and from savannas should account for both seasonal variation and differences between phenological guilds in patterns of assimilation.

Murphy and Lugo (1995) estimated that rates of primary productivity of dry forests (LAI = 2–4) in central America and the Caribbean range between 6 and 22 Mg ha^{-1} year^{-1}. Martinez-Yrizar (1995) determined that the gross primary productivity (GPP) of dry forests was 3.0 g C m^{-2} day^{-1}. More than 70% of tree canopy leaf area in north Australian savannas is evergreen; therefore canopy assimilation is dominated by the behavior of the evergreen species. If we assume a mean annual canopy assimilation rate of 7.5 μmol m^{-2} s^{-1} for a 4-h day (4 h at above-saturating irradiance) and a mean assimilation rate of 4 μmol m^{-2} s^{-1} for the remainder of an 11-h day, and an LAI of 1.0 (O'Grady et al. 1999), annual GPP is 9.15 Mg ha^{-1} year^{-1}, which is in the range of values cited by Murphy and Lugo (1995) for dry forests. If Australian savannas occupy 25% of the 7.6 million km^2 continent, and mean LAI is 0.75 (an LAI of 1 is representative of the wet end of the rainfall gradient along which savannas exist, but 0.5 is more representative of the arid end, hence an intermediate value of 0.75 is used), total GPP for the savanna is 1.25 Pg year^{-1}, or 3.1 g C m^{-2} day^{-1}, which is close to the estimate of 3.0 g C m^{-2} day^{-1} obtained by Martinez-Yrizar (1995). Despite the existence of a dry season, carbon flux to the canopy was only reduced by approximately 20% in the dry season, because water stored in the top 7 m of soil is sufficient to support high transpiration rates during the dry season and hence high photosynthetic rates (Cook et al. 1998). Furthermore, LAI of the tree canopy of savannas of north Australia varies seasonally by as little as 10% (O'Grady et al. 1999). Thus, the suggestion that

seasonal drought is a principal determinant of growth, productivity and carbon fixation (Murphy and Lugo 1995, Mulkey and Wright 1996) appears not to apply to the savannas of north Australia.

Diurnal patterns of assimilation

Usually, photosynthetic rates were higher in the morning than in the afternoon and the effect was more pronounced in the dry season than in the wet season (cf. Eamus and Cole 1997). Four reasons for this decline are proposed. First, leaf temperature is generally higher in the afternoon than in the morning (Eamus and Cole 1997, Prior et al. 1997*a*) as a result of both reduced transpirational cooling associated with reduced stomatal conductance (Fordyce et al. 1997, Prior et al. 1997*a*, 1997*b*) and warming of the ground throughout the day. This makes leaf temperatures supra-optimal, thereby reducing the photosynthetic rate (Prior et al. 1997*a*). Second, LAVPD is larger in the dry season than in the wet seson (Duff et al. 1997) and larger in the afternoon than in the morning (Duff et al. 1997). Stomata are sensitive to LAVPD (Eamus and Cole 1997, Meinzer et al. 1997, Myers et al. 1997) and thus increased LAVPD in the afternoon and in the dry season reduces stomatal conductance and hence assimilation rate (Eamus and Cole 1997, Myers et al. 1997). Consequently the C_i:C_a ratio generally declined with a decrease in photosynthetic rate between morning and afternoon (Eamus and Cole 1997, Figure 3c) indicating increased stomatal limitation to photosynthesis. Third, large water potential gradients may be generated within leaves when transpiration rates are high and this may cause reduced assimilation rates (Sharkey 1984). Finally, stomata are more sensitive to LAVPD when soil water content is low than when soil water content is high (Thomas and Eamus 1999).

Not all reductions in assimilation rate in the afternoon were associated with a decline in C_i:C_a ratio. Non-stomatal limitations were responsible for the afternoon decline in assimilation rates of *Eucalyptus miniata* in October and *Xanthostemon paradoxus* in February, as indicated by the increase in C_i:C_a ratio with declining assimilation rate (cf. Lauer and Boyer 1992). Kawamitsu et al. (1993) concluded that photosynthesis was influenced by VPD. In soils of northern Australia, where soil hydraulic conductance can be low, the supply of water to the root surface during the afternoon may limit water uptake.

In the mornings during the wet season, photosynthetic rate and the C_i:C_a ratio were essentially independent of LAVPD in all species. In contrast, in the mornings during the dry season, both photosynthetic rate and the C_i:C_a ratio declined with increasing LAVPD, indicating that LAVPD can influence assimilation directly. In agreement with the findings of Myers et al. (1997), there was no relationship between phenology and sensitivity to LAVPD (data not shown).

High transpiration rates may reduce photosynthetic rates (Sharkey 1984). However, in our study, increased transpiration rates were associated with either small increases in assimilation rate (wet season) or large increases in assimilation rate (dry season) followed by a plateau. Therefore, we conclude that, in the dry season, it is not high rates of transpiration that cause assimilation rate to decline, but some other factor associated indirectly with increased LAVPD or covarying with increased LAVPD (such as declining soil water content).

In all species, instantaneous transpiration efficiency (ITE; Eamus 1991) was higher in the dry season (May–September) than in the wet season (March) and after the initial rains (October). Such changes in ITE are expected, because resource-use efficiency increases when resource availability declines (Gulmon and Chu 1981).

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