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Changes in photosynthesis, xanthophyll cycle, and sugar accumulation in two North Australia tropical species differing in leaf angles

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Abstract

Two tropical species of North Australia, *Acacia crassicarpa* and *Eucalyptus pellita*, have similar leaf size and leaf structure but different leaf angles. *A. crassicarpa* with near vertical leaf angle directly reduced photon absorption and leaf temperature (T_l) and had relatively high photosynthetic activity (P_{max}) and low xanthophyll cycle activity. In contrast, *E. pellita* with a small leaf angle exhibited high T_l, low P_{max}, and high activity of xanthophyll cycle which was useful for the dissipation of excessive energy and reduction of photoinhibition. In the dry season, contents of soluble sugars including pinitol, sucrose, fructose, and glucose in *A. crassicarpa* increased whereas larger amounts of only fructose and glucose were accumulated in *E. pellita*. Different sugar accumulation may be involved in osmotic adjustment of leaves during water stress that makes photosynthesis more efficient. The leaf angle may be critical for developing different protective mechanisms in these two tropical tree species that ensure optimal growth in the high irradiance and drought stress environment in North Australia.

Additional key words: *Acacia*; diurnal changes; *Eucalyptus*; leaf angle; leaf morphology; osmoregulation; photoprotection.

Introduction

Plants have developed various strategies to prevent photoinhibitory damage and water deficiency at the molecular, cellular, and whole-plant levels (Ball *et al.* 1988, Chow 1994, Poulson *et al.* 2002, Falster and Westoby 2003). Photoprotection can induce various physiological adjustments including changes in leaf biochemistry, photochemistry, morphology, and anatomy (Quick *et al.* 1992, Marenco *et al.* 2001, Pastenes *et al.* 2005). Changes in leaf morphology and anatomy under high irradiance are usually associated with reducing intercepted radiation by reducing leaf size and/or having near vertical leaf angle. Artificial altering of leaf angle showed that reducing leaf angle (from vertical to horizontal) greatly increased leaf temperature (T_l), pool size of xanthophyll cycle, and reduced photosynthetic activity (Lovelock and Clough 1993, Falster and Westoby 2003, Liu *et al.* 2003). Some plants can alter leaf angle over short time intervals [min] by positioning the leaf blade parallel to the incident radiation thus decreasing the amount of photons reaching the leaf blade (Smith and Ulberg 1989, Griffin *et al.* 2004, Pastenes *et al.* 2005).

Photoprotection principally involves efficient dissipation of excess heat *via* chlorophyll (Chl) fluorescence and non-photochemical quenching and *via* the xanthophyll cycle (Chow 1994, Saccardy *et al.* 1998). High xanthophyll cycle activity is important in protecting the photosynthetic apparatus against photooxidative damage and this may vary between species, growth environment, and leaf position, and also diurnally (Thayer and Björkman 1990, Thiele *et al.* 1998, Havaux and Niyogi 1999). The accumulation of soluble sugars and sugar alcohols is a common metabolic response of plants to water stress which may be caused by abiotic factors such as drought, irradiance, cold, and salinity (Popp and Smirnoff 1995, Rontein *et al.* 2002, Murakeozy *et al.* 2003). Pinitol and sucrose are the major soluble saccharides that accumulate in plants under water stress and high sugar accumulation is probably very important in osmoregulation in plants under stress (Prior 1993, Smirnoff 1998, McManus *et al.* 2000).

In North Australia, the ambient irradiance is 1 700–2 400 μmol m^{-2} s^{-1} throughout the year (Boland *et al.*

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1990). This irradiance greatly exceeds that needed for maximum photosynthesis in tropical plants (Coles *et al.* 1994, Liu *et al.* 2003). The excessive light stress is greatly exacerbated in the dry season, DS (June–November), marked by cloudless sky, drought, and low humidity (20–30 %). The wet season, WS (December–May), which is accompanied by more than 90 % of the total rainfall (1 660 mm), is characterized by high cloud cover and high relative humidity.

Acacia crassicarpa is a tropical lowland tree with near vertical leaf angle (86.4º) which adapts well to various climatic and environmental conditions (Gunn and Midgley 1991). *Eucalyptus pellita* is a medium to tall forest tree with small leaf angle (39.2º) that is restricted to Eastern Australia (Doran and Turnbull 1997). Both species inhabit tropical environment where solar irradiation and temperature are high during the year. We studied changes in photosynthesis, xanthophyll cycle activity, and sugar accumulation in two tropical species differing in natural leaf angle in order to find how these tropical plants respond to high irradiance environment, are protected against photoinhibition, and maintain high productivity.

Materials and methods

Plants: The study was carried out using 3-year-old trees of *Acacia crassicarpa* and *Eucalyptus pellita* in the Howard Springs, 40 km south of Darwin (12ºS, 131ºE), North Australia, during the DS (October, the end of DS which means the lowest soil water content in the year) and WS (May, the end of WS represented by the highest soil water content) seasons. Eighteen leaves from six trees were sampled from each species. The experimental design in the field was a complete random block with 6 replicates. Three leaves were analysed per tree and six trees per species. Whenever possible, only the mid-section of the first fully expanded leaf in young branches was used for measurements and sample selection. Leaf discs of known area (1.77 cm^2) were rapidly removed from the middle part of a leaf, frozen in liquid nitrogen in pre-labelled aluminium bags, and stored at –80 ºC until analysis.

Leaf angle, structure, and leaf water potential: Leaf angle was measured with a hand-held Angle Meter (*PRO Smartlevel*, US patent 308644, Shanghai, China). Transverse sections of leaves were used to determine the size of the palisade, spongy mesophyll, and epidermis layers with the aid of a *Nikon* microscope (*Labophoto*) connected to a video camera (*JVC*, 8.5-mm MACRO) and television screen. Leaf water potential (ψ_l) was determined with a pressure chamber (*Soil Moisture Corporation*, USA). Three leaf samples from each tree were selected, sealed in plastic bags, and measured within 10 min.

Photosynthesis and related parameters: Maximal n et photosynthetic rate (P_{max}), photosynthetic photon flux density (PPFD), T_l, and stomatal conductance (g_s) were determined with a *LI-COR 6200* portable photosynthesis meter (*LI-COR Instrument*s, Lincoln, NE, USA). Measurements were initiated when CO_2 concentration in the 250 cm^3 leaf chamber approached ambient concentration. The flow rate of air through the system was set at 300 mmol s^{-1}. Humidity was regulated by adjusting the air flow through the desiccant tube. All measurements were made between 07:30–18:00 h for diurnals at given time point every 1.5 h or between 10:00–11:00 h for single point determinations. Measurements were done at least 6 times per treatment.

Analysis of xanthophylls and Chl: Three discs (~100 mg total fresh mass) were ground in a mortar and pestle in liquid N_2 and 3 cm^3 of cold 85 % acetone. The extract was placed on ice for 20 min and then centrifuged at 10 000×*g* for 6 min. The supernatant was transferred to a fresh tube and the pellet re-extracted with a small volume (2 cm^3) of 85 % acetone and re-centrifuged. The supernatant fractions were combined and filtered through a 0.45-mm syringe filter. Xanthophylls in the filtrate were subsequently analysed (3 replicates) by high-pressure liquid chromatography (model *3300*, *Varian Vistar* HPLC system; *Spherisorb ODS-1* column, 150.0×4.6 mm) as described by Thayer and Björkman (1990). For Chl measurement, leaf discs were ground in 80 % acetone containing 25 mM HEPES (pH 7.5). Total Chl amounts were determined according to Porra *et al.* (1989).

Extraction and analysis of sugars: Freeze-dried leaf discs (40 mg) were extracted in 5 cm^3 cold solvent (methanol : chloroform : water = 60 : 25 : 15) with a pestle and mortar. The mixture was vortexed and centrifuged at 3 500–4 000 rpm for 15 min. After volume determination, the supernatant was stored in a vial at 4 °C until analysis. Sugars were analysed as their trimethylsilyl imidazole (TMSi) derivatives using gas chromatography (GC) by the methods of Ford (1979). Xylitol (a five-carbon polyol) was used as an internal reference, as it is well separated from other sugars. A mixture of 0.40 cm^3 of the plant extract supernatant and 0.1 cm^3 xylitol solution (1 kg m^{-3}, in 20 % methanol), was dried in a 1-cm^3 vial, and 0.1 cm^3 of the derivatizing reagent (a mixture of TMSi and pyridine, 1 : 2, v/v) was added. The vial was vortexed rapidly for a few seconds to dissolve the sugars and left at room temperature overnight to complete the reaction. Samples (1–2 mm^3) were analysed by GC (*Varian 3300 Star #1*). A *DB-5* glass capillary column (30 m×320 μm i.d.) was used for analysis of sugars and sugar alcohols.

Statistical analysis: All data were analysed as general ANOVA and Tukey test by *Statistica* version *5.0* (*StatSoft*, Tulsa, OK, USA).

Results

Leaf angle and anatomy: Generally, leaves of *A. crassicarpa* had greater leaf angle (86.4º) while *E. pellita* had smaller leaf angle (39.2º) (Table 1). However, these two species had the similar leaf size, thickness, amounts of palisade and spongy mesophyll cells, and cuticle layers. Only a little difference in leaf epidermis layer was found: it was thinner in *A. crassicarpa* than in *E. pellita*.

Table 1. Leaf angle, size, and structure of 3-year-old *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia in the dry season. Means ± S.E. ($n = 30$). Values for epidermis and cuticle layer are the sum of the upper and lower layers.

Parameter	*Acacia crassicarpa*	*Eucalyptus pellita*
Leaf angle [°]	86.40 ± 1.31	39.20 ± 2.62
Leaf size [cm^2]	52.60 ± 2.12	48.40 ± 1.94
Leaf thickness[μm]	388.00 ± 2.97	375.00 ± 4.76
Palisade layer [μm]	178.00 ± 1.37	162.00 ± 2.28
Spongy mesophyll [μm]	181.00 ± 2.05	170.00 ± 4.79
Epidermis layer [μm]	11.20 ± 0.16	25.60 ± 0.37
Cuticle layer [μm]	18.10 ± 0.23	16.90 ± 0.31

Photosynthesis and related parameters *in situ* (Table 2): *A. crassicarpa* had double g_s than *E. pellita*. The incident irradiance on leaves of *A. crassicarpa* was 30 % less than that of *E. pellita*. Evidently leaves of *A. crassicarpa* with near vertical angle intercepted less radiation and had relatively higher P_{max} and g_s, and lower T_l compared to *E. pellita* with small leaf angle. T_l of the two species was higher in DS than in WS. T_l of *E. pellita* was 3 ºC higher than that of *A. crassicarpa* in WS, while the difference was 4.5 ºC in DS. Leaf water potential (ψ_l) decreased significantly and a corresponding decrease in P_{max} was observed in *E. pellita* in DS. However, ψ_l in *A. crassicarpa* did not change significantly between seasons even though P_{max} declined in DS.

Table 2. Photosynthesis and related parameters and xanthophyll contents in leaves of 3-year-old *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia during the dry (DS) and wet (WS) seasons. Determinations were carried at 10:00–11:00. Means ± S.E., $n = 5$.

Parameter	*Acacia crassicarpa*		*Eucalyptus pellita*	
	DS	WS	DS	WS
P_{max} [μmol m^{-2} s^{-1}]	10.50 ± 0.59	20.50 ± 1.09	6.09 ± 0.32	9.97 ± 0.76
Incident PPFD [μmol m^{-2} s^{-1}]	1302 ± 37	1222 ± 35	1868± 33	1770 ± 26
g_s [mol m^{-2} s^{-1}]	0.43 ± 0.02	0.62 ±0.01	0.15 ± 0.01	0.50 ± 0.01
T_l [°C]	34.50 ± 0.25	32.50 ± 0.22	39.00 ± 0.22	35.50 ± 0.32
Leaf water potential, Ψ_l [MPa]	−1.10 ± 0.08	−1.04 ± 0.06	−1.41 ± 0.09	−1.08 ± 0.07
Zeaxanthin [mmol mol^{-1}(Chl)]	9.25 ±0.76	7.80 ± 0.22	136.80 ± 18.50	32.70 ± 11.50
VAZ [mmol mol^{-1}(Chl)]	85.90 ± 3.54	51.10 ± 1.98	201.60 ± 11.30	92.10 ± 8.02

Zeaxanthin (Z) content and VAZ pool in the two species were higher in DS than in WS (Table 2). More than 2-fold Z content was found in DS than in WS in both species. The Z pool in *E. pellita* was more than 10-fold and VAZ pool 2-fold compared to that found in *A. crassicarpa*. Apparently the near vertical leaf angle greatly reduced excessive incident radiation, T_l, and xanthophyll cycle activity in *A. crassicarpa*.

Diurnal changes in photosynthesis and xanthophylls: In general, P_{max} was the greatest in the morning and the lowest at midday, and it recovered to high rate in the afternoon. Midday depression of P_{max} occurred at a relatively high irradiance and T_l. P_{max} was higher in *A. crassicarpa* (Fig. 1*A*) than in *E. pellita* (Fig. 1*B*) especially in the DS. g_s was much lower in DS than in WS in both species (Fig. 1*C,D*). The g_s dropped after 09:00 in both seasons and a dramatic decline was found in *E. pellita* in DS (Fig. 1*D*). In contrast, T_l increased from 09:00 and the increase was higher in DS in both species. The highest T_l (40.1 ºC) was found around 12:00 in *E. pellita* (Fig. 1*F*) when irradiance was the highest (data not shown) and the high T_l over 39 ºC was maintained till 15:00.

The diurnal changes in xanthophylls were dramatically different between the two species. *A. crassicarpa* showed little variation in contents of Z and violaxanthin, and in VAZ pool (Fig. 2*A,C,E*) throughout the day in both DS and WS. In contrast, the Z content in *E. pellita* increased from a barely detectable amount at 07:30 h to a maximum of >160 mmol mol^{-1}(Chl) at midday in the DS (Fig. 2*B*). The diurnal change of Z pool in WS was small. The VAZ content also increased in a similar manner in *E. pellita* in DS (Fig. 2*F*). The violaxanthin amount decreased in both species at midday and rose again in the late afternoon (Fig. 2*C,D*).

Leaf sugar contents: Content of pinitol increased by 20–40 % and contents of total sugars by 20–70 % in DS compared to that in WS in both species, apparently in response to increasing water deficit (Table 3). Total sugar content was comparable in both species but the pinitol content in *A. crassicarpa* was more than double than in *E. pellita.*

Fructose, sucrose, glucose, and *myo*-inositol contents increased in DS in both species. Content of fructose in *A. crassicarpa* was less than half of that in *E. pellita* while the sucrose content in *A. crassicarpa* was about double in both seasons. Glucose and *myo*-inositol contents were similar. Glucose content increased more than 2-fold in *A. crassicarpa* from WS to DS while that in *E. pellita* was only small. Pinitol was the major soluble sugar in *A. crassicarpa* in WS but in DS total soluble sugars, pinitol, fructose, sucrose, and glucose contents increased similarly. In *E. pellita*, fructose was the major sugar (about 50 % of total sugar) and glucose was the second one in both seasons.

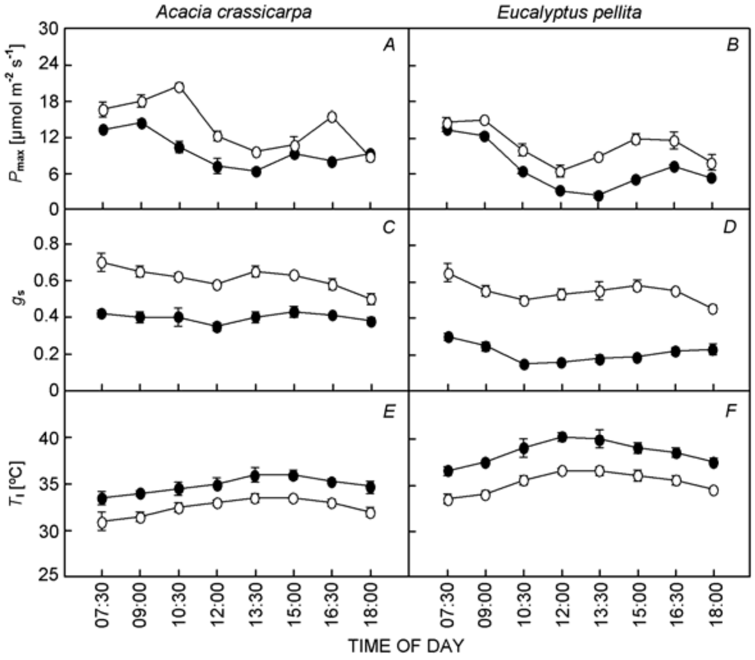

Fig. 1. Diurnal changes of photosynthesis (P_{max}), stomatal conductance (g_s), and leaf temperature (T_l) in 3-year-old trees of *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia during the dry (●) and wet (○) seasons.

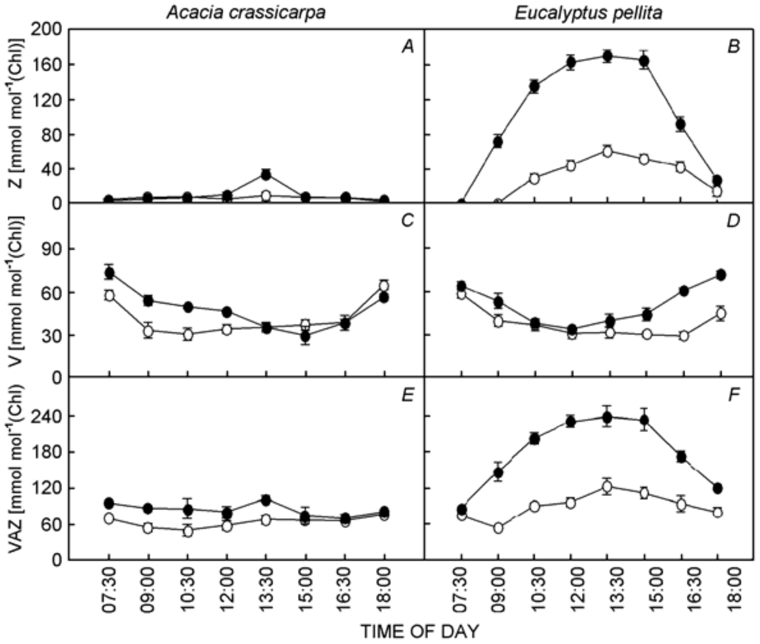

Fig. 2. Diurnal changes of xanthophyll contents (Z – zeaxanthin; V – violaxanthin) and VAZ (V+A, antheraxanthin, +Z) in leaves of 3-year-old *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia during the dry (●) and wet (○) seasons.

Table 3. The contents of pinitol and total sugars in leaves of 3-year-old *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia during the dry (DS) and wet (WS) seasons. Means ± S.E., *n* = 5. Samples were selected in the midday (12:00–13:00 h).

	Acacia crassicarpa		*Eucalyptus pellita*	
	DS	WS	DS	WS
pinitol [g kg^{-1}(DM)]	20.10 ± 0.28	15.90 ± 0.57	9.12 ± 0.63	5.51 ± 0.28
fructose [g kg^{-1}(DM)]	15.20 ± 1.28	4.82 ± 0.85	32.80 ± 1.96	17.60 ± 1.85
sucrose [g kg^{-1}(DM)]	16.70 ± 1.92	4.72 ± 1.01	7.71 ± 0.76	3.22 ± 0.31
glucose [g kg^{-1}(DM)]	18.20 ± 2.01	7.51 ± 1.21	12.50 ± 1.03	10.50 ± 0.73
myo-inositol [g kg^{-1}(DM)]	1.91 ± 0.03	1.12 ± 0.02	2.73 ± 0.05	2.23 ± 0.03
total sugars [g kg^{-1}(DM)]	72.10 ± 2.98	34.10 ± 2.49	64.80 ± 1.74	39.10 ± 1.08

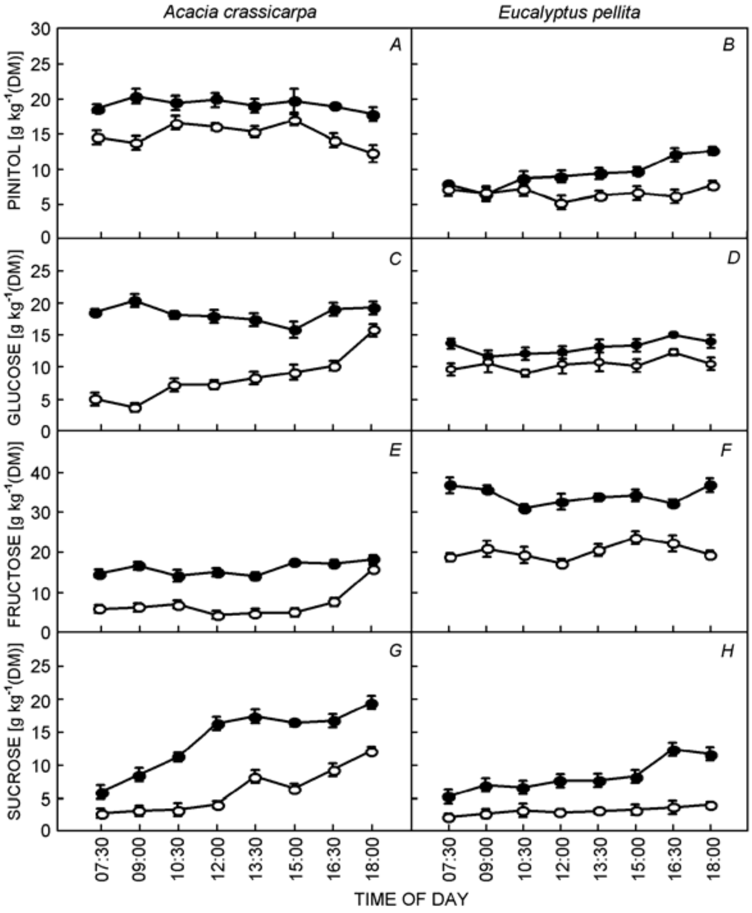

Fig. 3. Diurnal changes of the contents of pinitol, glucose, fructose, and sucrose in leaves of 3-year-old *Acacia crassicarpa* and *Eucalyptus pellita* growing in North Australia during the dry (●) and wet (○) seasons.

There was no dramatic diurnal variation in sugar contents in both species (Fig. 3). Pinitol amount was higher in DS but the content remained relatively constant throughout the day in both species (Fig. 3*A*,*B*). Glucose and fructose contents increased during the day in WS and glucose content increased in both seasons in *A. crassicarpa*. Sucrose amount increased during the day in both species.

Discussion

Interactions between high irradiance and high T_l or between high irradiance and water stress may result in photoinhibition (Ball *et al.* 1988, Marenco *et al.* 2001, Poulson *et al.* 2002, Falster and Westoby 2003, Griffin *et al.* 2004). Plants normally protect their photosynthetic apparatus from long-term photoinhibitory damage by reducing photon absorption and/or by increasing the capacity for energy dissipation *via* increased photosynthesis and xanthophyll cycle (Thiele *et al.* 1998, Havaux and Niyogi 1999). The two tropical species examined showed how these different adaptive strategies might be associated with leaf angle orientation, photosynthetic capacity, xanthophyll cycle, and sugar accumulation.

Reduction in photon absorption could result in carbon and energy savings because of reduced chloroplast repair costs due to photodamage on the D1 protein in photosystem 2 reaction centre (Chow 1994, Massacci *et al.* 1996, Poulson *et al.* 2002) and probably because of a reduced requirement for xanthophyll biosynthesis (Lovelock and Clough 1992, Saccardy *et al.* 1998). Such savings may contribute to higher $P_{\max}$ and total carbon fixed as observed for *A. crassicarpa* in our study. Xanthophyll/Chl ratios in mangroves were sensitive to irradiance under which the leaves developed (Lovelock and Clough 1992). The ratios decreased as irradiance declined over a vertical transect through forest canopy. Our results supported the above conclusions determined for mangroves.

A. crassicarpa has a near vertical leaf angle orientation and, thereby, avoids excessive incident irradiance, provides more effective heat loss, and protects against photoinhibition under excessive irradiance and high water deficit during DS by dissipating excessive energy *via* CO_2 fixation and xanthophyll cycle activity (Table 1). On the other hand, the leaf angle of *E. pellita* is smaller than that of *A. crassicarpa,* and the photosynthetic capacity is considerably less than that of *A. crassicarpa.* However, the eucalyptus has enormous xanthophyll cycle activity, especially the Z level was more than 10-fold and 15-fold that of *A. crassicarpa* in WS and DS, respectively (Table 2). These features could apparently protect the leaves against photoinhibition during the DS. If xanthophyll cycle helps to dissipate excessive photon energy and protects the leaf against photoinhibition, then the lack of such activity in *A. crassicarpa* compared to *E. pellita* would indicate that the near vertical leaf angle of *A. crassicarpa* is an effective morphological trait to reduce high irradiance which in turn prevents leaf from increasing temperature and provides a protective mechanism against photoinhibition. Conversely, the extremely high xanthophyll cycle activity in the eucalyptus is apparently associated with the protection of the photosynthetic apparatus from photodamage during water stress in DS.

$P_{\max}$ activity in *A. crassicarpa* declined from 20.5 μmol m^{-2} s^{-1} in WS to 10.5 μmol m^{-2} s^{-1} in DS. In contrast, the corresponding $P_{\max}$ values in the eucalyptus were 9.97 and 6.09 μmol m^{-2} s^{-1}, respectively, measured during 10:00–11:00. $P_{\max}$ dropped sharply which coincided with a serious decline of g_s especially in DS in the leaves of *E. pellita.* T_l increased after 09:00 in both species and both seasons (Fig. 1*E,F*), while a serious increase happened in DS in *E. pellita* in which it maintained a high value during afternoon. Generally, T_l values over 35 ºC significantly decrease the capacity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Ball *et al.* 1988, Crafts-Brandner and Salvucci 2000, Griffin *et al.* 2004), thereby limiting photosynthesis. The capacity of a plant to acclimate and maintain photosynthesis under high temperature is a critical factor in heat tolerance. We found that higher T_l caused the closure of stomata and reduced $P_{\max}$, which may be the main reason to explain the deep decline of $P_{\max}$ in *E. pellita* in DS. However, the difference in $P_{\max}$ between WS and DS was higher for *A. crassicarpa* but the difference between g_s in WS and DS was larger for *E. pellita*. Hence *E. pellita* is better adapted to drought stress due to an increment of instantaneous water use efficiency in the dry period. Moreover, ψ_l of *A. crassicarpa* did not differ significantly between DS and WS, indicating low drought stress at xylem scale.

Pinitol is the major soluble sugar present in mature leaves of clover when subjected to a significant water deficit and a good candidate for an osmoprotectant in plant leaves. Pinitol is important in osmotic adaptation of many plants including *Acacia* species (Prior 1993, Massacci *et al.* 1996, McManus *et al.* 2000, Streeter *et al.* 2001, Rontein *et al.* 2002, Griffin *et al.* 2004). There was a marked difference of sugar accumulation between acacia and eucalyptus examined in this study. Pinitol content in leaves of *A. crassicarpa* was higher than that in *E. pellita*. The leaf pinitol content in *E. pellita* was low [5.5–9.1 g kg^{-1}(DM)] compared to values of 15.9–20.1 g kg^{-1}(DM) in *A. crassicapa* in WS and DS, respectively (Table 3). Our results also agree with those of Prior (1993) that the sucrose content in water-stressed leaves of two acacia species remained high or even increased compared to control. The accumulation of pinitol and other sugars in all water-stressed tissues (in DS) of the studied tropical trees suggests that these compounds are important in osmoregulation. The difference in sugar accumulation type may relate to the species variation in response to water and saccharide metabolism.

In conclusion, we suggest that high irradiance, drought stress, and leaf morphology significantly alter the photosynthetic activity, xanthophyll cycle activity, and soluble sugar accumulation in leaves of *A. crassicarpa* and *E. pellita*. *A. crassicarpa* with near vertical leaf angle reduced directly photon absorption and T_l, and had high photosynthetic activity and pinitol accumulation. In contrast, *E. pellita* with a small leaf angle exhibited high T_l, low photosynthetic capacity, and high xanthophyll cycle activity which were useful for the dissipation of excessive energy and reduction of photoinhibition. The difference in sugar accumulation in leaves of the two species shows that these compounds are important in osmoregulation. Small leaf angle in *E. pellita* may be the main cause of high irradiance and high T_l that enhances the greater accumulation of xanthophylls and sugars. Our results are coincident with those of our previous studies with artificially changed leaf angle (Liu *et al.* 2003). We suggest that in natural conditions leaf angle may be critical in developing different protective mechanisms to adjust photosynthetic capacities, xanthophyll cycle activity, and sugar accumulation, maintaining optimal growth at high irradiance and drought stresses in North Australia.

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