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Ecophysiology of *Eucalyptus marginata* and *Corymbia calophylla* in decline in an urban parkland

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Abstract

Eucalypt trees are in decline throughout urban landscapes of south western Australia. This study investigated the cause of decline in *Eucalyptus marginata* and *Corymbia calophylla* trees in parkland and compared water and nutrient relations with healthy trees in adjacent bushland in Perth, Western Australia. It was hypothesized that: (i) trees were drought stressed through competition for soil water by the vigorous turf; (ii) excessive uptake of nitrogen, because of fertilizer application to turf, caused toxicity; and/or (iii) micronutrient (Cu, Fe, Mn and/or Zn) deficit was induced by high-pH irrigation water applied to turf around parkland trees. Leaf water potential showed a seasonal variation in the irrigated parkland trees and foliar $\delta^{13}\text{C}$ indicated that parkland trees generally had low water-use efficiency and were not drought stressed relative to bushland trees. Foliar N levels were not significantly different between parkland and bushland trees indicating that excess N uptake was not a factor in the decline. Foliar total Fe, 'metabolically active' Fe, Cu and Zn concentrations were not significantly different between parkland and bushland trees. Foliar manganese concentrations were indicative of deficiency and significantly lower in parkland trees ($5\text{--}14\ \mu\text{g g}^{-1}$) relative to bushland trees ($22\text{--}35\ \mu\text{g g}^{-1}$). It is concluded that application of alkaline irrigation water to the parkland site

reduced the plant-availability of Mn; however, our study of only one parkland site does not allow us to generalize the results across other parklands.

Keywords: alkaline; chlorosis; Dieback; Mundulla Yellows; tree decline; urban bushland

Introduction

Many scattered tree ecosystems are in a 'precarious state' (Manning *et al.* 2006). Urban parkland trees are valued for aesthetic, natural, historical and cultural significance. From an ecological perspective they provide habitat and improve biodiversity and connectivity between bushland reserves (Femández-Juricic 2000; Lumsden & Bennett 2005; Hodgkison *et al.* 2007). Urban parkland trees thus represent keystone structures which offer ecological benefits that are proportionately large relative to their biomass and/or density (Power *et al.* 1996). The decline of remnant, indigenous eucalypts in urban landscapes has received relatively little attention (Czerniakowski *et al.* 2006) despite the need to preserve and manage urban ecosystems (Stenhouse 2004) and the fact that urban ecosystems are one of the few growing habitats in Australia and worldwide (Johnston & Daniels 2006).

Manning *et al.* (2006) pointed out that scattered trees in disturbed landscapes are biological legacies that provide ecological continuity through time. However, trees in urban landscapes are often subjected to adverse conditions, including pollution (air and subsurface), soil compaction, mechanical disturbance, as well as altered water and nutrient regimes (Quigley 2004; Bidwell *et al.* 2006; Delgado *et al.* 2007). In a review of tree health across 11 British cities, over 50% of mortality in street and park trees was attributed to water and nutrient stress (Gilbertson & Bradshaw 1985). Street,

parkland, remnant and edge-trees generally experience high diurnal temperature extremes and low humidity (Whitlow *et al.* 1992; Kjelgren & Clark 1993; Taylor *et al.* 2001; Celestian & Martin 2004) relative to their bushland counterparts (Miller 1980). Such conditions can lead to water stress, decreased leaf internal CO₂ concentrations and subsequently a greater isotopic ratio of ¹³C to ¹²C (δ¹³C) of photosynthate produced (Flexas *et al.* 2006). Water stress has been implicated as a contributing factor to rural tree decline in agricultural landscapes (Landsberg & Wylie 1983; Crombie & Milburn 1988; Close *et al.* 2008) and unfavourable water relations have been reported in manganese-deficient *Abies alba* (Hiltbrunner & Flückiger 1996).

In order to sustain growth during the dry summer months, parks, gardens and other turfed areas are regularly irrigated and fertilized (Miyamoto *et al.* 2005). Where available, irrigation with groundwater has been adopted in southern Australia, because drinking water resources have become increasingly limited. In the Botanic Garden of Kings Park (Perth, Western Australia), a recent shift to an automated irrigation system that delivers 2.5 times more water to turfed areas, relative to the volume of water delivered before installation of the new system, has significantly hastened symptoms of tree decline as perceived by arboricultural management. The decline was characterized by leaf yellowing and interveinal chlorosis, death of branch tips, defoliation and ultimately tree death. Similar symptoms in other eucalypt species growing in disturbed environments throughout southern Australia have been referred to as ‘Mundulla Yellows’ (MY) decline (Czerniakowski *et al.* 2006). Recent research indicated that MY is caused by abiotic factors (Luck *et al.* 2006) such as high soil pH and/or nitrate content (Czerniakowski *et al.* 2006) and is similar to the phenomenon of ‘lime-induced chlorosis’ observed in tree crops grown in calcareous soils in the Mediterranean (Bavaresco *et al.* 1999; Fernández & Ebert 2005). Excessive amounts of N have also been found to induce decline of eucalypts in modified landscapes (Landsberg *et al.* 1990; Granger *et al.* 1994).

In the present study, water and nutrient relations of *Eucalyptus marginata* (Sm.) (jarrah) and *Corymbia calophylla* ((Lindl.) K.D.Hill & L.A.S.Johnson) (marri) were examined in declining parkland trees and compared with those of healthy bushland trees. We hypothesized that (i) parkland trees were drought stressed through competition for soil water by the vigorous turf; (ii) excessive uptake of nitrogen, due to fertilizer application to turf, caused toxicity to parkland trees; and/or (iii) micronutrient deficit (Cu, Fe, Mn and/or Zn) was induced by high-pH irrigation water applied to turf around parkland trees.

Materials and Methods

Species and site characteristics

Eucalyptus marginata (Sm.) (jarrah) and *C. calophylla* ((Lindl.) K.D.Hill & L.A.S.Johnson) (marri) often co-occur and, prior to European settlement, were distributed throughout the south-west of Western Australia where mean annual rainfall averaged between 650 and 1250 mm (Boland *et al.* 1992). The species share a similar latitudinal distribution from 29 to 35°S, commonly occur on lateritic soils and extend between 10 and 200 km inland, where elevations rarely exceed 300 m above sea level.

Perth (31.9°S 115.8°E) has a Mediterranean-type climate of warm dry summers and cool wet winters. Conditions during the experimental period (2003–2006; Fig. 1–Bureau of Meteorology 2006) were close to the long-term averages.

Parklands and streetscapes, including the parkland study site within the botanic garden of Kings Park, have been created as part of the urban development of Perth city where bushland understorey is cleared and turfed with introduced grass species leaving original trees for shade or aesthetic landscape elements. We have observed that within parkland areas, soils have a distinct upper humic horizon of around 20–30 cm depth from the surface, built up through long-term turf management that includes mowing and verti-draining to 150 mm (see next section). Below the humic horizon is a white, silty sand to depth (>1 m) that is mottled yellow in places.

Turf management

Bore water that supplies the irrigation requirements of the botanic garden within Kings Park is characterized by high calcium carbonate levels ($185 \mu\text{g g}^{-1}$) and is alkaline (pH 8.4). At the end of 2003, the irrigation regime changed from manual sprinkler placement to a fully automated system. Under the manual system, turf was irrigated in an irregular pattern, every 2–3 days. Under the automated system, irrigation was set to apply between 70% and 80% of the daily pan evaporation value during the dry summer months. Class A pan evaporation rates averaged 8.2 mm per day in January (Bureau of Meteorology 2006). This equated to approximately double the volume of bore water applied under the manual system. Irrigation was not carried out in winter.

A poly-coated prill fertilizer high in urea and potassium, but excluding phosphorus (NPK, 22:0:18), was applied to the turf from spring (early November) at a rate of $35 \text{ kg nitrogen ha}^{-1}$ every 6–8 weeks. Around mid December, a solution of iron and a separate solution of manganese were applied to the turf at a rate of 32 and 25 kg ha^{-1} , respectively. In January, turf-wear dependent, water soluble nitrogen (Barmac CoRoN Urea Based and Nuturf Nitrosert Triazone liquids) (5 kg N ha^{-1}) and sulfate ($7\text{--}8 \text{ kg S ha}^{-1}$) was applied to the turf between solid prill applications. Application of ammonium

sulfate to the turf at 40 kg ha^{-1} was conducted either during the week before or after a 3-month cycle of verti-mowing (aeration to 150 mm soil depth with a 19 mm solid tyne, flick of 10° , every 6 cm^2) to facilitate recovery of the turf.

Sampling and experimental design

Plant water relations and nutritional status of parkland trees at 'Synergy Parkland' (referred to as Parkland hereafter), within the botanic garden of Kings Park, were compared with healthy bushland trees less than 1 km away (referred to as Bushland hereafter). Close *et al.* (2007) developed a five-level, species-specific ranking system for the assessment of *E. marginata* and *C. calophylla* trees suffering decline in the botanic garden of Kings Park. Using the system of Close *et al.* (2007) we assessed the range of decline severity present in 'Synergy Parkland' and selected five representative (trees that ranged from minor- to severe-decline severity) *E. marginata* and five *C. calophylla* trees at the Parkland site. Five *E. marginata* and five *C. calophylla* trees were selected at the Bushland site. Only two sites were selected given the need to minimize the time taken to move equipment between sites. The sites were approximately 4 ha in area each and delineated by a sharp boundary up to which native vegetation had been historically cleared. The parkland contained approximately 15 trees per ha that were relatively evenly distributed and relatively evenly split between *E. marginata* and *C. calophylla*. The density of trees at the bushland site was typical of native jarrah woodland of western Australia that contains around 593 stems per ha (Koch & Samsa 2007). The number of replicates (five trees of each species at each site) was determined by the length of time each measurement involved, and the need to minimize the effects of diurnal variation. Parkland trees were surrounded by open ground covered with turf while bushland trees were in relatively undisturbed woodland. Bushland trees were within 5 m of a fire-break edge. This was necessary to gain access with a vehicle and cherry picker for *in situ* measurement of gas exchange in each tree crown. Gas exchange and leaf

water potential were measured in November (spring) 2003, May (autumn) 2004, August (winter) 2004 and February (summer) 2005.

Leaf water potential

Leaf water potential was measured using a Scholander pressure chamber (PMS Instruments, Corvallis, OR, USA). Measurements were taken at predawn and midday on the days that gas exchange was measured. Five shoot sections, approximately 10 cm long with two or three leaves were cut from all five individuals of each species at each site. Sampling was always done on the northern side of the crown, where, at midday, leaves would be fully sun exposed.

Leaf gas exchange

Gas exchange was measured on intact leaves using a Li-Cor 6400 portable infra-red gas analyser (LI-COR Inc. Lincoln, NE, USA). Leaves were exposed to a photosynthetic photon flux density (PPFD) of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ at all times and in all seasons. Leaf chamber carbon dioxide (CO_2) concentration was controlled between 360 and 375 $\mu\text{mol mol}^{-1}$ with reference CO_2 concentration maintained at 380 $\mu\text{mol mol}^{-1}$. Vapour pressure and temperature in the chamber were maintained as close as possible to that of ambient air. Measurements were made on the youngest, fully expanded healthy leaves located on the north side of the crown. Five leaves were measured on each tree, and five individual trees were assessed for both species at each site from an elevated work platform (cherry picker). Leaves measured for gas exchange were collected and later measured for leaf area on a back-lit flatbed scanner at a scanning resolution of 0.2 μm with images analysed using WinRhizo

Software (WinRhizo V3.0.3 1995, Regent Instruments, QC, Canada). Instantaneous water-use efficiency (WUE) was calculated as [photosynthesis]/[transpiration].

Isotope composition

Foliage collected from *E. marginata* and *C. calophylla* in summer 2005 and summer 2006 was analysed for carbon ($\delta^{13}\text{C}$) isotope composition. Five branches with healthy leaves free from insect attack were harvested from the north side of each individual, placed in paper bags, then into a drying oven for 4 days at 70°C within 12 h for later analyses. The dry leaf material was ground using a hammer mill then finally a ball mill to <0.6 mm. $\delta^{13}\text{C}$ analysis was performed using continuous flow mass spectrometry (Roboprep + Tracermass Ion Ratio Mass Spectrometer – Europa Scientific, Crewe, UK). $^{13}\text{C}:^{12}\text{C}$ ratios of the CO_2 produced by combustion at 1000°C in an oxygen atmosphere were then compared against those obtained by combustion of a cornflour standard (ANCA 53), calibrated in turn against the international standard NBS-22. Analytical precision was based on multiple replicate analyses for $\delta^{13}\text{C}$ ($\pm 0.2\%$) relative to the PeeDee Belemnite standard.

Foliage mineral composition

The same leaf material collected for isotope composition was sub-sampled for nutrient analyses. Dry leaf material was powdered using a ball mill with canisters and bearings lined with a hard plastic coating to prevent iron contamination of the samples in 2006, but not in 2005. For this reason results from 2006 only are presented. Nitrogen concentration was determined colourimetrically (indophenol blue method) using an Autoanalyser system after digestion with sulphuric acid and hydrogen peroxide (Yuen & Pollard 1954). Another subsample of leaf material was digested with a mixture of nitric and

perchloric acids (McQuaker *et al.* 1979), and then analysed by inductively coupled plasma–atomic emission spectroscopy (ICP-AES – Varian Vista axial spectrometer, Palo Alto, CA, USA) to determine concentrations of phosphorus, potassium, calcium, magnesium, sulfur, boron, copper, iron, manganese and zinc. The measure of total iron included apoplastic iron that is not ‘metabolically active’ according to the ‘iron chlorosis paradox’ (Morales *et al.* 1998; Bavaresco *et al.* 1999; Römheld 2000). Fe is the only plant nutrient that does not necessarily show a correlation between the total concentration in the plant tissue and the degree of deficiency (for a review see Mengel 1994). For this reason foliar active iron concentration was determined using the method outlined by Guzman *et al.* (1986) and analysed by ICP-AES.

Statistical analysis

Individual trees were considered as the units of replication. Homogeneity of variances was assessed using Cochran's test and data transformed (square root or \log_{10}) if group variances were heterogeneous or not normally distributed. The data were analysed using a split-plot design (repeated measures for leaf water potential and gas exchange data) in the statistical software package JMP (SAS Institute). Tree species were analysed separately. Trees were nested within habitat and treated as a random factor, season was treated as a fixed factor. Results were considered significantly different at the $P < 0.05$ level. Tukey *post hoc* tests were employed to analyse for differences between parkland and bushland trees within season and differences were considered significant at the $P < 0.05$ level. Carbon-isotope ratios did not differ significantly between materials sampled in 2005 and 2006 and thus were pooled for analysis.

Results

Water availability of bushland and parkland trees

Predawn leaf water potential (Ψ_{Lpd}) in parkland trees of both species varied little throughout the year (−0.5 to −1.1 MPa) compared with that of trees in the bushland (−0.5 to −1.4 MPa for *C. calophylla* and −0.5 to −2.2 MPa for *E. marginata*, respectively) (Fig. 2a,b). Similarly, midday leaf water potential (Ψ_{Lmd}) in parkland trees was steady between −1.5 and −2 MPa throughout the year (Fig. 2c,d) while that of bushland trees fluctuated seasonally, especially for *E. marginata*, which displayed very negative Ψ_{Lmd} values (below −3.2 MPa) in autumn 2004 (Fig. 2d). The different seasonal patterns in leaf water potential between parkland and bushland trees were reflected in a significant interaction (habitat × season) for both *C. calophylla* ($\Psi_{Lpd}F_{3,24} = 24.532$, $P < 0.0001$: $\Psi_{Lmd}F_{3,24} = 12.030$, $P < 0.0001$) and *E. marginata* ($\Psi_{Lpd}F_{3,24} = 30.595$, $P < 0.0001$: $\Psi_{Lmd}F_{3,24} = 38.823$, $P < 0.0001$). Tukey *post hoc* tests indicated significant differences within seasons in Ψ_{Lpd} (Fig. 2a,b) and Ψ_{Lmd} (Fig. 2c,d) between trees in the parkland and bushland.

Seasonal gas exchange of bushland and parkland trees

Photosynthesis in bushland trees was greatest during spring 2003 and winter 2004 (Fig. 3a,b) when temperatures were cool to mild and the soil profile was sufficiently wet from winter rains (Fig. 1). Bushland trees had relatively low levels of photosynthesis in autumn 2004 and summer 2005 which corresponded to hot, dry conditions. In parkland trees, there was little variation in rates of photosynthesis between spring 2003, autumn 2004 and winter 2004, with maximum rates of photosynthesis recorded in summer 2005.

The seasonal patterns in photosynthesis for parkland and bushland trees were reflected in a significant interaction effect (habitat \times season) for *C. calophylla* ($F_{3,24} = 18.8546$, $P < 0.0001$) and *E. marginata* ($F_{3,24} = 10.4772$, $P = 0.0001$). Tukey *post hoc* tests indicated significant differences within seasons between trees in the parkland and bushland (Fig. 3a,b).

Trends in stomatal conductance (Fig. 3c,d) were similar to those for photosynthesis with significant interaction effects (habitat \times season) for *C. calophylla* ($F_{3,24} = 21.6923$, $P < 0.0001$) and *E. marginata* ($F_{3,24} = 3.6077$, $P = 0.0279$). Tukey *post hoc* tests indicated significant differences within season between *C. calophylla* (Fig. 3c) but not *E. marginata* (Fig. 3d) trees in the parkland and bushland.

There was a significant interaction effect (habitat \times season) on instantaneous WUE in *C. calophylla* ($F_{3,24} = 13.1981$, $P < 0.0001$). There was no significant interaction (habitat \times season) on WUE in *E. marginata* ($F_{3,24} = 2.5224$, $P = 0.0818$) but effects of habitat ($F_{1,24} = 13.6319$, $P = 0.0061$) and season ($F_{3,24} = 26.3975$, $P < 0.0001$) were significant. Tukey *post hoc* tests indicated significant differences within season in WUE between bushland and parkland trees (Fig. 3e,f).

Carbon-isotope discrimination in bushland and parkland trees

Carbon-isotope ratios ($\delta^{13}\text{C}$) were significantly less negative in bushland than in parkland trees for *C. calophylla* (bush = $-27.62\text{‰} \pm 0.257$, park = $-29.14\text{‰} \pm 0.314$; habitat effect $F_{1,18} = 14.040$, $P = 0.0015$) and *E. marginata* (bush = $-27.49\text{‰} \pm 0.220$, park = $-28.84\text{‰} \pm 0.364$; habitat effect $F_{1,18} = 10.091$, $P = 0.0052$).

Nutrition of parkland and bushland trees

Leaf N concentrations were not significantly different between bushland and parkland trees (Table 1). Leaf P and K concentrations were significantly lower in bushland than in parkland trees. There were no significant differences in leaf Na, total Fe, metabolically active Fe, or Cu between parkland and bushland trees. Parkland trees generally had less than 25% the concentration of Mn relative to bushland trees (Table 1). Leaf Zn concentrations were not significantly different between bushland and parkland *C. calophylla* and were significantly greater in parkland than in bushland *E. marginata* (Table 1). Results of nutrient analyses of leaves sampled in 2005 (not shown) were very similar to those presented for material sampled in 2006 for all leaf nutrients, except iron which was probably because of iron contamination during the leaf grinding process in 2005.

Discussion

We found significant differences in leaf water potential, gas exchange, leaf $\delta^{13}\text{C}$ and nutrient concentrations between parkland trees in decline and healthy bushland trees of *E. marginata* and *C. calophylla*. Bushland trees showed seasonal patterns in water relations consistent with rainfall: more negative water potentials and higher instantaneous WUE during the dry autumn 2004 and summer 2005 relative to the wet spring 2003 and winter 2004 seasons (trends similar to those reported by Crombie *et al.* 1988; Crombie 1992). Crombie *et al.* (1988), reported a seasonal range of -0.35 to -2.02 MPa for *E. marginata* and -0.27 to -1.30 MPa for *C. calophylla*. It is possible that our results were compounded by the edge effect (Taylor *et al.* 2001) of bushland trees being within 5 m of an access track. That is lower humidity in summer and higher soil water availability in winter because of run-off. We found pre-dawn water potentials at the low end of the range reported by Crombie *et al.* (1988; -0.5 MPa for both *E. marginata* and *C. calophylla*) during the wet spring 2003 and winter

2004 seasons, but at the upper end (around -2.25 MPa for *E. marginata* and around -1.25 MPa for *C. calophylla*) of the range during the dry autumn 2004 and summer 2005 seasons.

Parkland trees generally had aseasonal water relations, and foliar carbon-isotope ratios indicated lower WUE of parkland than bushland trees. Values of -28.5% to -29.5% were similar to $\delta^{13}\text{C}$ values for phloem sap of irrigated *E. globulus* trees (-28.4%) from the south coast of Western Australia (Pate & Arthur 1998). We conclude that parkland trees were utilizing irrigation water during the summer months and avoiding summer drought stress. This contrasts to studies on the water relations of eucalypts suffering rural tree decline. Landsberg and Wylie (1983) and Crombie and Milburn (1988) reported lower midday water potentials and greater transpiration in declining, relative to healthy eucalypts and concluded that this may in part be due to the generally younger leaves of declining eucalypts that have inherently higher conductance rates than leaves of the primary foliage. We found no trend of greater transpiration in parkland trees and midday water potentials were generally less negative in parkland than in bushland trees during the dry autumn 2004 and summer 2005 seasons. Thus the differences we observed between parkland and bushland trees in leaf water potential and transpiration may have been due to the effects of irrigation, rather than decline per se and our first hypothesis, that water stress in parkland trees may be caused by competition for soil water with vigorous turf, as a factor in parkland tree decline seems unlikely. However, we caution that, because of the logistical restrictions of studying only one parkland and one bushland site, conclusions from the study cannot be generalized across different parkland and bushlands.

Total foliar N concentrations did not differ significantly between habitats and were generally within the reported ranges of 8.0 – 10.2 mg g^{-1} for *C. calophylla* and 6.5 – 10.3 mg g^{-1} for *E. marginata* in Western Australia (Judd *et al.* 1996). This result did not support our second hypothesis (of excessive N uptake and tree toxicity) and parkland trees did not suffer from N toxicity, unlike *E. ovata* and *E.*

camphora within a rural system of south-eastern Australia where the use of N fertilizers led to excessive tree N uptake, toxicity and tree decline (Granger *et al.* 1994).

We found that concentrations of Cu, metabolically active Fe and Zn were not significantly different between parkland and bushland trees. This result did not support our third hypothesis that high alkalinity of irrigation water decreased the availability of soil pH-dependent micronutrients. However, consistent with our third hypothesis, Mn concentrations were significantly lower in parkland relative to bushland trees, with levels well below normal ranges (Judd *et al.* 1996) of 50–70 $\mu\text{g g}^{-1}$ for *C. calophylla* and 30–180 $\mu\text{g g}^{-1}$ for *E. marginata* in Western Australia. A strong cause and effect link between Mn deficiency and parkland tree decline, exemplified by the onset of pervasive chlorosis, is probable. According to empirical observations by arbour staff, parkland tree decline has accelerated since irrigation with alkaline bore water increased in 2003. Mn available to plants in the soil decreases when pH is greater than 6.5 (Lambers *et al.* 1998). Tree decline has been associated with high soil pH and relatively low foliar Mn levels in *Acer rubrum* and *A. saccharum* growing in streetscapes and parklands (Kielbaso & Ottman 1976; Smiley *et al.* 1986) and in *Quercus alba* in an arboretum Messenger (1986). Messenger (1986) reported that declining *Q. alba* trees were exposed to significantly elevated soil pH following downslope run-off containing dissolved CaCO_3 from a recently constructed road and carpark, relative to healthy trees upslope from the constructions. Mn deficiency in *A. saccharum* and *A. rubrum* was corrected by stem injection of MnSO_4 (Kielbaso & Ottman 1976), while soil amendments with buried Mn chelates and soil acidification rectified Mn deficiency in *Q. alba* (Messenger & Nesbit 1998). Further, *E. gomphocephala*, a species indigenous to south west Australia that is adapted to calcareous, coastal, high pH soils (Boland *et al.* 1992), has not shown symptoms of decline in managed turf areas of the botanic garden of Kings Park. Thus we conclude that irrigation with high-pH (8.4) bore water is rendering Mn plant-unavailable in soil solution, probably due to precipitation as oxides and/or carbonates (Epstein & Bloom 2005) and that Mn deficiency may be contributing to the decline of *E. marginata* and *C. calophylla* within the botanic garden of Kings Park. Mn deficiency may be contributing to the significantly lower rates of

photosynthesis of parkland *E. marginata* relative to bushland *E. marginata*, during the wet spring 2003 and winter 2004 seasons, given the link between Mn deficiency and decreased photosynthetic performance (Cregg *et al.* 2004).

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Figure 1. Rainfall and temperature (average of daily maxima) data for the 3 months preceding gas exchange measurements from the Perth 'Mt Lawley' weather station (Australian Bureau of Meteorology at 31.9192S, 1151.8728E, 24.9 m above sea level) approximately 5 km from the experimental sites. Error bars are standard errors of the mean.

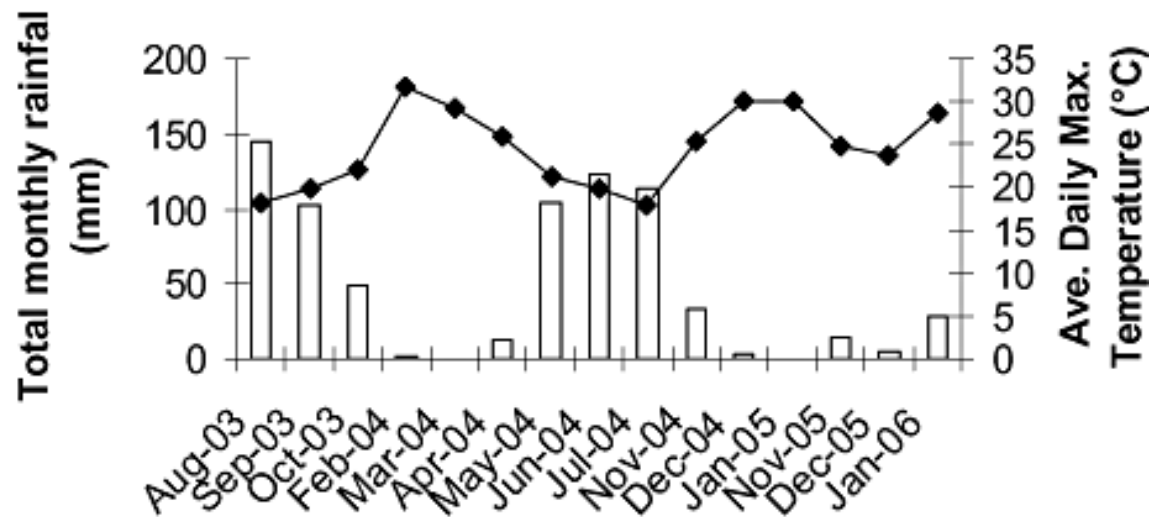


Figure 2. Predawn (a,b) and midday (c,d) leaf water potential (MPa) of *Corymbia calophylla* and *Eucalyptus marginata* in parkland (park) and native bushland (bush). Error bars are standard errors of the mean. Asterisks denote a significant difference using Tukey *post hoc* tests between parkland and bushland trees at $P = 0.05$ level.

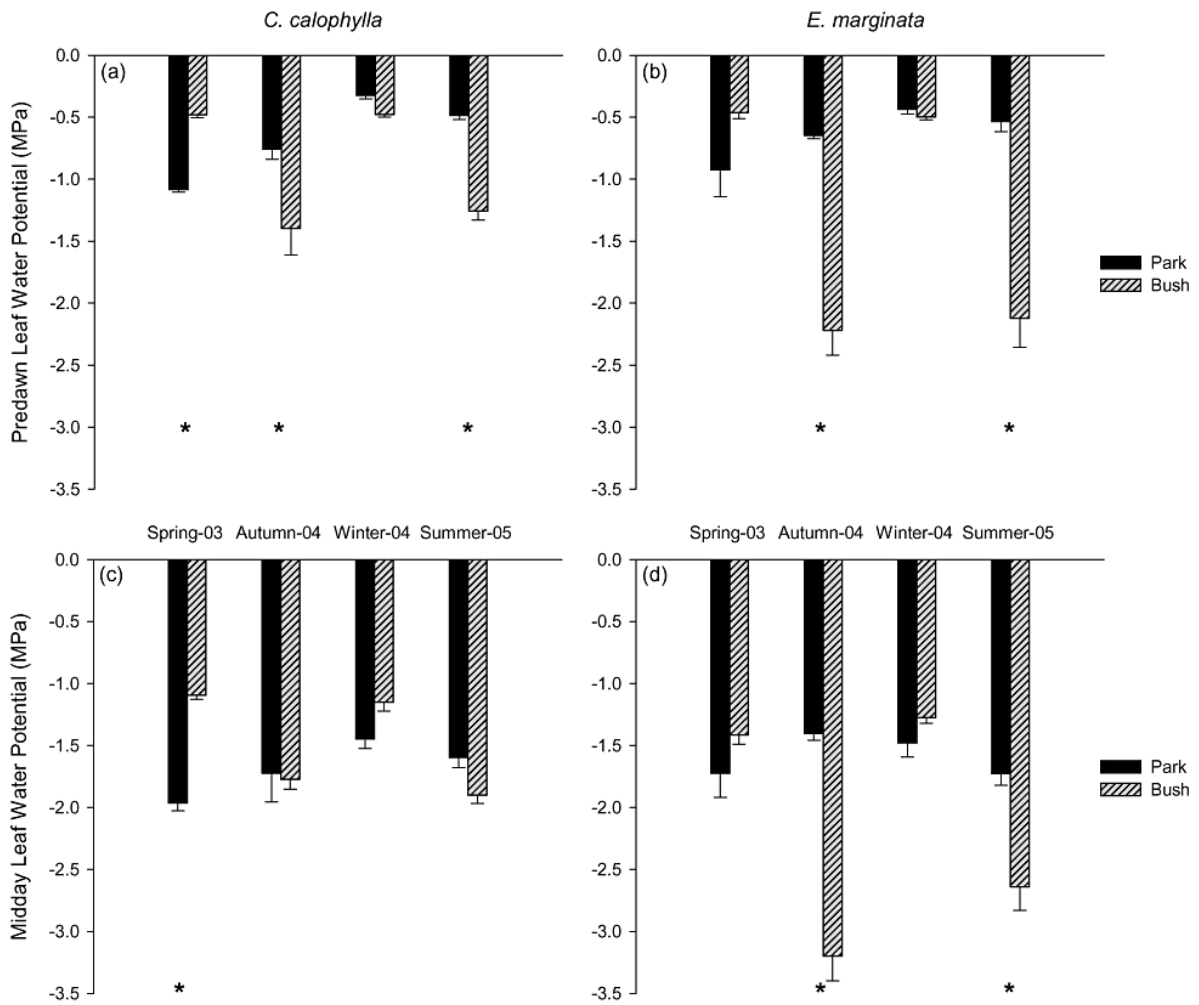


Figure 3. Photosynthesis (a,b), stomatal conductance (c,d) and instantaneous water-use efficiency (e,f) of *Corymbia calophylla* and *Eucalyptus marginata* in parkland (park) and native bushland (bush). Error bars are standard errors of the mean. Asterisks denote a significant difference using Tukey *post hoc* tests between parkland and bushland trees at $P = 0.05$ level.

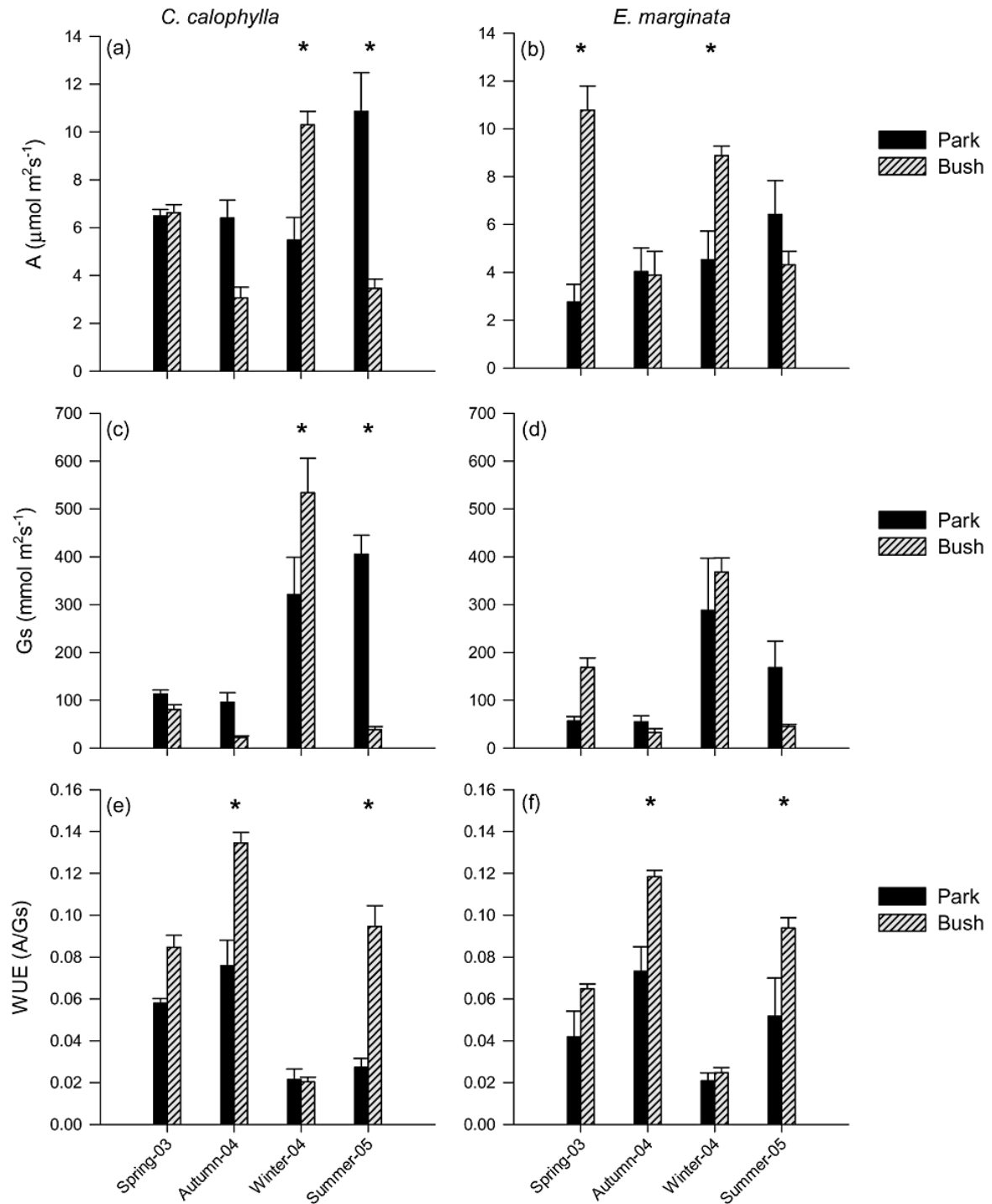


Table 1. Foliar macro- and micro-nutrient concentrations from *Corymbia calophylla* and *Eucalyptus marginata* in parkland and native bushland collected in Summer 2006

Nutrient	<i>E. marginata</i>			<i>C. calophylla</i>		
	Bushland	Parkland	$F_{1,8}$	Bushland	Parkland	$F_{1,8}$
Nitrogen (mg g^{-1})	11.30 \pm 0.66	10.64 \pm 0.34	0.774	15.18 \pm 0.98	13.6 \pm 0.83	1.518
Phosphorus (mg g^{-1})	0.470 \pm 0.020	0.620 \pm 0.049	14.286	0.620 \pm 0.037	0.960 \pm 0.068	19.267
Potassium (mg g^{-1})	4.74 \pm 0.26	6.30 \pm 0.90	2.792	9.32 \pm 0.47	14.32 \pm 0.94	22.527
Sodium (mg g^{-1})	4.84 \pm 0.39	4.00 \pm 0.57	1.484	3.86 \pm 0.13	3.80 \pm 0.93	0.004
Copper ($\mu\text{g g}^{-1}$)	5.62 \pm 0.51	11.68 \pm 3.13	3.644	6.20 \pm 0.88	7.26 \pm 0.76	0.230
Iron ($\mu\text{g g}^{-1}$)	48.80 \pm 1.24	53.60 \pm 7.45	0.404	57.00 \pm 5.42	77.00 \pm 21.05	0.847
Active iron ($\mu\text{g g}^{-1}$)	5.44 \pm 2.79	16.98 \pm 4.17	0.094	18.80 \pm 2.37	34.80 \pm 16.06	0.972
Manganese ($\mu\text{g g}^{-1}$)	21.80 \pm 0.92	13.02 \pm 3.11	7.337	34.20 \pm 6.35	6.62 \pm 0.97	18.431
Zinc ($\mu\text{g g}^{-1}$)	10.62 \pm 1.28	22.00 \pm 3.52	9.220	36.40 \pm 3.74	35.00 \pm 6.04	0.039

Error bars are standard errors of the mean.