

Vulnerability of native savanna trees and exotic *Khaya senegalensis* to seasonal drought

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## Abstract

Seasonally dry ecosystems present a challenge to plants to maintain water relations. While native vegetation in seasonally dry ecosystems have evolved specific adaptations to the long dry season, there are risks to introduced exotic species. African mahogany, *Khaya senegalensis* Desr. (A. Juss.), is an exotic plantation species that has been introduced widely Asia and northern Australia, but it is unknown if it has the physiological or phenotypic plasticity to cope with the strongly seasonal patterns of water availability in the tropical savanna climate of northern Australia. We investigated the gas exchange and water relations traits and adjustments to seasonal drought in *K. senegalensis* and native eucalypts (*Eucalyptus tetradonta* and *Corymbia latifolia*) in a savanna ecosystem in northern Australia. The native eucalypts did not exhibit any signs of drought stress after three months of no rainfall and probably had access to deeper soil moisture late into the dry season. Leaf water potential, stomatal conductance, transpiration and photosynthesis all remained high in the dry season, osmotic adjustment was not observed. Overstorey leaf area index (LAI) was 0.6 in the native eucalypt savanna and did not change between wet and dry seasons. In contrast, the *K. senegalensis* plantation in the wet season was characterized by a high water potential, high stomatal conductance and transpiration and a high LAI of 2.4. In the dry season, *K. senegalensis* experienced mild drought stress with a predawn water potential -0.6 MPa. Overstorey LAI was halved, stomatal conductance and transpiration drastically reduced, while minimum leaf water potentials did not change (-2 MPa) and no osmotic adjustment occurred. *K. senegalensis* exhibited an isohydric behaviour and also had a lower hydraulic vulnerability to cavitation in leaves, with a P50 of -2.3 MPa. The native eucalypts had twice the maximum leaf hydraulic conductance but a much higher P50 of -1.5 MPa. *K. senegalensis* has evolved in a wet-dry tropical climate in west Africa (600 to 800 mm) and appears to be well suited to the seasonal savanna climate of northern Australia. The species exhibited a large phenotypic plasticity through leaf area adjustments and conservative isohydric behaviour in the six months dry season while operating well above its critical hydraulic threshold.

## Introduction

Seasonally dry ecosystems occur in many regions of the world, including Mediterranean or tropical savannas, and the long annual dry season presents a challenge for plants to maintain hydration and turgor. Periods of ample rainfall and soil moisture alternate with long periods of high evaporative demand, lack of rainfall and declining soil moisture. Native vegetation in seasonally dry ecosystems have evolved multiple strategies to adjust to these climate extremes (Eamus and Prior 2001; Goldstein et al. 2008). As such, introducing new or exotic species into these seasonally dry climates can be risky if the drought tolerance strategies of the exotic plants are unknown.

The dominant vegetation of tropical north of Australia is savanna. Tree-grass ecosystems span some 2 million km<sup>2</sup> and stretch from northern Western Australia across to north Queensland and typically occur above 500 to 600 mm annual rainfall (Fox 2001). Over the last decade, the region has been mooted for agricultural and forestry expansion (Ross 2009; Webster et al. 2009). An exotic plantation species that is gaining popularity in northern Australia is African mahogany, *Khaya senegalensis* Desr. (A. Juss.). This species originates from savanna regions in north-west Africa, where it occurs in riverine forests and within the higher rainfall savanna woodlands (Orwa et al. 2009). It has been introduced widely across China, Vietnam, Malaysia, Indonesia and Sri Lanka for forestry plantations and amenity plantings (Arnold et al. 2004). In northern Australia, the success of early experimental plantings of *K. senegalensis* established from the 1960's, to the 1990's highlight that this species has wide suitability to climatic conditions and produces high quality timber from both young and old stands (Armstrong et al. 2007; Nikles et al. 2008). However, detailed physiological studies of this suggested 'suitability' are still lacking. Hence, it is unknown if *K. senegalensis* has the appropriate physiological properties to make it a suitable commercial species for the seasonally dry savanna climate of northern Australia. A key issue is the physiological or phenotypic plasticity to cope with the strongly seasonal patterns of water availability. Most of the annual rainfall in Australian savannas occurs in the wet season between November and April,

whereas the months between May and October represent a dry season with almost no rainfall. Some native species avoid the effects of drought through phenological adjustments like drought deciduousness (Williams et al. 1997), however the bulk of the dominant evergreen *Eucalyptus* and *Corymbia* species employ other adaptations such as deep rooting, low variability in leaf water potentials and effective control of transpiration via stomatal and canopy adjustment (Eamus and Prior 2001; Hutley et al. 2001).

There are inherent uncertainties about survivability when exotic plantations tree species are introduced into an environment with seasonal extremes and soils with low water holding capacity (Cook et al. 1998). Plantations are usually monocultures of a fixed density and sometimes with strategic thinnings applied. As trees grow taller the leaf area index (LAI) may exceed that of the surrounding native vegetation potentially impacting on water resources if plantation size is significant (Polglase and Benyon 2009). It is unclear if an exotic species such as *K. senegalensis* when established in dense monoculture plantations can employ physiological adjustments to lower water potentials (by osmotic or elastic adjustment), impose sufficient stomatal control of transpiration and/or show a phenological plasticity to survive the long dry season. If their physiological or phenological plasticity is limited, this species may be particularly vulnerable to the long dry season, especially if they have high vulnerability to cavitation in their xylem and cannot respond to the drying soil and higher evaporative demand by lower water potentials.

The aim of this study was to investigate the drought adaptation of *K. senegalensis* in comparison to native eucalypt trees in a typical north Australian savanna.

The objectives were to (1) determine gas exchange and water-relations traits of common eucalypt species and *K. senegalensis*, (2) evaluate the adjustment of these water relations traits in response to an annual dry season, and (3) assess the vulnerability to prolonged drought based on the overall water-use and drought adaptation of the species for commercial forestry.

## Material and Methods

### *Site description*

We established a study area where native savanna vegetation was neighboured by a *K. senegalensis* plantation, which allowed us to study water relations of both systems. The study sites were located within the Daly River catchment (-13.04°S, 131.42° E), in the Northern Territory of Australia, about 200 km south of Darwin. The climate in the study region is characterized by a monsoonal climate with constantly high temperatures and strong wet and dry seasons. The mean annual rainfall in the last 30 years in the region was around 1200 mm and the mean annual temperature was approximately 34 °C (Douglas River climate station 014901, ca. 34 km NE from the study sites, Bureau of Meteorology, [www.bom.gov.au](http://www.bom.gov.au)). Around 98% of the annual rainfall falls in the wet season, which typically lasts from October to April. The dry season from May to September receives less than 20 mm of rainfall in small and erratic rainfall events.

The *K. senegalensis* plantation was established with a planting density of 800 stems per hectare in January 2007. The adjacent savanna contains *Eucalyptus tetradonta* F.Muell., *E. miniata* A.Cunn. ex Schauer and *Corymbia latifolia* F.Muell. as the dominant overstorey tree species, of which *E. tetradonta* and *C. latifolia* were sampled. *Corymbia* and *Eucalyptus* are two closely related genera in the family of Myrtaceae and are both commonly called ‘eucalypts’, hence we will refer to the *E. tetradonta* and *C. latifolia* both as eucalypts throughout the manuscript.

We established a paired site design where six replicated individuals of each species were randomly selected within a block in the savanna (*E. tetradonta* and *C. latifolia*) and in the *Khaya* plantation. The paired sites were approximately 100 m apart and both sites were located on the same soil type. Soils of both the plantation and adjacent savanna sites were red kandosol soils (after Isbell 2002), deep sands grading to sandy loams of approximately 5 m depth. Depth to groundwater ranges from 30 to 50 m at this location. Hence, our design was a replication of trees in paired sites, a design that is very common in ecophysiological studies. The trees at both locations were exposed to the same

climatic conditions in regard to irradiance, temperature and rainfall. We cannot exclude any potential differences in some soil parameters; however, the trees grew on the same red kandosol soil type, the soils in the region are generally very uniform in structure and the *Khaya* plantation showed a high degree of uniformity in regard to productivity, height and shape of trees. Hence, any potential differences in the ecophysiological responses of *Khaya* and the eucalypts resulting from minor differences in soil parameters are likely to be small.

We selected six individuals of *K. senegalensis*, *E. tetradonta* and *C. latifolia* for the ecophysiological measurements with measurement campaigns in March (wet season) and September 2013 (late dry season). The native *Eucalyptus* and *Corymbia* trees were 4-6 m tall and of similar height to the *K. senegalensis* individuals. For all trees, leaves for gas exchange and water relations measurements were accessed from branches less than 4 m above ground. For the wet season sampling, the two sites (plantation and savanna) were approximately 100 m apart and we sampled native trees 20-30 m from the savanna edge and *K. senegalensis* trees 3 – 4 rows (12-16 m) from the edge of the plantation. The savanna site that was sampled in March was burned by a low intensity wildfire in June, hence we selected a different paired site for the dry season measurements in September for both the savanna and the plantation sites. The March and September sites were approximately 500 m apart. Wet season measurements were carried out in late March 2012 towards the end of the wet season (running October – April). Heavy overnight rainfall and overcast morning conditions characterized the March measurements. Dry season measurements were carried out in early September 2012. Clear skies with some afternoon cloud cover but no rainfall characterized September weather conditions.

#### *Stomatal conductance and transpiration*

Stomatal conductance ( $g_s$ ) and transpiration ( $E$ ) were measured using a steady state porometer (LI-1600; Li-Cor, Lincoln, NE, USA) as described in (Kahmen et al. 2008). Diurnal measurements were taken on March 26<sup>th</sup> and September 11<sup>th</sup> every two hours throughout the day starting at 8 am

(sunrise 6.55 am in March, 6.45 am in September) and finishing at 5 pm local time (sunset 6.55 pm in March, 6.45 pm in September) in March, and at 6 pm in September resulting in six individual measurement occasions. We measured gas exchange of three fully expanded outer canopy leaves on six individual trees of each species on each measurement occasion. Areas of major degradation or major venation on leaves were avoided. The average daily stomatal conductance and transpiration were calculated by averaging the measurements of each of the six measurement occasions.

### *Leaf water potential*

Maximum leaf water potential was measured at pre-dawn ( $\Psi_{\text{pre}}$ ) and minimum leaf water potential after midday ( $\Psi_{\text{min}}$ ) on the 26<sup>th</sup> March and 10<sup>th</sup> September by measuring one leaf per individual tree from 6 replicate trees per species using a pressure chamber (Model 3000, Soilmoisture Equipment Corp. Santa Barbara, CA, USA). Leaves were cut from branches using secateurs, placed into a sealed bag and measured within 1-2 minutes of collection. The pre-dawn measurements were taken at 6 am and minimum measurements between 1:00 and 2:00 pm local time.

### *Pressure volume curves*

Pressure-volume (pV) curves were constructed from a minimum of 5 individual leaves of each tree species from samples taken early in the mornings of 25<sup>th</sup> March and 9<sup>th</sup> September, between 7:30 and 8:00 am. Compound leaves were collected from *K. senegalensis* and small branches collected from *E. tetradonta* and *C. latifolia*. The ends of these samples were recut under water immediately and placed in water filled buckets to rehydrate during transport back to the laboratory (approximately 1 hr, which was sufficient to rehydrate branches to full turgor). Pressure volume curves were plotted using  $1/\Psi_{\text{leaf}}$  against relative water content (RWC) at regular intervals as the leaves desiccated slowly on the bench (Callister et al. 2006). Leaf water potential was measured as described before using a pressure chamber until the values stopped decreasing or exceeded the safe measurement range of the pressure chamber (-7.0 MPa). The parameters of osmotic potential at full

turgor ( $\pi_{100}$ ), water potential at zero turgor ( $\Psi_{\text{tp}}$ ), relative water content at zero turgor ( $\text{RWC}_{\text{tp}}$ ) and bulk modulus of elasticity ( $\epsilon$ ), were estimated by a pV curve fitting routine based on Schulte and Hinckley (1985) and downloaded from landflux.org.

### *Leaf hydraulics*

Leaf hydraulic conductance was measured using the timed rehydration method (Brodribb and Holbrook 2003) to calculate  $K_{\text{leaf}}$ :

$$K_{\text{leaf}} = C \cdot \ln(\Psi_o/\Psi_f) / t$$

where  $C$  = capacitance,  $\Psi_o$  = leaf water potential before rehydration,  $\Psi_f$  = leaf water potential after rehydration and  $t$  = length of rehydration period. Leaf hydraulic conductance was only measured during the dry season in *E. tetradonta* and *K. senegalensis* using the same trees that were sampled for the pV measurements. Small branches were cut with a tree pruner early in the mornings of 10<sup>th</sup> September, placed in plastic bags and transported back to the lab within one hour. Branches were recut underwater and allowed to rehydrate for a minimum of four hours before being dried on the bench for varying periods of time. Leaf hydration measurements were undertaken over the next three days on adjacent or paired leaves for each  $K_{\text{leaf}}$  measurement using 30 – 40 leaf pairs to construct each vulnerability curve. Maximum  $K_{\text{leaf}}$  for each species was determined by fitting a 3-parameter sigmoidal function to the variation of  $K_{\text{leaf}}$  with initial  $\Psi_o$ . Leaf area was estimated using ImageJ software (National Institutes of Health, Bethesda, MD) on dry leaves. Pre- and post-turgor loss point capacitance was measured from the slope of leaf RWC and water potential (Brodribb and Holbrook 2003) for each species and compared to values obtained using a fast rehydration method (Nardini et al. 2012). The ratio between pre- and post-turgor loss point capacitance varied depending on which method was used. As the ratio affects the decline in hydraulic conductance past turgor loss point, post-turgor loss capacitance was excluded from calculations of hydraulic



conductance. A minimum of three leaves for both *E. tetradonta* and *K. senegalensis* pre- and post-turgor loss point were sampled from the same shoots collected for  $K_{\text{leaf}}$  measurements.

#### *A-c<sub>i</sub> curves*

Two portable photosynthesis systems (Li-6400, LiCor Inc., Lincoln, NE, USA) were used to measure the response of photosynthesis to intercellular CO<sub>2</sub> concentration (*A-c<sub>i</sub>* curve) (Cernusak et al. 2011). The two systems were cross-calibrated, and gave unbiased results. A minimum of 3 leaves per tree were sampled from 4 – 6 individual trees of each species totalling 12 – 18 leaves from each tree species on each of the two measurement occasions. Canopy access was achieved using ladders accessing young, fully mature leaves in all species. The CO<sub>2</sub> concentration ( $\mu\text{mol mol}^{-1}$ ) of the leaf cuvette was altered in the following sequence: 400, 200, 50, 50, 200, 325, 400, 600, 800, and 1200 ppmv CO<sub>2</sub>. A measurement of photosynthesis was logged approximately every two minutes after a step change in CO<sub>2</sub> concentration. Irradiance during the *A-c<sub>i</sub>* curve measurements was set at 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetically active radiation (PAR), supplied by an artificial light source (6400-02B LED, LiCor Inc.). Mean site values for leaf temperature during measurements ranged from 28°C at the end of the wet season (March) to 38°C at the end of the dry season (September). The *A-c<sub>i</sub>* curves were analyzed using the spreadsheet utility (version 2007.1) provided by (Sharkey et al. 2007). The spreadsheet utility fits the photosynthesis model of (Farquhar et al. 1980) to the observed CO<sub>2</sub> response curve. Estimates are generated of the maximum Rubisco carboxylation rate,  $V_{\text{cmax}}$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ); the electron transport rate,  $J$  ( $\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$ ). The spreadsheet utility provides estimates of these parameters normalized to 25°C to facilitate comparisons with measurements made at other leaf temperatures.

#### *Leaf area index*

Leaf area index (LAI) of stands in the savanna and *K. senegalensis* plantation were estimated using hemispherical photos according to (Macfarlane et al. 2007). Stands were photographed on the 26<sup>th</sup>

of March and 11<sup>th</sup> of September. Thirty-six hemispherical pictures were taken in the *K. senegalensis* stand on a randomly allocated grid in an area of 30 x 40 m. The savanna site was measured by taking 11 photographs along 100 m transects at 10 m intervals, with two transects photographed in total (22 pictures).

### *Data analysis*

Statistical analysis was undertaken using Statistica Version 11 (StatSoft, Inc) and the 'R' package (version 3.0.2, R Development Core Team, 2013). Two sample t-tests in Minitab were used for tests of difference in all cases, except pV curve analysis, for which a Tukey HSD post-hoc test was applied after a two-way ANOVA analysis in R. We tested for variation between the seasons and among the species in photosynthetic parameters using analysis of variance. Post hoc tests for pairwise difference between species and seasons were carried out using Tukey's tests. Results were considered significant at  $p \leq 0.05$ .

## **Results**

### *Water relations*

The leaf water potentials indicate that no species was drought stressed in the wet season (Figure 1). The  $\Psi_{pre}$  was around -0.2 MPa in all species, whereas the  $\Psi_{min}$  was around -2 MPa. In the dry season the eucalypts displayed similar  $\Psi_{pre}$  and  $\Psi_{min}$  values, also indicating a lack of drought stress. Conversely, *K. senegalensis* exhibited a significantly lower  $\Psi_{pre}$  of around -0.6 MPa in the dry season, whilst the  $\Psi_{min}$  was similar to the wet season. The pV curve parameters showed little variation between the wet and dry season in all species (Table 1). *K. senegalensis* showed no significant differences in any pV curve parameter between wet and dry season. In the eucalypts, we observed significantly lower  $\pi_{100}$  and  $\Psi_{tp}$  in the wet season. Hence, there were more osmotically

active substances and a lower water potential at zero turgor in the wet season compared to the dry season in both eucalypts. *E. tetradonta* also had a lower  $\epsilon$  at the end of the dry season, indicating more elastic cell walls than the other species. The  $RWC_{\text{tlp}}$  did not change in any species between the wet and dry season measures.

#### *Leaf gas exchange*

*K. senegalensis* had the highest  $g_s$  at  $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$ , which occurred in the wet season (Figure 2). The transpiration of leaves was similar among all species in the wet season. In the dry season however, both eucalypts maintained similarly high values of  $g_s$  and  $E$  whilst *K. senegalensis* showed significant lower rates of  $g_s$  and  $E$ . There were no changes in  $g_s$  or  $A$  between wet and dry season in *E. tetradonta* but both parameters significant decreased for *K. senegalensis* in the dry season. Both eucalypts had much greater  $A$  (around  $15 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) compared to *K. senegalensis*, which had only half of that value in the wet, and a fifth of that value in the dry season. We observed similar trends for  $V_{\text{cmax}}$  and  $J$  where both eucalypts had much greater values compared to *K. senegalensis*. However, there were no significant differences in  $V_{\text{cmax}}$  and  $J$  between wet and dry season measures for any species.

#### *Leaf hydraulic conductivity*

There were significant differences in the leaf hydraulic conductivity between *E. tetradonta* and *K. senegalensis* (Figure 3). *E. tetradonta* had more than double the leaf hydraulic conductivity at full hydration ( $\sim 40 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) compared to *K. senegalensis* ( $\sim 16 \text{ mmol m}^{-2} \text{ s}^{-1}$ ). However, the hydraulic conductivity decreased more rapidly for the eucalypt as water potential declined. As a consequence, the water potential at which 50% of conductivity is lost (P50) was  $-1.5 \text{ MPa}$  in *E. tetradonta* and  $-2.3 \text{ MPa}$  in *K. senegalensis*. This difference was even greater for the water potential at which 88% conductivity of leaves is lost (P88), with *E. tetradonta* at  $-3.0 \text{ MPa}$  compared to  $-4.8 \text{ MPa}$  for *K. senegalensis* (Figure 3).

## LAI

During the wet season, overstory LAI within the *K. senegalensis* plantation reached 2.4 but was reduced by half in the dry season. This dry season LAI in the open-forest savanna canopy was four times lower than Khaya (~0.6, Table 3) but was aseasonal.

## Discussion

*K. senegalensis* is an exotic plantation species originating from the savannas of central west Africa and our data demonstrate that it is well suited to thrive and survive in the savanna regions of northern Australia. There are some physiological differences in the way *K. senegalensis* maintains its water status compared to native savanna trees. The eucalypt trees in this savanna ecosystem showed remarkably little change in all measured ecophysiological parameters to the long dry season. Despite three months without rainfall and high temperatures none of the measured water relations or gas exchange parameters or LAI changed in the eucalypt savanna.

The lack of changes in  $\Psi_{pre}$  clearly indicates that the eucalypts in the savanna were not drought stressed and had access to ample soil moisture at the end of the dry season. There are a number of reported case studies, where the  $\Psi_{pre}$  of *E. tetradonta* did not fall below -0.6 MPa in the dry season (Eamus et al. 2000; Kelley et al. 2007; Myers et al. 1997). Previous studies of savanna water use have described similar aseasonal patterns leaf water relations (Prior and Eamus 1999) and tree transpiration (Hutley et al. 2000; Hutley et al. 2001; Kelley et al. 2007) leading to the conclusion that savanna basal area is presumably regulated over longer timescales to the available rainfall and fire (Beringer et al. 2011). Using water release data of the deep red kandosols soils of the site (Hutley et al. 2011b) the plant available moisture store over the top 2.5 m is ~245 mm, adequate for the 180 to 200 mm tree transpiration that is likely at an annual rainfall of 1100 mm in this savanna (Hutley et al. 2001). As such, adequate levels of soil moisture availability are reflected in the leaf

scale data of this and previous studies. A key question is the ability *K. senegalensis* to maintain function over the annual 6 months dry season.

*K. senegalensis* had three times the leaf area in the wet season compared to the savanna canopy, and this declined significantly to ~1.2 by the late dry season, presumably in response to mild drought stress. The bulk of the native savanna stand water use in the wet season can be attributed to the grassy understorey (Hutley et al. 2000), whereas the water use by native eucalypt trees often does not change between seasons (Hutley et al. 2000; O'Grady et al. 1999). The lack of drought stress in the eucalypts was reflected in the lack of osmotic adjustment or adjustments of turgor loss point. In fact,  $\pi_{100}$  was lower in the wet season compared to the dry season, which indicates that the eucalypt leaves had more osmotically active substances in the wet season compared to the dry season, which explains the small degree of negative osmotic adjustment. The measured  $\pi_{100}$  was similar to the range reported previously (Myers et al. 1997; Prior and Eamus 1999) and it is possible that the trees at the site measured in the dry season simply had a different  $\pi_{100}$  baseline compared to the trees that were measured in the wet season because these were different stands and not the identical trees. Osmotic adjustment has been observed before in *E. tetradonta* (Prior and Eamus 1999), but other reports indicated that adjustment was absent in the dry season (Myers et al. 1997). Hence, like in other studies (Arndt et al. 2008; Merchant et al. 2010) it is possible that osmotic adjustment is only triggered by significant water deficits, which were absent in our study and probably uncommon.

The lack of drought stress also led to a similarly high gas exchange in eucalypts in both seasons. Eucalypts in savannas often show reductions in stomatal conductance and transpiration in the dry season to limit water loss (Duff et al. 1997; Myers et al. 1997; Prior et al. 1997) and this has also been observed in other savanna regions of the world (Bucci et al. 2008; Goldstein et al. 2008). This is triggered by a greater evaporative demand and lower soil water potentials in the dry season.

However, the reductions in gas exchange are also often accompanied by a significant reduction in stand leaf area so that the water-use of individual trees often does not differ between wet and dry

season (Hutley et al. 2001) or is even greater in the dry season (O'Grady et al. 1999). The physiological or phenotypical (e.g. reduced leaf area) plasticity that has been reported before for eucalypt savannas but also Neotropical savannas (Bucci et al. 2003) was not apparent in our study as the deep soil water content in the dry season was sufficient to meet evaporative demand by the tree canopy (see above).

We observed a different drought adaptation in the *K. senegalensis* plantation. In the wet season, the LAI of the *K. senegalensis* stand was four times larger compared to the savanna and this was accompanied by a high  $g_s$  and  $E$ , 30% higher than the savanna species (Figure 2). Hence, *K. senegalensis* trees experienced a mild drought stress in the dry season and responded very conservatively in regard to water loss until the end of the dry season where canopy leaf area adjustment occurred. The trees lost half of the total leaf area and reduced water loss by reducing  $g_s$  to 20% of its wet season value, which significantly reduced  $E$  in the dry season. These adjustments to reduce water loss were not accompanied by osmotic or elastic adjustments; all water relations parameters, including  $\Psi_{\min}$ , remained unchanged between wet and dry season. This response is typical of an isohydric species, where tight stomatal regulation maintains a fairly constant minimum leaf water potential from day to day and under water limiting conditions (Tardieu and Simonneau 1998). The isohydric behaviour contrasts with anisohydric plants, where the minimum water potential decreases with changes in evaporative demand and changes in soil matric potential and stomatal control is less pronounced until a threshold is reached (Larcher 2003). Isohydric species reportedly keep the minimum water potential well above water potentials at which loss of hydraulic conductivity is critical (McDowell et al. 2008). This is true for *K. senegalensis*, where the minimum water potential (-2.0 MPa) was higher than the water potential at which 50% loss of conductivity (P50) occurred in the leaves (-2.3 MPa) and much greater than P88 (-4.8 MPa). The P88 is regarded as a 'point-of-no-return' threshold that has been linked to the minimum recoverable water potential in some angiosperm trees (Barigah et al. 2013; Delzon and Cochard 2014; Urli et al. 2013).

This low risk of cavitation comes at a cost of having a relatively slow hydraulic pathway, as the maximum hydraulic conductance of *K. senegalensis* leaves was approximately half of the value for *E. tetradonta* on a per area basis. Therefore, *E. tetradonta* expressed a much riskier hydraulic behaviour. Their maximum leaf hydraulic conductance of  $39.6 \text{ mmol m}^{-2} \text{ s}^{-1}$  was at the high end of reported values for tree species (Johnson et al. 2011), but the hydraulic pathway was also much more vulnerable as water potential declined because the eucalypt had a much narrower hydraulic safety margin compared to *K. senegalensis* as it operated just above  $\Psi_{\text{tp}}$  (-2.1 to -2.6 MPa).

*K. senegalensis* had a much lower net photosynthesis ( $9 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) compared to the eucalypts, which had almost double the photosynthetic rate. The lower  $A$  was a consequence of a lower maximal Rubisco carboxylation velocity ( $V_{\text{cmax}}$ ) and electron transport rate ( $J$ ) in *K. senegalensis* compared to the eucalypts. The values of  $V_{\text{cmax}}$  and  $J$  of the eucalypts are well within the range reported for savanna eucalypts (Cernusak et al. 2011). However, neither  $V_{\text{cmax}}$  nor  $J$  were impacted in the dry season in *K. senegalensis*, indicating that the significant reductions in  $A$  in the dry season were a consequence of a reduced  $g_s$  rather than damages to the photosystem. It is possible that the low  $A$  is an adaptation to the large seasonal leaf turnover and hence a lower investment into the photosynthetic apparatus of leaves with a short life span. The large reductions in leaf area in *K. senegalensis* are not a consequence of damages to the photosynthetic apparatus or of leaf water potentials that have passed hydraulic thresholds. It is unclear what triggers the reductions in leaf area, but it is an effective way of reducing stand water use in the dry season and keeping soil moisture losses to a minimum.

Savanna eucalypts displayed a range of physiological and phenotypic adjustments in response to drought. They probably have a greater potential of adjustment by closing stomata, adjustment of osmotic and turgor loss points or, at a critical water potential threshold, canopy leaf area adjustment. The variation in ecosystem level gas exchange during the dry season in north Australian savannas is likely regulated via changes in leaf area index in response to increasing aridity rather than by changes to leaf performance (Cernusak et al. 2011; Hutley et al. 2011a). Overall, *K.*

*senegalensis*, showed similar adaptations to seasonal drought than Neotropical savanna trees. Many Neotropical savanna species also show an isohydric behaviour with an homeostasis of  $\Psi_{\min}$ , strong stomatal control of water loss in the dry season and seasonal leaf area adjustments (Bucci et al. 2003; Bucci et al. 2008; Franco et al. 2014; Goldstein et al. 2008). This confirms that isohydric behaviour paired with phenotypic plasticity is a highly successful adaptation to seasonal drought in a wide range of savanna ecosystems.

## **Conclusion**

The native eucalypts in savanna ecosystems in northern Australia are well adapted to the annual water limiting dry season and employ a large range of adjustments that allow a fine balance between carbon gain and water loss in relation to the available soil water. However, the eucalypts in our study were not drought stressed in the dry season and consequently did not adjust any of the measured water relations or photosynthetic parameters. Although *K. senegalensis* is not locally adapted it is nevertheless well suited to the climatic conditions that are occupied by northern Australian savannas. *K. senegalensis* had a lower photosynthesis compared to eucalypts but had a high stomatal conductance and transpiration and a much greater leaf area in the wet season. *K. senegalensis* is an isohydric species with a large potential for phenotypic plasticity by adjusting leaf area on a seasonal basis. It probably has a limited ability to adjust the osmotic potential or turgor loss point of leaves. In an environment that has a relatively predictable wet season with high temperatures, irradiance and evaporative demand, it seems that leaf area adjustments are a favourable drought adaptation for *K. senegalensis* as it allows a maximizing of carbon gain in the wet season. Consequently, *K. senegalensis* trees are well suited to the monsoonal climate of Northern Australia and it has a low vulnerability to the long dry season.

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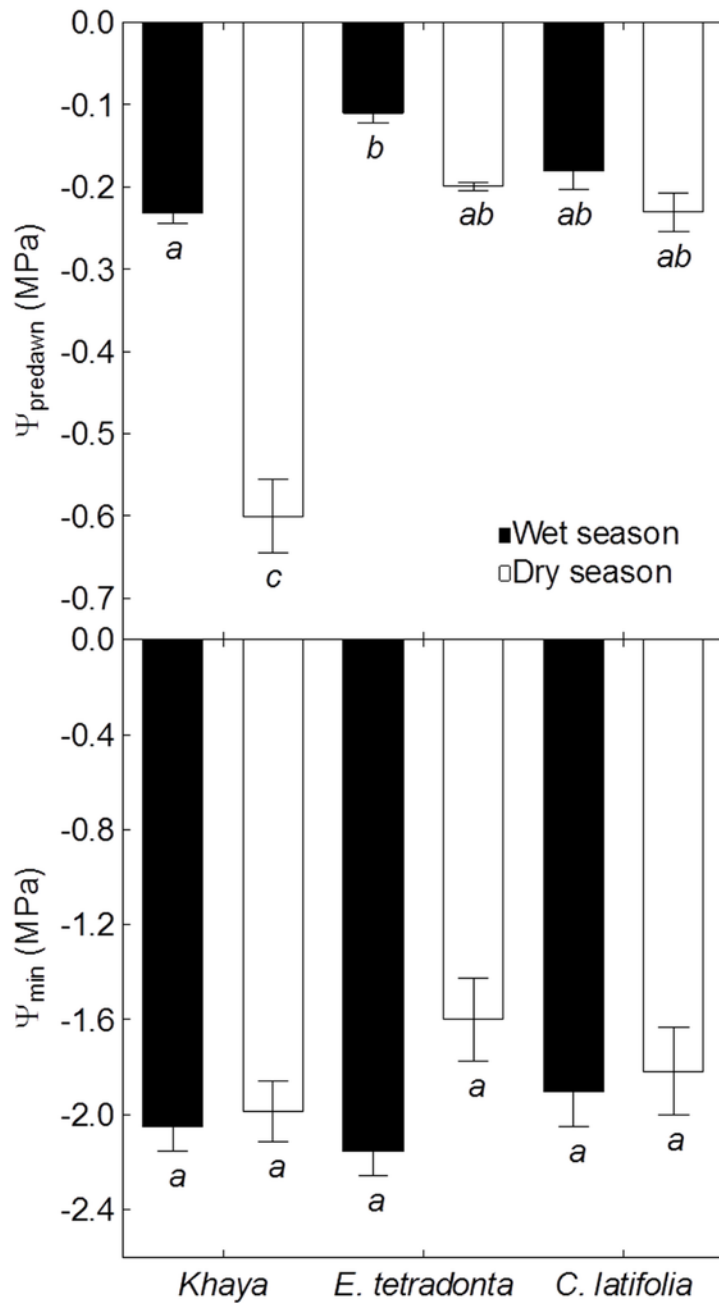
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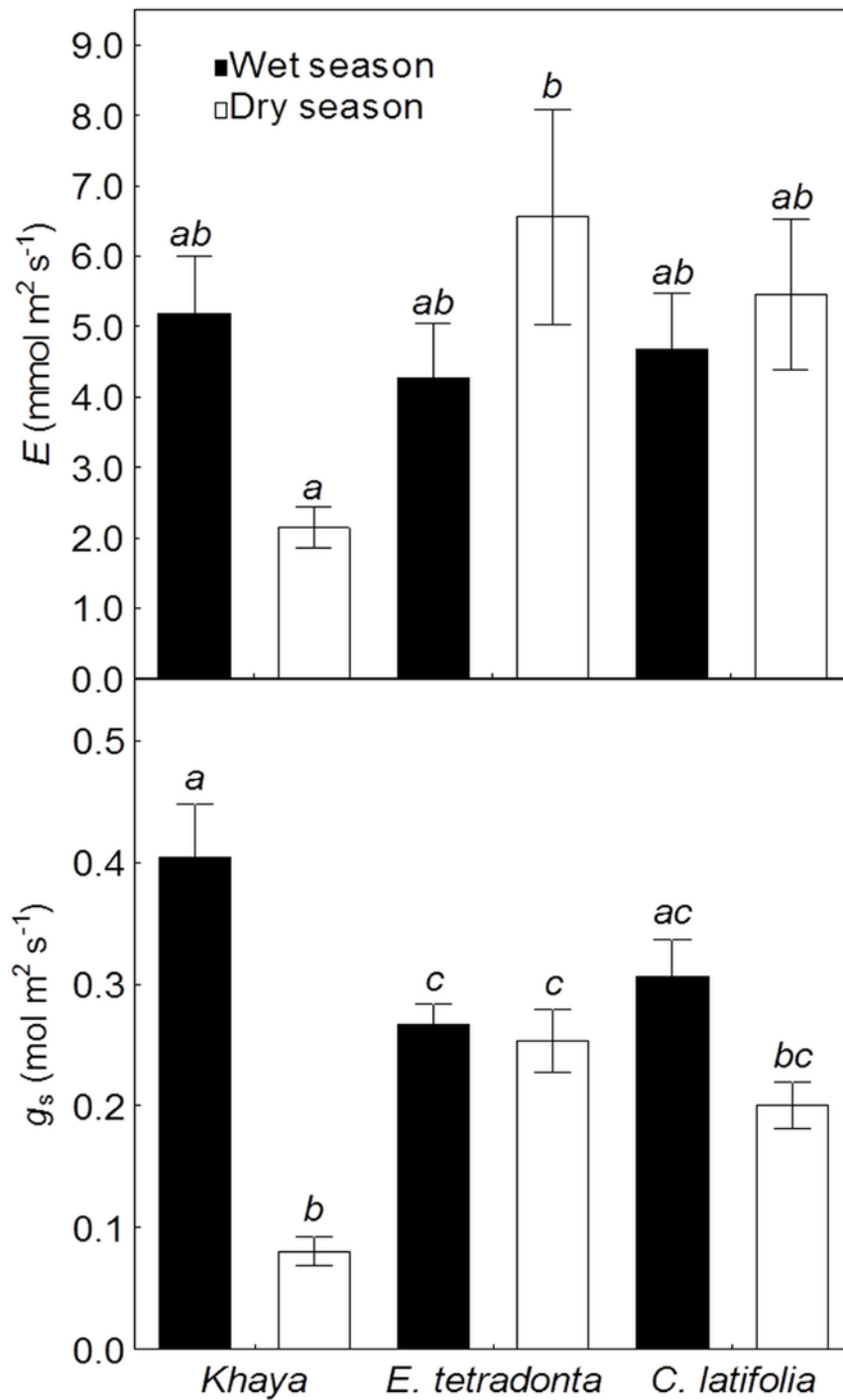
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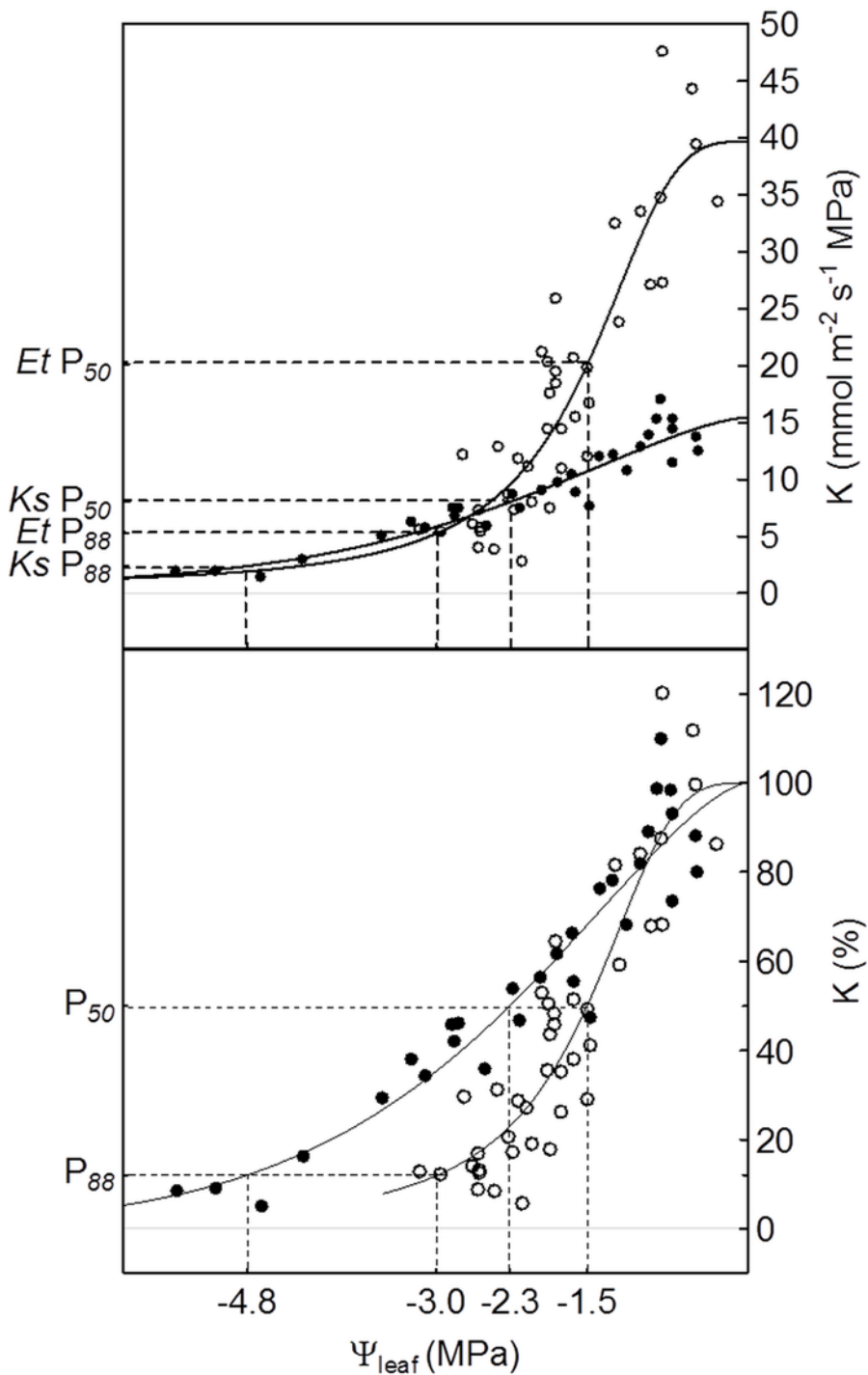
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**Figure 1.** Predawn and minimum water potential of leaves of *Khaya senegalensis*, *Eucalyptus tetradonta* and *Corymbia latifolia* at WhyNot station in the Northern Territory, Australia at the end of the wet season (March, closed bars) and dry season (September, open bars);  $n = 6$ , error bars are SE, letters indicate significant differences ( $p \leq 0.05$ ) between species and season (ANOVA, LSD).



**Figure 2.** Transpiration ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) and stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ) of leaves of *Khaya senegalensis*, *Eucalyptus tetradonta* and *Corymbia latifolia* at the end of the wet season (March, closed bars) and dry season (September, open bars);  $n = 6$ , error bars are SE, letters indicate significant differences ( $p \leq 0.05$ ) between species and season (ANOVA, LSD).



**Figure 3.** a) Leaf hydraulic conductivity ( $K$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ) and b) percent  $K$  across a range of water potentials for *Khaya senegalensis* (Ks, open circles) and *Eucalyptus tetrodonta* (Et, filled circles). The water potential at 50% loss of conductivity ( $P_{50}$ ) or 88% loss of conductivity ( $P_{88}$ ) are indicated for each species on the x-axis of the lower panel. The absolute  $K$ -values for  $P_{50}$  and  $P_{88}$  for each species are indicated on the y-axis of the upper panel.



**Table 1.** Pressure volume curve parameters of *Khaya senegalensis*, *Eucalyptus tetradonta*, and *Corymbia latifolia* leaves in March (wet season) and September (dry season) in northern Australia and the difference between wet and dry season. Presented are osmotic potential at full turgor ( $\pi_{100}$ ), water potential at turgor loss point ( $\Psi_{\text{tlp}}$ ), bulk modulus of elasticity ( $\epsilon$ ) and the relative water content at turgor loss point ( $\text{RWC}_{\text{tlp}}$ ),  $n = 10$ , different letters indicate statistically significant differences between season and species (ANOVA, Tuckey post hoc,  $p \leq 0.05$ ), an asterisk denotes a significant difference between wet and dry season (ANOVA, Tuckey post hoc,  $p \leq 0.05$ ).

Species	Wet season				Dry season				Wet – dry difference			
	$\pi_{100}$	$\Psi_{\text{tlp}}$	$\epsilon$	$\text{RWC}_{\text{tlp}}$	$\pi_{100}$	$\Psi_{\text{tlp}}$	$\epsilon$	$\text{RWC}_{\text{tlp}}$	$\pi_{100}$	$\Psi_{\text{tlp}}$	$\epsilon$	$\text{RWC}_{\text{tlp}}$
<i>K. senegalensis</i>	-2.23 <sup>a</sup>	-2.65 <sup>a</sup>	15.0 <sup>b</sup>	0.84 <sup>b</sup>	-2.18 <sup>a</sup>	-2.77 <sup>a</sup>	11.0 <sup>b</sup>	0.83	-0.04	-0.11	4.0	0.01
<i>E. tetradonta</i>	-2.27 <sup>a</sup>	-2.52 <sup>a</sup>	27.6 <sup>a</sup>	0.89 <sup>a</sup>	-1.85 <sup>b</sup>	-2.13 <sup>b</sup>	16.5 <sup>b</sup>	0.88	0.42 <sup>*</sup>	0.39	11.1 <sup>*</sup>	0.01
<i>C. latifolia</i>	-2.41 <sup>a</sup>	-2.67 <sup>a</sup>	28.9 <sup>a</sup>	0.91 <sup>a</sup>	-2.11 <sup>ab</sup>	-2.35 <sup>b</sup>	26.2 <sup>a</sup>	0.91	0.30 <sup>*</sup>	0.32 <sup>*</sup>	2.7	0.01

**Table 2.** Gas exchange parameters for *Khaya senegalensis*, *Eucalyptus tetradonta*, and *Corymbia latifolia* leaves in March (wet season) and September (dry season) in northern Australia. Stomatal conductance, net photosynthesis and the ratio of the internal to ambient CO<sub>2</sub> mole fractions ( $C_i/C_a$ ) were measured at irradiance of 1600  $\mu\text{mol}$  photosynthetically active radiation (PAR)  $\text{m}^{-2} \text{s}^{-1}$  and  $C_a$  of approximately 380  $\mu\text{molm}^{-2} \text{s}^{-1}$ . The maximal Rubisco carboxylation velocity ( $V_{\text{cmax}}$ ) and electron transport rate ( $J$ ) were determined at irradiance of 1600  $\mu\text{mol}$  PAR  $\text{m}^{-2} \text{s}^{-1}$  from CO<sub>2</sub> response curves. Values shown are the mean of 12 to 18 leaves for each species in each season; standard errors are shown in parenthesis. Values within a column not followed by a common letter differed from each other at  $p \leq 0.05$ .

Season	Species	Net Photosynthesis ( $\mu\text{molm}^{-2} \text{s}^{-1}$ )	Stomatal conductance ( $\text{mmolm}^{-2} \text{s}^{-1}$ )	$C_i/C_a$	$V_{\text{cmax}}$ at		Temperature leaf °C
					25°C ( $\mu\text{molm}^{-2} \text{s}^{-1}$ )	$J$ at 25°C ( $\mu\text{molm}^{-2} \text{s}^{-1}$ )	
Wet	<i>Khaya senegalensis</i>	8.8 (0.9) b	0.210 (0.030) b	0.75 (0.02) a	34.4 (4.7) b	44.9 (2.6) b	31.5 (0.3) b
Dry	<i>Khaya senegalensis</i>	3.9 (0.3) c	0.041 (0.003) c	0.55 (0.01) b	43.7 (5.3) b	44.8 (3.1) b	34.4 (0.3) c
Wet	<i>Eucalyptus tetradonta</i>	15.3 (0.7) a	0.329 (0.025) a	0.75 (0.01) a	67.6 (3.4) a	87.9 (5.1) a	29.7 (0.3) a
Dry	<i>Eucalyptus tetradonta</i>	14.9 (1.0) a	0.326 (0.046) a	0.72 (0.02) a	68.8 (4.1) a	84.0 (3.5) a	33.7 (0.3) c
Dry	<i>Corymbia latifolia</i>	15.3 (1.2) a	0.367 (0.052) a	0.73 (0.02) a	73.7 (5.4) a	83.6 (6.8) a	33.3 (0.4) c

**Table 3.** Leaf area index (LAI) of a *Khaya senegalensis* plantation and neighbouring native savanna in the wet season (March) and dry season (September) in northern Australia. Values within a column not followed by a common letter differed from each other at  $p \leq 0.05$ .

<b>Vegetation type</b>	<b>Season</b>	<b>LAI</b>	<b>s.e.</b>	<b>n</b>
<i>K. senegalensis</i>	wet	2.4 a	0.05	36
<i>K. senegalensis</i>	dry	1.2 b	0.03	35
<b>Savanna</b>	wet	0.7 c	0.02	22
<b>Savanna</b>	dry	0.6 c	0.02	22