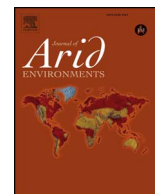




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Contrasting ecophysiology of two widespread arid zone tree species with differing access to water resources

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ABSTRACT

Arid environments can support the seemingly unlikely coexistence of species tolerant of, or sensitive to, dry soil moisture. Here, we examine water-use and carbon-gain traits in two widespread tree species in central Australia: *Acacia aptaneura* and *Eucalyptus camaldulensis*. The former has a shallow root distribution and relies on soil moisture, while the latter is groundwater dependent. We hypothesised that *A. aptaneura* would exhibit a suite of characteristics that confer tolerance to low soil moisture, in contrast to *E. camaldulensis*. Consistent with our hypotheses *A. aptaneura* was relatively more anisohydric than *E. camaldulensis* (seasonal leaf water potential of -7.2 to -0.8 MPa *cf.* -1.4 to -0.3 MPa). Additionally, compared to *E. camaldulensis*, *A. aptaneura* had lower water potential at turgor loss (-2.5 *cf.* -1.1 MPa); a larger Huber value; smaller, narrower and thicker phylloides/leaves; and larger photosynthetic capacity (J_{max}); and larger water-use efficiency. Further, water-use efficiency for *E. camaldulensis* was similar to species receiving annual rainfall of 1500 mm, despite annual rainfall of 348 mm. We conclude that mean annual rainfall is the dominant determinant of water and carbon relations for *A. aptaneura*, but not *E. camaldulensis*. This has important implications for ecosystem-scale transpiration and primary productivity across this arid zone.

1. Introduction

Water is a fundamental resource for plants. Consequently, water availability is a key factor limiting terrestrial plant production globally, particularly in arid and semi-arid regions. In these regions many ecosystems are dependent upon groundwater, which is also important in sustaining human settlements and agriculture (Eamus et al., 2006). Sustainable management of groundwater for these competing interests is challenging, particularly when little is known about the functioning of groundwater-dependent ecosystems. In Australia, arid and semi-arid regions occupy 70% of the continent (Eamus et al., 2006). These dryland ecosystems are often assumed to be of low productivity because they have very little water to sustain photosynthesis, and therefore growth, for prolonged periods. However, the productivity of semi-arid regions can be a dominant contributor to global terrestrial carbon strength. For example, during 2011 there was a global land carbon sink anomaly due to exceptionally large primary productivity in the semi-arid regions of the Southern Hemisphere (Poulter et al., 2014). The

majority of this anomaly (60%) was attributed to exceptional productivity in the semi-arid vegetation of Australia during a period of extreme precipitation (Poulter et al., 2014). Understanding the functional controls on plant water-use and carbon uptake in semi-arid Australia is therefore of importance for local, sustainable management of groundwater and for regional, continental and global terrestrial carbon budgets.

A dominant vegetation type in semi-arid Australia is the Mulga woodlands and shrublands which occupy 20% of continental Australia (Maslin and Reid, 2012). These woodlands and shrublands are dominated by the Mulga complex of 12 closely related *Acacia* species, including *Acacia aneura* F.Muell. ex Benth and *Acacia aptaneura* Maslin & J.E.Reid, which together are the most widely distributed and studied species of Mulga (<http://www.ala.org.au>; Fig. 1a; Eamus et al., 2016). Species from the *Acacia* genus are known to form a symbiosis with nitrogen-fixing bacteria (Schulze et al., 2014). A second important vegetation type is the River Red Gum forests, which are almost exclusively dominated by *Eucalyptus camaldulensis* Dehnh. These forests are largely

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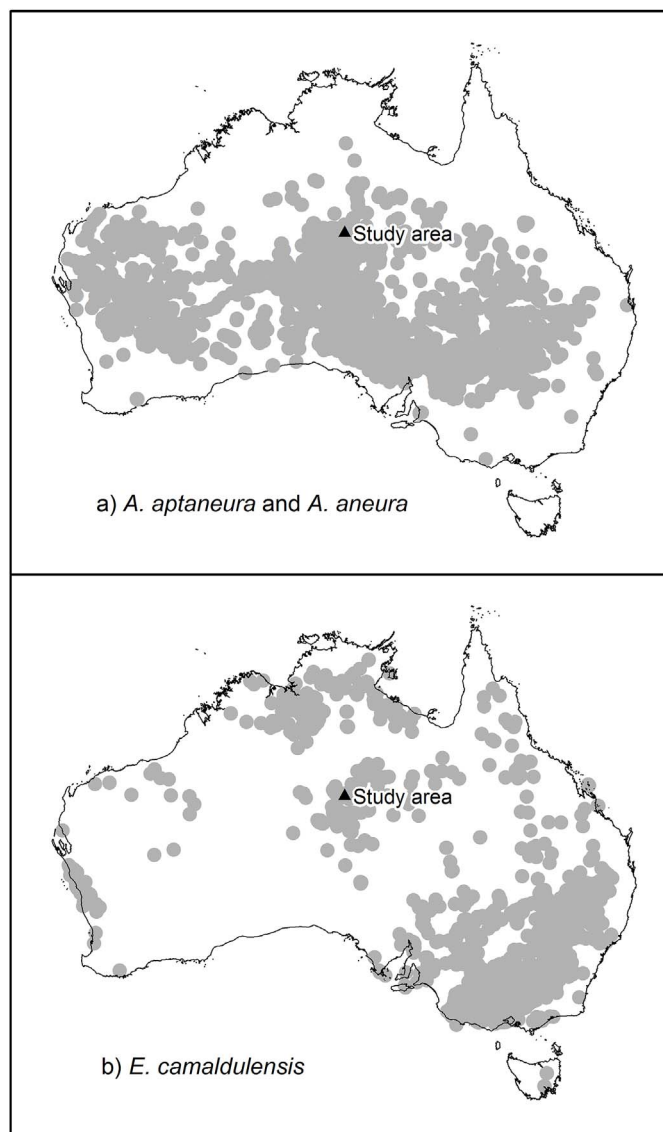


Fig. 1. Distribution records for (a) *A. aptaneura* and *A. aneura* and (b) *E. camaldulensis*, each point represents one or more observation of the species. Both *A. aptaneura* and *A. aneura* records are presented as they were classified as the same species until 2012, and they are both part of the Mulga complex of species (Maslin and Reid, 2012). Records are from the Atlas of Living Australia (<http://www.ala.org.au>). Also shown is the location of the study area.

restricted to narrow riparian corridors (Fig. 1b). However, *E. camaldulensis* is more widely distributed across the continent than *A. aneura* or *A. aptaneura* (Fig. 1) and is the most widely distributed of all *Eucalyptus* species. The distribution of *E. camaldulensis* within riparian zones may allow year-round access to groundwater in addition to soil moisture (O'Grady et al., 2009). In contrast, Mulga species are located away from riparian zones, have a shallow root distribution (< 5 m), with most roots occurring close to the surface (< 30 cm) (Cleverly et al., 2016a). Consequently, Mulga trees experience large seasonal fluctuations in access to moisture because of the pronounced seasonality of rainfall in central Australia.

Given differing access to water between *A. aptaneura* and *E. camaldulensis*, these species are likely to have water and carbon relations that differ in multiple ways, despite experiencing the same rainfall, solar radiation, temperature and vapour pressure deficit. Indeed, a recent study of seven co-occurring species within the Ti-Tree basin in central Australia demonstrated that, compared to *E. camaldulensis*, *A. aneura* had significantly larger xylem vessel wall thickness and stem

density and significantly smaller xylem conductive area (Santini et al., 2016). This is consistent with the theory of ecohydrological niche separation, which proposes that differing access to water between species is a fundamental process underlying species co-existence within a single biome (Araya et al., 2011; Peñuelas et al., 2011). A key mechanism underlying ecohydrological niche separation is the regulation of water loss by stomata. At one extreme, species which regulate stomatal conductance (g_s) to maintain a more constant (and relatively high) minimum leaf water potential (Ψ_{leaf}) are classified as isohydric (Tardieu and Simonneau, 1998). Species displaying little regulation of g_s can experience large fluctuations in minimum Ψ_{leaf} and are classified as extremely anisohydric. Isohydric species tend to occur in mesic areas where they can avoid drought-induced hydraulic failure and are often classified as drought avoiders, in contrast to anisohydric species which are relatively drought-tolerant (McDowell et al., 2008). The precise definition of iso/anisohydric remains problematic with contrasting definitions discussed by Martínez-Vilalta and García-Forner (2016). Furthermore, tight regulation of Ψ_{leaf} may not always be associated with tight regulation of g_s during drought (Martínez-Vilalta and García-Forner, 2016). However, seasonal comparisons of the behaviour of g_s and Ψ_{leaf} and measurements of maximum rates of photosynthesis and photosynthetic potential of co-occurring species experiencing differing soil water availability allows us to answer the questions: do these two species exhibit contrasting behaviours in g_s and Ψ_{leaf} consistent with a definition of iso/anisohydric; and does isohydry constrain photosynthesis more than anisohydry?

Anisohydric species tolerate low soil water availability due to several biophysical properties related to maintaining cell turgor. Loss of turgor in guard cells results in stomatal closure and loss of cell turgor more generally results in cessation of growth (Cowan, 1977). The Ψ_{leaf} at which cells lose turgor (the turgor loss point; Ψ_{TLP}) varies across species and is positively correlated with water availability within and across ecosystems (Bartlett et al., 2012; Mitchell and O'Grady, 2015). A related trait is cell wall elasticity. Low elasticity results in a steeper decline in Ψ_{leaf} with declining relative water content, promoting the maintenance of water potential gradients between the leaf and soil which facilitates water uptake by roots as soils dry (Kozłowski and Pallardy, 2002). The combination of low Ψ_{TLP} and low cell wall elasticity enables anisohydric plants to continue transpiring and fixing carbon at lower levels of soil moisture content than for isohydric plants. Plants may also tolerate low soil moisture content through morphological adaptations. At the leaf-scale, small, thick and narrow leaves can prevent wilting at high levels of desiccation, thereby avoiding cell damage (Cunningham et al., 1999; Niinemets, 2001). At the branch-scale, a large Huber value (i.e. low ratio of leaf area to sapwood area) reduces the risk of xylem cavitation (Zolfaghar et al., 2014).

Plants with little access to soil moisture are likely to have relatively low rates of g_s . However, low g_s may be partially compensated for by increased allocation to foliar N, which can increase the capacity to maintain photosynthesis (Evans, 1989; Vogan and Maherali, 2014). This “resource substitution” has previously been demonstrated in multiple species (Taylor and Eamus, 2008). Primary measures of photosynthetic capacity include the rate parameters of the enzyme kinetic processes which drive photosynthesis, specifically V_{max} (maximum rate of carboxylation) and J_{max} (maximum rate of electron transport; Farquhar et al., 1980). A larger investment in leaf tissue, specifically leaf mass per area (LMA) can also enhance photosynthetic capacity by increasing foliar N on a leaf-area basis. However, plants with a large LMA allocate more resources, including nitrogen, to building thick cell walls. Consequently, LMA is negatively correlated with photosynthetic nitrogen-use efficiency (PNUE) (Hikosaka, 2004). A large photosynthetic capacity can result in increased leaf-scale intrinsic water use efficiency (WUE_i , the ratio of C assimilation to stomatal conductance; Farquhar et al., 1989; Dawson et al., 2002), and many drought tolerant plants have increased WUE_i compared to drought avoiding plants (Moreno-Gutierrez et al., 2012). Furthermore, WUE_i increases with

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