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Shallow soils negatively affect water relations and photosynthesis in two semi-arid *Eucalyptus* species

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ABSTRACT

Water relations of saplings of two *Eucalyptus* species (*E. leptopoda* Benth. and *E. loxophleba* Benth.) were investigated on engineered cover systems (soil spread over mine waste rock) with soil depths of 0.3, 0.5 and 0.7 m in a semi-arid climate during summer. Objectives were (1) to assess the influence of soil depth on plant water availability; and (2) to better understand the impact of water availability and diurnal environmental fluctuations on key physiological parameters such as transpiration (*E*), stomatal conductance (g_s), net photosynthesis (*A*), intercellular CO_2 concentration (C_i), and mid-day leaf water potential (Ψ_{MD}) as they relate to regulation of plant water status. Physiological responses of plants to environmental factors differed between plants in shallow versus deep soils and species. Plants on deeper soils were less affected by high vapour pressure deficit (VPD), temperature, and irradiance due to increased plant available water, partly provided by their less confined roots, resulting in higher overall g_s, *E*, *A*, and Ψ_{MD}. Stomatal closure reduced *A* but not C_i, indicating that high temperature and radiation were also significantly contributing to the diurnal decline in *A* through reversible photoinhibition. Greater soil depth in natural (semi-) arid ecosystems and on constructed or restored substrates may minimise plant sensitivity to higher temperature, VPD and irradiance through plant available moisture, especially in areas most vulnerable to climate warming and drying.

1. Introduction

Plant establishment and survival in water-limited ecosystems are largely governed by soil water availability (Noy-Meir, 1973; Grayson et al., 2006). In these systems, plants rely on stored soil water during long periods of drought between unpredictable rainfall events under conditions of high evapotranspiration. Soil depth is a key determinant of water storage capacity, and in seasonally dry climates, it correlates strongly with vegetation type (Beard and Pate, 1984; Borchert, 1994, Li et al., 2012). Soil texture and organic matter content affect plant water availability through their influence on soil pore size, hydraulic conductivity, and moisture retention capacity (Bhaskar and Ackerly, 2006; McDowell et al., 2008). In general, some coordination exists between soil textures and associated soil hydraulic characteristics, plant water use strategies, and soil depths (Li et al., 2012). For instance, more negative leaf water potentials (Ψ_l) were associated with a shrub species growing in a fine textured soil compared to Ψ_l of the same species growing in a coarse textured soil; abundant pore spaces within the fine textured soil hold water at more negative soil water potentials Ψ_s increasing the requirement to decrease Ψ_l under drought conditions thus facilitating water extraction (Sperry and Hacke, 2002). Finer textured soils may also be associated with shallower roots systems due to smaller soil pore spaces resulting in greater Ψ_s ranges, shallower wetting, and impedance to root penetration (Sperry and Hacke, 2002). This stresses the link between plant traits or strategies and soil profiles/textures in water limited systems.

Water availability to plants also depends on the depth distribution of soil water and roots, especially in deeper soils. The depth distribution of soil water is highly dynamic and influences root growth but is also influenced itself by plant water uptake (Schymanski et al., 2008), hydraulic lift or redistribution of water by plants (Neumann and Cardon, 2012), and root effects on soil hydraulics (Nulsen et al., 1986).

Arid ecosystems characteristically have very low leaf area indices (LAI, m^2 of leaf area per m^2 of ground area) due to the lack of reliable access to soil water and associated physiological stress (Asner et al., 2003; Valladares and Sánchez-Gómez, 2006). Transpiration (*E*) is the loss of water through stomata, the same pores that allow diffusion of carbon dioxide (CO_2) from the atmosphere into the leaves for photosynthesis (*A*; Lombardini, 2006). Aridity-adapted species are generally considered to be conservative water users, i.e. they have low rates of

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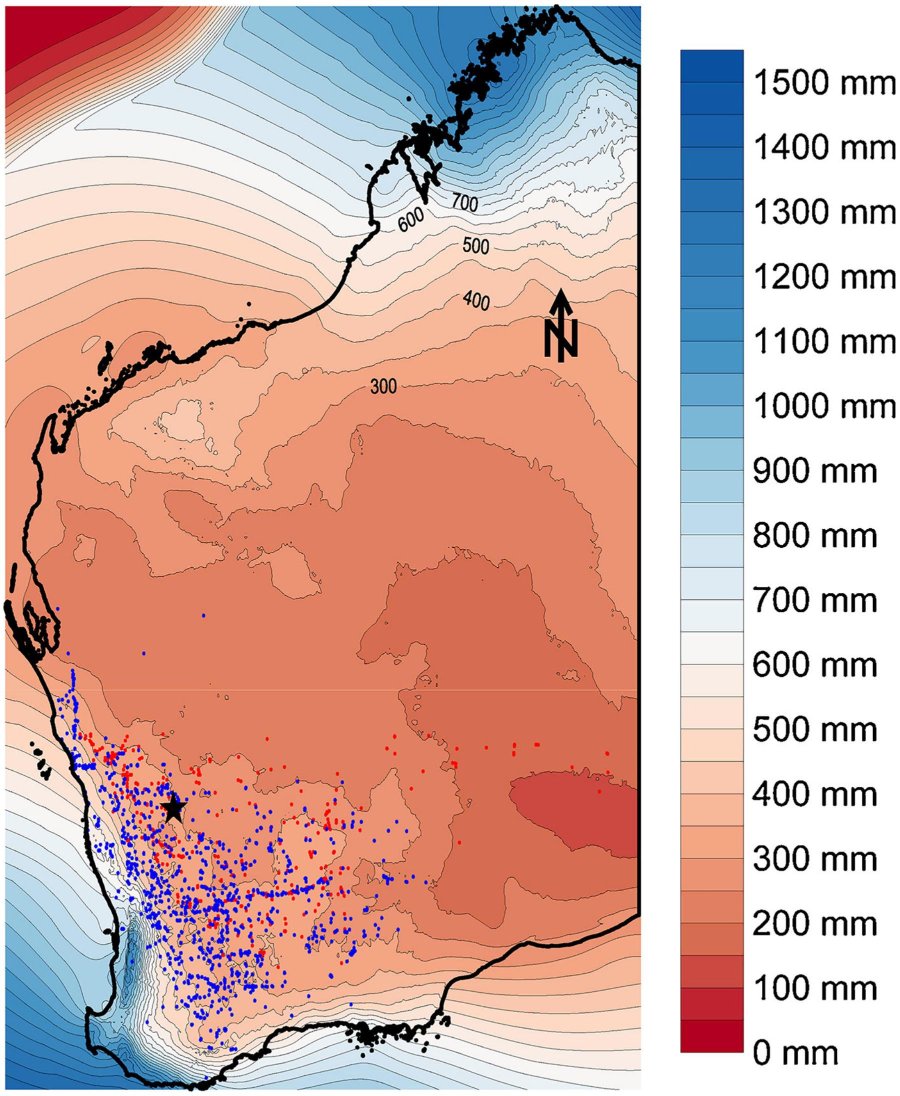

Fig. 1. The distribution of *E. leptopoda* (Benth; red circles) and *E. loxophleba* (Benth; blue circles) (Atlas of Living Australia, https://www.ala.org.au/), and average annual rainfall (Bureau of Meteorology, http://www.bom.gov.au/) for Western Australia (Australian Government, http://www.data.gov.au); the black star on the map denotes the study site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

water use per unit biomass due to low rates of *E*. Stomata ultimately control the balance between water loss and CO_2 uptake in response to soil water status and abiotic environmental factors (Lombardini, 2006). Maximum stomatal conductance (g_s) of arid species is not necessarily low (Körner, 1995), indicating that effective stomatal regulation is vital to balancing water use to optimise growth and survival. High stomatal conductance (g_s) can result in high *A*, growth, and leads to evaporative cooling of foliage in hot summer conditions, but risks dehydrating leaf tissue and depleting soil water (Lombardini, 2006; Chaves et al., 2016). Low g_s is a safer strategy but reduces growth, and is ineffective for water conservation if neighbouring plants have higher water use and growth rates, as competition for water by larger plants with higher *E* and g_s will deplete shared soil water reserves (Fowler, 1986; Van Der Waal et al., 2009). The stomatal aperture can be reduced in response to environmental cues such as low soil moisture availability and vapour pressure deficit (VPD), directly as a result of the turgor loss of guard cells (hydropassive closure), and indirectly through signalling by production of abscisic acid (ABA) in roots and leaves (hydroactive closure) (Luan, 2002; Lombardini, 2006; Brodribb et al., 2014). Faced with extreme evaporative demand where the boundary between semi-arid and arid areas is defined by potential evapotranspiration that is five times the annual rainfall (Barrow, 1992), and uncertain timing of the next rainfall event, arid-zone plants are expected to regulate stomatal opening in a way that minimises the risk of dehydration and maximises the productive use of water. Stomatal behaviour may therefore be different for species that evolved in deep vs. shallow soils or sandy vs. clayey soils, and similarly, for plants of the same species growing in (and phenotypically adjusting to) soils that differ in soil depth or texture. However, evolution has led to a variety of trait combinations dealing with aridity, and it has been shown that different species, even if belonging to the same genus and growing in similar soil, can differ significantly in a range of traits associated with drought tolerance (Lamoureux et al., 2016). As soil moisture content varies with depth, due to precedent weather, soil physical properties as well as plant root water uptake, its influence on stomatal regulation is difficult to resolve, but likely to vary among species that differ in their soil and climatic preferences.

In addition to the complex effect of soil moisture on plant water status, g_s also varies diurnally in response to a decline in plant hydration from a pre-dawn maximum to a diurnal minimum, and due to fluctuations in atmospheric evaporative conditions. Mid-day depression and early morning peaks in g_s, *A*, and *E* have been described in numerous studies (e.g. Eamus and Cole, 1997; Prior et al., 1997). Because *A* and *E* are both influenced by g_s, leaves need to balance between maximising carbon gain, while minimising evaporative water loss