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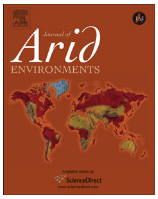

Informing arid region mine-site restoration through comparative ecophysiology of *Acacia* species under drought

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ABSTRACT

Establishing vegetation on disturbed sites in arid environments is difficult due to decreased water availability caused by altered soil properties: depth, compaction, and hydraulic characteristics. Plants cope with moisture stress through a combination of traits, including physiological strategies such as anisohydry and isohydry. We used a typical mine restoration substrate in a glasshouse pot experiment to investigate drought tolerance of nine Pilbara region *Acacia* species classified according to habitat preferences defined by preferred soil type: alluvial (fine textured), sandy, rocky, and generalists without a clear soil preference. Seedlings were examined to (1) determine physiological shoot, and morphological shoot and root traits associated with drought tolerance, and (2) identify if these traits were correlated with species' soil preferences. Species from alluvial, rocky, and one sandy soil species were more anisohydric. These species had higher stomatal conductance at more negative leaf water potentials. Alluvial soil species had greater total biomass allocation to lateral roots, whereas two coarser textured soil species had high allocation to tap roots. Soil preference was a poor predictor of plant water relations, presumably due to complex soil profiles in nature associated with widely differing hydraulic characteristics, and interactions among plant functional traits influencing water uptake, transport and loss.

1. Introduction

Plant establishment for vegetation restoration on mine-impacted sites is often challenging, especially in arid environments where moisture deficits pose a considerable hindrance. In such conditions, water availability may be further compromised by alteration of soil hydraulic characteristics by machinery (e.g. compaction), and lack of topsoil to construct profiles with the required depth and moisture holding capacity (Sheoran et al., 2010). Better understanding of physiological and morphological adaptations to drought may aid species selection and substrate design resulting in enhanced establishment of plant species in restored areas, such as former mine sites (Grierson et al., 2011). Although studies have presented useful information concerning species response to drought, some knowledge gaps exist regarding the traits and strategies used for assessment of drought tolerance (e.g. Bartlett et al., 2012; Galmés et al., 2007; Valladares and Sánchez-Gómez, 2006). Remaining physiologically active under moisture stress hinges on the ability to tolerate high water tensions in the xylem which enables continued moisture uptake from a drying soil (Bhaskar and Ackerly, 2006). Although physiological adaptations are essential to drought tolerance, soils and plant-soil interactions strongly affect those adaptations, thus influencing plant available water across climates (Hacke et al., 2000; Jury and Horton, 2004; Sperry and Hacke, 2002).

Plant adaptations to drought in seasonally dry environments are essential for their survival. To maximise long-term carbon gain, and nutrient use efficiency (Gray, 1983), many species in these environments are evergreen and have long-lived leaves with low nutrient concentrations, low leaf area to mass ratios, low photosynthetic rates, and high root:shoot ratios (Ackerly, 2004; Kummerow et al., 1977; Mooney and Dunn, 1970). Another advantage for survival in drought prone environments is high tolerance to low water potentials in xylem tissues to avoid cavitation. High wood density and its associated resistance to cavitation has been shown to be an effective drought adaptation (Hacke et al., 2001). Plants may also cope with moisture stress through physiological controls such as anisohydric and isohydric strategies. Under declining soil water potentials (Ψ_s), anisohydric plants typically have more negative leaf water potentials (Ψ_l), maintain higher stomatal conductance (g_s), and often have wider Ψ_l ranges (Barnes, 1986; McDowell et al., 2008). Conversely, isohydric plants reduce g_s in response to decreasing Ψ_s thus maintaining more constant Ψ_l to

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avoid water transport failure (McDowell et al., 2008; Sperry et al., 2002). However, even within semi-arid to arid systems, plant adaptations to drought vary as different combinations of traits provide drought tolerance across varying soil types and associated hydraulic properties.

Plants grow on a range of soil types that have different hydraulic characteristics with textures ranging from heavy clays to coarse sands (Hacke et al., 2000). Plant water availability is largely a function of soil texture through the influence of pore size, hydraulic conductivity, and moisture retention capacity (Bhaskar and Ackerly, 2006; McDowell et al., 2008). Therefore, varying soil textures present different challenges for plant water extraction (Bristow et al., 1984) and species associated with different soil types often have different morphological traits and water use strategies to facilitate plant water uptake (McDowell et al., 2008; Westoby and Wright, 2006), suggesting a close coordination between plant traits or strategies and soil profiles/textures (Westoby and Wright, 2006). For instance, populations of shrub species growing on fine-textured soils generally have more negative Ψ_l than populations of the same species growing on coarse textured soils (Sperry and Hacke, 2002). These more negative Ψ_l reflect the smaller and more abundant pore spaces in fine textured soils that hold water at more negative Ψ_s (Sperry and Hacke, 2002). Additionally, plant rooting depth may be influenced by moisture retention across soil textures (Jackson et al., 2000). Plants on sandy soils are required to grow roots into deeper moist soil layers due to low soil moisture retention capacity of sands (Sperry and Hacke, 2002). Deep growth in coarser textured soils is also supported by greater oxygen availability at depth, and easier root penetration, especially in sandy soils (Sperry and Hacke, 2002). In finer textured soils deep root growth is reduced due to broader Ψ_s ranges as a result of smaller pore spaces, shallower wetting, and impedance to root penetration (Sperry and Hacke, 2002). This stresses the importance of quantifying drought adaptation across soil types within the same water limited environment.

The Pilbara region in NW Australia is semi-arid to arid, and is prone to periods of severe seasonal drought (Van Vreeswyk, 2004). Despite severe moisture deficits it hosts a large plant diversity with 1094 native vascular species, including 150 conservation significant species, on 21 soil groups forming 44 plant-soil associations (EPA, 2014; Van Vreeswyk, 2004). The Pilbara is mostly dominated by *Triodia-Acacia-Eucalyptus* alliances, however, species within these genera vary across sub-regions and soil types (Beard, 1975; Van Vreeswyk, 2004), and thus are expected to exhibit functional differences reflecting adaptations to varying soil types. The region is rich in mineral resources producing more than 90% of Australia's iron ore (DMP, 2012). Active and pending mining tenements cover 91.8% of the Pilbara, and thus large areas will require restoration of native flora due to mining disturbance (EPA, 2014). Because mining restoration substrates differ from naturally occurring soils in depth, compaction, and hydraulic characteristics, physiological and morphological plant responses to drought stress in these substrates are largely unknown. Therefore, it is of value (1) to examine how the ecophysiological and morphological mechanisms of drought tolerance differ among common Pilbara species when grown on a common mine site restoration substrate, and (2) to determine whether potential differences are related to species' preferred soil types. The latter would suggest that specific adaptations to local soil types or profiles occur and are expressed even when species are grown on a common substrate.

In this study, nine Pilbara *Acacia* species were grown in a typical mine site restoration substrate in a glasshouse experiment with the following aims: (1) determine the physiological shoot, and morphological shoot and root traits associated with drought tolerance, and (2) determine if these traits differed between their preferred soil types. We hypothesised that, when faced with soil moisture deficit, *Acacia* species with a tendency to keep stomata open for longer, allowing further decreases of plant water potentials, would be associated with lower osmotic potentials at full hydration (π_{sat}) and greater biomass investment in lateral roots. We also expected such species to typically occur in more fine-textured alluvial soils than more coarse-textured sandy and rocky soils.

2. Materials and methods

2.1. Study species

Nine Pilbara *Acacia* species from four contrasting preferred soil types were chosen for this study. Species were categorised according to their soil preferences based on evidence gathered from literature, online flora descriptions (Flora Base, http://florabase.dpaw.wa.gov.au/) and expert consultations. Soil preference categories are as follows:

- alluvial (fine textured) soil species: *Acacia aneura* Benth., *A. citrinoviridis* Tindale & Maslin, and *A. cowleana* Tate;
- sandy soil species: *A. coriacea* subsp. *pendens* R.S.Cowan & Maslin and *A. stellaticeps* Kodela, Tindale & D.A.Keith;
- rocky soil species: *A. pruinocarpa* Tindale and *A. maitlandii* F.Muell.; and
- generalist species: *A. bivenosa* DC. and *A. ancistrocarpa* Maiden & Blakely.

Although study species were categorised according to these soil preferences, we recognise that within-species variation in distribution patterns exists, e.g. related to ecotypes or interactions with climate. Soil preferences indicated here reflect the preferred soil types in which these species are most commonly found.

2.2. Experimental design

The experiment was conducted in a glasshouse mimicking the climate in the species' native habitats. Air temperature was approximately 32 °C during the day and 25 °C at night (Appendix A). During the growth stage (14 August 2013–14 February 2014), automated shade cloths on the glasshouse structure were raised when outside temperature reached 30 °C or more which reduced sunlight by 60%. During the experimental period (15–25 February 2014) plants received natural light which peaked on average at approximately 1500 μmol m^2 s^{-1} during mid-day; shade cloths were not deployed, however, the glasshouse structure reduced light by 25%. Plants were grown in 2.8 L free-draining pots (diameter 16.5 cm, height 16.5 cm). Pots were lined with a fine synthetic mesh and a thin layer of gravel (0.40 kg) to retain soil, and inhibit root growth out of the pots. Each pot was filled with soil (2.60 kg; see details below), and then topped with a thin layer of gravel (0.30 kg) to limit soil water evaporation. Soil was kept moist and allowed to settle for one week prior to sowing.

Acacia species seeds were collected from the Pilbara and obtained from the Botanical Gardens and Parks Authority (Kings Park, Perth, Western Australia). Seeds were scarified in near-boiling water prior to sowing. Ninety pots were sown with five seeds from one of nine *Acacia* species. Ten additional pots were left without plants to quantify soil evaporation rates. A standard block design was used across five benches in the glasshouse, each *Acacia* species having two pots (one well-watered, one water-stressed) per bench. Pots were randomised within each block. Pots were watered to field capacity during the growing stage, by hand for the first month, and by micro-irrigation three times daily for one minute thereafter. After six months, one healthy seedling (of representative size for its species) was kept per pot, and the extras were cut at the stem-soil interface.