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Seasonal variations in tree water use and physiology correlate with soil salinity and soil water content in remnant woodlands on saline soils

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A B S T R A C T

Ecophysiological studies of remnant woodlands in saline environments are scarce. We investigated seasonal fluctuations in soil water and salinity together with leaf and branch traits (area-based maximum assimilation (A_{max}), foliar nitrogen, specific leaf area (SLA) and Huber value (H_v)) and sap velocities of *Eucalyptus macrorhyncha* at four semi-arid sites in south-eastern Australia. Summer and winter soil salinities (10 cm depth) were 15–35 dS m^{-1} and 8–10 dS m^{-1} respectively. Gravimetric soil water content in the upper 20 cm was 2–5% in summer and 7–23% in winter, resulting in a significant inverse correlation between soil water and soil salinity. We found significant correlations between soil conditions and plant traits and function across seasons. Soil water content was significantly correlated with foliar N, SLA, H_v and maximum sap velocity while soil salinity was significantly correlated with A_{max}, H_v and maximum sap velocity. Correlations indicate co-variation of soil conditions and plant physiology in response to environmental conditions such as solar radiation and vapour pressure deficit (D). *E. macrorhyncha* tolerates the dual stresses of high salinity and low soil water during summer. While the plants appeared unhealthy, our data show that remnant vegetation can remain functional even in close proximity to saline scalds.

1. Introduction

Dryland salinity is widespread across Australia and other semi-arid regions of the globe (Lambers, 2003). Rising water tables bring salts to the surface of the soil (Eberbach, 2003) after clearing of deep-rooted perennial native vegetation has resulted in increased groundwater recharge (Lambers, 2003; Rengasamy, 2010). This serious land-degradation restricts agricultural productivity as increased salt concentrations and waterlogging of soils associated with dryland salinity can reduce plant growth and threaten plant survival (Sun and Dickinson, 1995). Studies testing methods for rehabilitation of saline soils have identified native salt-tolerant species which can be planted on salt-damaged soils and potentially improve soil quality (Bell, 1999). However, little is known about the ecophysiology of remnant vegetation remaining on saline soil (Pannell and Ewing, 2006). Consequently, the extent to which different native species respond to soil salinity *in situ* is not clear (Cramer and Hobbs, 2002).

Soil salinity affects plant function in a number of ways, for example, increased salinity reduces growth of stems, leaves and roots (Kayama et al., 2003; Myers et al., 1996; Rubinigg et al., 2004) in forest and greenhouse studies. The accumulation of salts in or below the root zone generally results in reduced tree growth and water use, and sometimes tree death (Macar et al., 1995; Sun and Dickinson, 1995; Feikema and Baker, 2011). High soil salinity can lead to changes in the soil-plant hydraulic conductance (Kayama et al., 2003; Rengasamy, 2006), leading to decreased tree water-

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use (Doody et al., 2009) which can end with death of non-halophytes (Akeroyd et al., 1998; Boland et al., 1996; Macar et al., 1995; Teobaldelli et al., 2004). This decreasing water-use may be a result of reductions in leaf area (Hatton et al., 1995, 1998; Myers et al., 1998) or increased soil-to-leaf hydraulic resistance (Teobaldelli et al., 2004).

While the effects of high salinity on tree growth and tree water-use have been studied within many plantations (Benyon et al., 2001; Morris and Collopy, 1999; Hatton et al., 1998), few reports examine photosynthesis, growth and water-use of remnant vegetation on saline sites (Akeroyd et al., 1998; Barrett et al., 2005; Pannell and Ewing, 2006; Bann and Field, 2010; Bui, 2013). In one of the few studies of effects of salinity and waterlogging on native species *in situ*, Barrett et al. (2005) found very little measurable effect on pre-dawn leaf water potential, stomatal conductance and foliar ion concentrations, even when tree health was visibly compromised. These results highlight the need to examine the ecophysiological response of native trees *in situ* because visible symptoms and impaired ecophysiological function may not always be correlated. Similarly, Marchesini et al. (2013) found predawn leaf water potentials at disturbed and undisturbed sites were unchanged despite lower gravimetric water content and lower electrical conductivity at disturbed semi-arid woodland sites. However, Bui (2013) identifies salt as a major ecological driver over geological and more recent time-scales in semi-arid areas. He suggests that salt has been largely ignored as an ecological driver and soil salinity should be considered together with other factors such as soil water and fire when exploring vegetation community composition (Bui, 2013). Pannell and Ewing (2006) advocate for cost effective management options to prevent expansion of salinised areas. Without adequate data on remnant vegetation, their value in the fight against salinity is not clear.

Seasonal variations in soil salinity are associated with seasonal rainfall (Tomar and Gupta, 1985; Srivastava and Jefferies, 1995; Rengasamy, 2010) and changes in watertable depth (Jackson et al., 1956; Peck, 1978). Heavy rains and rising watertables dilute salt in the soil while drier periods are associated with higher salinities due to evaporation and transpiration of soil water. Seasonal measurements are therefore required to capture the full range of combinations of environmental conditions which occur naturally. Trees in semi-arid regions affected by dryland salinity also have to tolerate winter frosts and high evaporative demands in summer. Seasonal patterns in function often reflect changing environmental conditions. For instance, the strong relationship between tree water-use and solar radiation (R_n), vapour pressure deficit (D) and soil water content (θ) is often exploited in simple empirical models of stand transpiration for well-coupled forest canopies (e.g. Whitley et al., 2008). In this study, we explored the patterns of θ and soil salinity associated with coarse seasonal patterns of water relations and productivity of remnant eucalyptus species in a region affected by dryland salinity. Specifically, we measured transpiration rates, hydraulic architecture, photosynthesis and leaf traits as well as θ and soil salinity across four sites in summer and winter and used correlation analysis to explore co-variation of plant function and soil conditions.

2. Materials and methods

2.1. Study site and species

The study sites were located near Crookwell, an agricultural and pastoral district in the southern Tablelands of New South Wales (34.4572 S, 149.4690 E, elevation 887 m). All sites had open forest with a grass understorey and very few shrubs and were within 3 km of each other. Site 1 at Laggan Corner was dominated by *Eucalyptus dives* Schauer (peppermint) directly adjacent to a saline scald, where salt crystals were forming on the soil surface and vegetation was absent due to the high concentrations of salt. Site 2 (also at Laggan Corner) was dominated by *Eucalyptus rossii* R. Baker & HG Smith (scribbly gum) and was 300 m from the nearest visible saline scald. *Eucalyptus macrorhyncha* F. Muell. ex Benth (red stringybark) occurred at both sites 1 and 2 as did *E. rossii*. Sites 3 and 4 at Laggan Dam were equally dominated by *Eucalyptus goniocalyx* F. Muell. ex Miq. (box), *E. macrorhyncha* and *E. dives*. Site 3 was directly adjacent to a saline scald while site 4 was over 200 m from the saline scald. Trees closest to the saline scald appeared unhealthy with discoloured leaves.

Winter sampling took place in July 2003 and summer sampling occurred in January 2004. *E. macrorhyncha* was studied at all four sites. *E. rossii* and *E. goniocalyx* were also studied at Laggan corner and Laggan dam respectively but data are not shown because these data were very similar to those for *E. macrorhyncha*. Red stringybark is wide-spread in south-eastern NSW and locally dominant in dry schlerophyll forests and woodlands. It is hardy, tolerating frosts and occasional snow (Boland et al., 2006). Six sample trees were identified within two plots at each site (three trees per plot). All plant measurements were conducted on these trees. Leaf and branch samples were selected haphazardly from within 5 m of the ground.

This research was conducted during a prolonged and extreme drought lasting three years, with severe water deficiencies with rainfalls in the lowest 5% of historical totals (Bureau of Meteorology, 2003). The region is characterised by a long-term mean annual rainfall of 861 mm but is located in a rain shadow so the sites commonly experience drought conditions with extended periods (months to years) with little rainfall. There is slightly more rain in winter than summer and average temperatures are 10–27 °C in summer and 0–10 °C in winter (Fig. 1). Climate data were obtained from the nearest Bureau of Meteorology station at Crookwell Post Office (approximately 8 km to the south of the experimental sites).

2.2. Soil salinity and water content

The soil is defined as coarsely cracking grey and brown clays (NSW Natural Resource Atlas, http://nratlas.nsw.gov.au, accessed on 22nd July 2013). The soil type is a sodosol (Isbell, 2002) and is classed as sodic saline soil according to Rengasamy's (2010) categories. Particle size analysis indicated the clay content was approximately 30%. Five soil samples were collected from the base of each of the six sap flow sample trees to assess salt content of the soil at each of the four sites. Approximately 1000 cm^3 were excavated at a depth of 10 cm and transported in a zip-lock bag to the laboratory. An aqueous saturated paste extract (of 50 mL water to 10 g air-dried soil) was produced by shaking the sample for 5 min then allowing to settle for an hour, following the methods of Rhoades (1982). The electrical conductivity (dS cm^{-1}) of this solution was measured with a conductivity meter (YSI Incorporated, Ohio) and divided by 100 to produce values of dS m^{-1}. The salinity of the saturated paste extract was multiplied by 8.6 (for a sandy clay loam) to determine the salinity experienced by roots (Taws, 2003). The remaining soil was dried to constant weight (110 °C) and weighed to determine soil water content. As our sites were privately owned, we did not have permission to dig deep holes so we were limited to non-invasive soil measurements in this project.

2.3. Photosynthesis

Photosynthesis was measured as maximum (light saturated) assimilation (A_{max}) with a HCM-1000 Portable Photosynthesis System (PPS) (Walz, Germany). Measurements were taken in the morning (between 0930 and 1130) and in the afternoon (between