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Topographical and seasonal trends in transpiration by two co-occurring *Eucalyptus* species during two contrasting years in a low rainfall environment

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ABSTRACT

Understanding the strategies that confer resilience on natural woodlands in drought prone environments is important for the conservation of these and similar ecosystems. Our main aim in this 2-year study was to assess traits (sapwood area, sapwood density and leaf area index) that control transpiration in *Eucalyptus camaldulensis* and *E. microcarpa* in a natural forest in which topographical variation created surface soils of sandy clay in a depression (clay-zone) and of loamy sand underlain by a dense profile on the terraces (sand-zone). The clay-zone had a wetter profile due to extra water supply through subsurface lateral flow from the adjoining, topographically higher, sand-zone. In the clay-zone, the differences between the two tree species in their hydraulic attributes were large and rates of water use were widely divergent. Rates of transpiration per unit land area (E_c) and canopy conductance of *E. camaldulensis* that was dominant in the clay-zone were about 50% lower than those for *E. microcarpa* in the same zone. This was in marked contrast to the behavior of trees growing in the sand-zone where water availability was persistently low and variations in sapwood density, sapwood area and canopy conductance were narrow. This resulted in almost identical rates of water use for the two species in the sand-zone, despite *E. microcarpa* dominating the stand. Contrary to many previous studies, sapwood density was positively correlated with E_c in these eucalypt species, while the proportion of trunk area assigned to sapwood declined with sapwood density. Consequently in this low rainfall environment, with prolonged dry seasons, dense sapwood safeguards against turgor loss, and possibly xylem embolism, thereby allowing E_c to be sustained under extremely low soil-water availability. We concluded that variation in hydraulic traits is less likely where trees are under persistent water-stress than where the stress is short and relatively mild. We developed single functions for predicting E_c for the two species by integrating their responses to micrometeorological and soil-water conditions.

1. Introduction

Remnants of native woody vegetation are an important resource for understanding the pre-existing eco-hydrological processes on highly disturbed landscapes. In semi-arid Australian environments, where European settlement resulted in large scale land clearance, remnants of woody vegetation are a testimony to their capacity to adjust their transpiration in response to short- and long-term variability in rainfall and meteorological conditions over the millennia. Adjustment of transpiration by manipulating traits at ecological (population density), structural (leaf area index, rooting depth), anatomical (size and density of water conducting tissues, density and location of stoma), physiological (stomatal conductance) and biochemical (osmotic adjustment) levels is well known (Wullschleger et al., 1998; Bucci et al., 2004; Meinzer, 2003; Baldocchi and Xu, 2007). Disparate species may modify several of these traits to differing degrees to maintain transpiration in a given environment resulting in *functional convergence* (Meinzer, 2003), i.e. attainment of similarity in transpiration through different strategies. This was demonstrated by the parity in transpiration of *Melaleuca* spp. and *Eucalyptus* spp. growing in contiguous sites having differing water availabilities arising through topographical

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variation. This parity arose by compensatory behavior of leaf area index and sapwood area in the two species (Kelley et al., 2007).

Variability in soil texture exerts profound influence on long-term availability of soil-water and can permanently modify structural and physiological traits associated with water-uptake in woody species (Alder et al., 1996; Hultine et al., 2005; Kelley et al., 2007; Mitchell et al., 2008). Alder et al. (1996) observed that trees growing on a dry slope had low canopy conductance stemming from reduced hydraulic conductance in their stem and root due to xylem embolism in a particularly dry year (Alder et al., 1996). Hultine et al. (2005) reported that desert mesquite (*Prosopsis velutina*) produced larger conduit diameters on a loamy clay, on which xylem cavitation occurred at higher xylem pressure in the stem, than on a coarser loam soil. Similar responses in plant-water relations due to repeated transient ponding or flooding are known to prime the tree to effectively extract water over an extended range of soil-water availability (Sperry and Hacke, 2002). *Eucalyptus* trees subjected to prolonged flooding tolerated much lower soil-water potential (−3.5 MPa) before wilting compared with non-flooded plants (−3.1 MPa) (Myers and Neales, 1984). The capacity to withstand low soil-water potential has been associated with improved osmotic adjustment in trees that experience frequent flooding (Alder et al., 1996). Similarly transpiration was more responsive to vapour pressure deficit in cottonwood (*Populus fremontii*) trees subjected to perennial flooding than in those subjected to intermittent flooding (Gazal et al., 2006).

Anatomical characteristics of the stem, especially sapwood density, are known to impact hydraulic conductivity and the capacity of the tree to withstand prolonged limited soil-water supply. For instance, high sapwood density tends to constrain water conductivity, but also safeguards against xylem embolism (Koch and Fredeen, 2005; Mitchell et al., 2008; Stratton et al., 2000). Thus species with dense sapwood are able to maintain water conduction at much lower leaf water potentials and, hence, lower levels of soil-water availability, than species having low sapwood density. Small variations in sapwood density generally induce large variations in hydraulic properties of the tree, including vulnerability to xylem embolism, and its capacity to respond to transient micrometeorological conditions (Bucci et al., 2004; Stratton et al., 2000; Koch and Fredeen, 2005).

Recent studies in the arid environments of Australia, however, found trait variation amongst plant species to be particularly limited under arid conditions (Mitchell et al., 2008; O'Grady et al., 2009). Mitchell et al. (2008) observed limited trait variation amongst several woody species on soil with prolonged poor water supply, where convergence of water use strategies was more likely, compared with soil having good water storage capacity. Understanding these trade-offs amongst traits that control water use by trees, is important to management of regional water resources, salinity control and management of sensitive ecosystems. In this paper, we analyzed transpiration for two co-occurring eucalypt species that dominate a remnant forest in which the terrain caused strong differences in texture and hence water supply of surface soils in southeastern Australia. Our objectives were to (1) identify the dominant anatomical and physiological traits that control transpiration in the two species under extended drought conditions and (2) quantify seasonal and annual transpiration by the trees and characterize its relative sensitivity to micrometeorological and soil-water conditions.

2. Materials and methods

2.1. The site

This study was undertaken at the Reef Hills State Park (36°36′S, 145°56′E or AMG Zone 55, Easting 403442, Northing 594857) located near Benalla in Victoria, Australia. It covers 2032 ha and the vegetation can be generally classified as Heathy Dry Forest (Muir et al., 1995). The park forms part of Box-Ironbark forests and woodlands of almost three million hectares that covers almost 13% of the state of Victoria in Australia (Parks Victoria, 2007). Annual rainfall for the district is about 670 mm with almost one third of this falling during winter (June–August) when cold westerly winds dominate and mean daily temperature falls below 10 °C; occasionally the minimum temperature falls to 0 °C and frosts occur especially from mid-winter to early spring. Summers are generally warm to hot with daily mean temperature of 20.6 °C, and is generally dry except for occasional heavy storms. The park was heavily grazed after the cessation of mining in the early decades of the twentieth century, the declaration of the park as a reserve has since alleviated grazing and facilitated recovery of the native vegetation. There was limited routine harvesting of wood for fuel and timber up until 1988 when the practice was stopped, and there has been no record of wildfires in recent decades. The park has substantial sapling undergrowth (Meers and Adams, 2003), and at the commencement of this study in 2006, the dominant tree species were approximately 50 years old.

We chose a single block of approximately one hectare (62 m × 160 m) that was dominated by *Eucalyptus camaldulensis* (Red River Gum) and *E. microcarpa* (Grey Box) as over-storey species. The understory was dominated by *Acacia pynantha* (Golden Wattle) and *A. meamsii* (Black wattle) and there was a seasonal groundcover of *Joycea pallida* (Wallaby Grass) and isolated tussocks of *Poa sieberiana* (Tussock-grass). The soil had a duplex profile of coarse textured topsoil underlain by heavy textured clayey subsoil. Salinity measured as electrical conductivity increased from an average of 0.15 dS/m in the near-surface layer to 0.7 dS/m at 3 m depth. The bulk density (Mg/m^3) rises from 1.21 in the top 0.2 m layer to 1.43 at 0.5 m depth and 1.75 at 1.0 m; the density was >1.5 at

Table 1
Textural composition for the soil on each of the two topographic zones and the limits for volumetric water content (θ) for the whole 6 m soil profile measured during the study in the two soils during 2006–2007 at Reef Hill, Australia.

Depth layers (m)	Clay-zone				Sand-zone			
	Sand	Silt	Clay	Texture	Sand	Silt	Clay	Texture
Particle composition (%)								
0.0–0.2	49.5	19.4	31.1	Clay loam	74.3	16.6	9.1	Loamy sand
0.2–1.5	31.9	16.0	52.1	Clay	37.3	12.6	50.2	Clay
1.5–3.0	49.4	15.5	35.2	Clay loam	45.8	12.3	41.9	Clay loam
3.0–6.0	56.3	16.3	27.4	Clay loam	52.3	10.3	37.4	Clay loam
Water limits for the whole 6.0 m profile								
Maximum θ (m^3 m^{-3})	0.32 ± 0.034				0.28 ± 0.022			
Minimum θ (m^3 m^{-3})	0.24 ± 0.028				0.23 ± 0.009			
Water holding capacity (%)	13.0				13.3			