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Sapwood capacitance is greater in evergreen sclerophyll species growing in high compared to low-rainfall environments

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Summary

1. The capacitative release of water from sapwood allows photosynthesis to continue for longer into dry periods, both diurnally and seasonally. However, costs of high capacitance include increased vulnerability to xylem cavitation. The degree of reliance on stored water is predicted to differ among environments as a result of this trade-off.

2. Xylem water potential and sapwood capacitance were measured on 32 evergreen sclerophyll shrub and tree species in eastern Australia, sampled from four sites contrasting in soil nutrients and rainfall.

3. Capacitance calculated over species' typical shoot water potential operating range was threefold higher for species from high compared to low-rainfall sites, and 1·5-fold higher for species from high compared to low-nutrient sites.

4. To determine whether these site differences were related to extrinsic (e.g. water availability) or intrinsic (e.g. species anatomical construction) factors, we calculated capacitance at two common operating ranges; that is, the mean range in water potential observed for low-rainfall species ($\Delta\Psi_{\text{low rain}}$) and the mean range for high-rainfall species ($\Delta\Psi_{\text{high rain}}$). While no difference was seen between low- and high-rainfall species in release of stored water across $\Delta\Psi_{\text{high rain}}$, across $\Delta\Psi_{\text{low rain}}$, the high-rainfall species released 38% more stored water than low-rainfall species. Presumably these differences reflect underlying differences in anatomy, such as wood density, which was lower in high-rainfall species.

5. These results accord with predictions that (i) species from wetter sites exhibit less negative stem water potentials and high sapwood capacitance, enabling them to maintain function under variable conditions characterized by many short, dry periods, while (ii) species from low-rainfall sites have wood anatomies conferring tolerance to very low water potentials, with low sapwood capacitance, enabling them to survive longer through unpredictable and extended periods of low rainfall. The finding that the degree to which species rely on stem-stored water varies with site rainfall suggests that changes in drought regimes (e.g. incidence, duration and severity) under future climates could differentially affect species according to the capacitance properties of their woody tissues.

Key-words: cumulative water release, midday water potential, plant hydraulic strategies, pre-dawn water potential, stem water storage, wood density

Introduction

Water is critical for carbon assimilation in plants: an unavoidable cost of photosynthesis is evaporative water loss (transpiration). Reliance on soil water makes plants vulnerable to unpredictable rainfall events, run-off and evaporation, and competition from neighbours. One way that plants overcome a mismatch between supply and transpirational demand for water when resources are scarce or unpredictable is to store water in various tissues (Holbrook 1995; Cruiziat, Cochard & Améglio 2002). Sapwood

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capacitance is a commonly used measure of tissue water storage.

The hydraulic capacitance of plant tissues (units: kg m^{-3} MPa^{-1}) is defined as the mass of water that can be extracted per unit change in water potential (Cruiziat, Cochard & Améglio 2002). Transpiration from leaf surfaces produces a gradient in water potential throughout the plant hydraulic system, but also between hydraulic elements (xylem, tracheids) and their surrounding tissues (e.g. parenchyma, fibres), which can result in stored water being released into the transpiration stream (termed sapwood capacitance). These water stores may be recharged overnight from soil water when water potential gradients within stems are favourable for refilling (Steppe *et al.* 2005; Meinzer *et al.* 2010), and more slowly recharged and depleted over longer (seasonal) time-scales. Stored water in woody stems is believed to be released by a combination of mechanisms (Tyree & Yang 1990; Ewers & Cruiziat 1991; Hunt, Running & Federer 1991; Tyree & Zimmermann 2002), most notably: (i) capillarity: water is removed from apoplastic and intracellular capillary spaces at the slender tips of embolized fibres, vessels and tracheids, and in cracks between cells or along rays; (ii) elasticity: water is removed from living cells, such as ray and axial parenchyma, fibres, bark phloem, pith and cambial tissues, through osmotic water movement mediated by elastic cell walls. This process is assumed to be behind the regular diurnal shrinking and swelling of plant stems, and some authors suggest that this is the mechanism by which the majority of water is stored (Cruiziat, Cochard & Améglio 2002); (iii) release of water bound in the cell walls of xylem tissue (suggested by Hunt, Running & Federer (1991) to be a major store; and (iv) on seasonal time-scales, cavitation of intact xylem vessels, tracheids or fibres, and (less commonly) from air-seeding of specialized water storage cells (Tyree & Zimmermann 2002).

Three rather distinct phases can often be recognized in water release curves (Fig. 1a), presumably reflecting the ordered removal of water from different storage compartments (Tyree & Yang 1990; Hunt, Running & Federer 1991; Tyree & Zimmermann 2002). Rapid water release characterizes 'phase I'. In this phase, water is presumably removed from both elastic and capillary water stores. Capillary storage relies on surface tension and the radius of curvature of the gas–water interface, which changes rapidly as water potentials decline, resulting in significant water release at high (weakly negative) water potentials (e.g. above −0·6 MPa; Tyree & Yang 1990; Holbrook 1995). The water release curve is flatter during 'phase II'. Presumably, water released during this phase is largely from sites of elastic storage (Cruiziat, Cochard & Améglio 2002) and, increasingly so at more negative water potentials, from xylem cavitation. Phase III, less commonly observed experimentally since it occurs at very negative water potentials, is steeper again and presumably reflects further, and perhaps irreversible, water release via cavitation (Tyree & Yang 1990; Tyree & Zimmermann 2002).

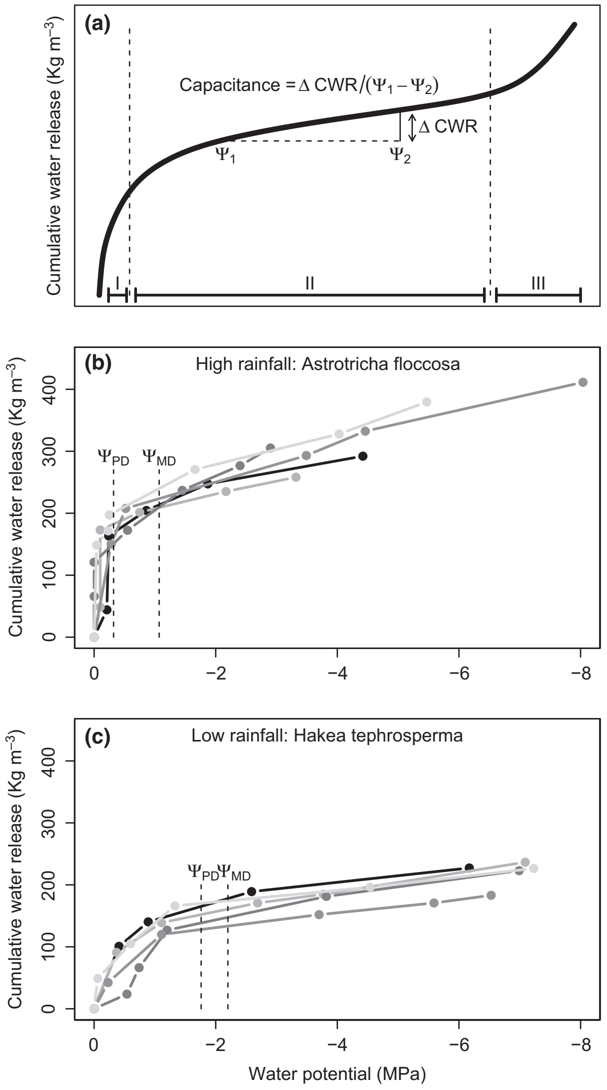

Fig. 1. (a) Schematic of an idealized sapwood cumulative water release (CWR) curve in relation to sapwood water potential. Capacitance is calculated as the ratio of CWR to $\Delta\Psi$ corresponding to a particular water potential interval of interest. Following Tyree & Zimmermann (2002) three phases of water release can be recognized; see text for details. (b) Water release curves measured on five replicate plants of the high-rainfall species, *Astrotricha floccosa* (Araliaceae), one of the least sclerophyllous study species. Each line is a replicate. (c) Water release curves measured on five replicate plants of a needle-leaved low-rainfall species, *Hakea tephrosperma* (Proteaceae), one of the most sclerophyllous study species. Vertical dotted lines on the two lower plots indicate predawn (Ψ_{PD}) and midday (Ψ_{MD}) shoot water potentials, measured in spring, which were used to define the native water potential operating range ($\Delta\Psi_{native}$) for capacitance calculations. Note that the *x*-axis runs from zero (left) to increasingly negative water potentials (to the right).

The capacitative release of water from storage compartments should slow changes in xylem water potential and leaf water status brought about by transpiration (Gartner & Meinzer 2005). Presumably the advantage of such a mechanism is that gas exchange through stomata may be sustained for longer during the day and/or longer into the dry season (Tyree *et al.* 1991; Goldstein *et al.* 1998;

Phillips *et al.* 2003; Borchert & Pockman 2005; Scholz *et al.* 2007). Water stored in woody plant tissues may contribute between 6% and 50% of daily transpiration (Waring & Running 1978; Waring, Whitehead & Jarvis 1979; Schulze *et al.* 1985; Tyree & Yang 1990; Machado & Tyree 1994; Goldstein *et al.* 1998; Kobayashi & Tanaka 2001; Maherali & DeLucia 2001; Phillips *et al.* 2003; Meinzer, James & Goldstein 2004; Scholz *et al.* 2007). Capacitance may also allow tall trees to overcome resistance to axial water transport as hydraulic path length increases (Goldstein *et al.* 1998; Mencuccini & Magnani 2000; Phillips *et al.* 2003), as well as play a protective role by preventing the desiccation of certain tissue types, such as reproductive structures (Holbrook 1995).

However, production of sapwood with high capacitance presumably comes at a cost: several studies have shown that higher capacitance sapwood is more vulnerable to vessel cavitation (Pratt *et al.* 2007; Meinzer *et al.* 2008b; Sperry, Meinzer & McCulloh 2008). Perhaps this should not be surprising, given that water release during cavitation is one mechanism for maintaining hydraulic integrity (Hölttä *et al.* 2009). Sapwood capacitance has also been shown to be higher in species with lower wood density (Scholz *et al.* 2007; Meinzer *et al.* 2008a; McCulloh *et al.* 2012), presumably because interspecific variation in wood density is strongly driven by the fraction of fibre fields that are lumen rather than wall (Chave *et al.* 2009) and thus related to water storage. Since high wood density confers, among other traits, mechanical strength (Onoda, Richards & Westoby 2010) and possibly defence against biological attack (Chave *et al.* 2009), this suggests that high wood density and high sapwood capacitance sit at either end of a trait spectrum representing a trade-off between tissue longevity and hydraulic efficiency.

Incorporating theory around the costs and benefits of sapwood capacitance, Meinzer *et al.* (2009) hypothesized that species adapted to withstanding very negative xylem water potentials avoid cavitation by relying on wood structural features that increase hydraulic safety margins and that also result in low capacitance. By contrast, species typically operating at far less negative water potentials have structural features that engender high capacitance, buffering transpiration-induced fluctuations in xylem tension by transiently releasing stored water and maintaining minimum xylem water potentials above critical values (Meinzer *et al.* 2009). These two strategies may be rephrased in terms of drought tolerance and drought avoidance, respectively. These terms describe the process by which physiological functioning is maintained under drought conditions by employing traits that allow plants to persist despite low plant water potentials and soil water, vs. those traits that increase access to water or reduce water loss (Salisbury & Ross 1992).

In this study, we quantified the sapwood capacitance of branch samples from 32 evergreen, sclerophyllous shrub and tree species growing in high- and low-rainfall environments, and on high- and low-nutrient soils, in eastern Australia. Based on the literature cited above, we predicted that species from wetter sites would have higher sapwood capacitance than those from drier sites, enabling them to survive predictable and frequent short dry periods ('drought avoiders'). By contrast, species from low-rainfall sites, the 'drought tolerators', were predicted to have lower sapwood capacitance, and thus, higher implied hydraulic safety, enabling them to survive long and unpredictable periods of low rainfall.

Perhaps most commonly capacitance has been calculated as the slope of a line fitted to the initial, approximately linear and most rapidly changing phase of the water release curve where water potentials are high (i.e. phase I, Fig. 1a; Meinzer *et al.* 2003; McCulloh *et al.* 2012). However, for our species and sites, we found that this lacked relevance to water potentials experienced by plants under field conditions. Species from the high-rainfall sites were generally found to operate within the early part of phase II (e.g. −0·5 to −1 MPa), and low-rainfall species were operating well within phase II (commonly around −3 to −4 MPa), even at dawn when xylem water potentials should be at their least negative. Consequently, we calculated capacitance as the cumulative water release (CWR) over (divided by) the 'native operating range' ($\Delta\Psi_{\text{native}}$) of each species; that is, from pre-dawn shoot water potential (Ψ_{PD}) to midday shoot water potential (Ψ_{MD}), measured in spring as part of a previous study. Calculated this way, differences in capacitance among species (and among sites) could arise via differences in CWR, in the width of their operating range ($\Delta\Psi_{\text{native}}$), or in both. In turn, these differences might relate to differences in the intrinsic shape of their water release curves, to the region of their water release curve in which they are operating (Ψ_{PD} being the quantifiable starting point), or to both. Differences in the intrinsic shape of water release curves, testable via comparisons made over common water potential intervals, are likely to be related to differences in wood anatomy (e.g. proportions of parenchyma, rays and fibre wall; proportions and diameters of vessels, tracheids and fibres). Here, we use wood density as a rough index of the anatomical construction of stems. We quantify relationships between capacitance, CWR, $\Delta\Psi_{\text{native}}$, and wood density across species, and among sites; we explore these relationships using both cross-species and phylogenetic independent contrast comparisons to determine whether cross-species relationships are due to repeated coordinated shifts across the phylogeny, or to a few, deep divergences.

Materials and methods

SITE AND SPECIES SELECTION

The site selection design was the same as that used in several previous studies (Wright, Reich & Westoby 2001; Wright & Westoby 2002); that is, two sites were chosen at higher rainfall (Ku-ring-gai Chase National Park, coastal eastern Australia; mean annual rainfall 1220 mm) and two at lower rainfall (*ca.* 500 km west at

Round Hill Nature Reserve; mean annual rainfall 390 mm). Higher-nutrient sites (clay-rich soils) and lower-nutrient sites (sand-rich) were chosen within each rainfall zone (total soil phosphorus contents at high-rainfall sites were 442 and 94 p.p.m., and at low rainfall 250 and 132 p.p.m., respectively; Wright, Reich & Westoby 2001). All four sites lie along a common latitudinal band (mean annual temperature 17·5 °C) and experience approximately aseasonal rainfall. Eight evergreen tree and shrub species were sampled at each site giving a total of 32 species from 12 plant families (see Table S1, Supporting information). These 32 species were chosen from the larger species list of Wright, Reich & Westoby (2001) because they were the more common species found at each site and also represented a wide range of plant families.

Stem samples *c.* 300 mm long and 4–6 mm in diameter were taken from the outer canopy from five individuals of each species at each site. This diameter was chosen for consistency with other studies of the same species that used 10 mm^2 sapwood cross-sectional area as a standard measurement point (e.g. Pickup, Westoby & Basden 2005). Samples were stored in a fridge (*ca.* 3 °C) in sealed plastic bags with a piece of moist paper towel and analysed within 3 weeks of collection. All samples were collected between February and April 2008.

MEASUREMENT OF SAPWOOD HYDRAULIC PROPERTIES

Water release curves were generated using the methods outlined by Meinzer *et al.* (2003). Prior to the analysis of sapwood water potentials (Ψ_s), stems were cut into three segments, 10 mm long and *ca.* 3·6 mm in diameter with bark and cambium removed. The sapwood segments were allowed to rehydrate for 12 h in distilled water. Following rehydration, the segments were quickly blotted dry, weighed and secured together in a single thermocouple psychrometer chamber (83 series; JRD Merrill Specialty Equipment, Logan, UT, USA). Each psychrometer chamber was placed in a water bath at 30 °C and allowed to equilibrate for 2–2·5 h before measurements were taken with a 12-channel digital psychrometer (Cooling current: 5 mA, Cooling time: 30 s, Delay time: 3 s, 85 series, JRD Merrill Specialty Equipment). Microvolt outputs from the psychrometer were automatically logged to a computer via an amplifier (50× amplification) and digital oscilloscope operating in data logger mode (DS1M12 Stingray; USB Instruments, Glasgow, UK). The output from the psychrometer was recorded as the mean voltage in the plateau region of the output following cessation of peltier cooling (typically recorded over a 2 s period; Andraski & Scanlon 2002). Following the first set of measurements, the psychrometer chambers were removed from the water bath, opened and the sapwood was allowed to partially dehydrate in a low temperature (*ca.* 40 °C) drying oven. The partially dried samples were then reweighed and resealed inside the chambers for further measurement of sapwood water potential. Between all measurements, psychrometer chambers were thoroughly cleaned with distilled water, ethanol and degreaser (ULS-Ultrasolve; Electrolube, Leicestershire, UK). Measurements were repeated 6–7 times until sapwood relative water content was less than 50%. A calibration curve was determined for each psychrometer chamber using filter paper soaked in a set of salt solutions of known water potential.

Curves of CWR (kg m^{-3}) against Ψ_s were generated for each replicate of each species (see Fig. 1b,c for example curves). CWR was calculated from sapwood relative water content (RWC):

$$\mathrm{RWC} = \frac{(W_f - W_d)}{(W_s - W_d)} \qquad \text{eqn 1}$$

where W_f is sapwood fresh weight, W_s is sapwood saturated weight determined after 24 h hydration, and W_d is sapwood dry weight determined after drying in an oven for more than 48 h at 60 °C (notation is taken from Meinzer *et al.* 2003; Lenz, Wright & Westoby 2006). CWR was calculated as:

$$\mathrm{CWR} = (1 - \mathrm{RWC}) \times (W_s - W_d) \times \left(\frac{(\rho \times 1000)}{W_d}\right) \qquad \text{eqn 2}$$

where ρ is wood density (g cm^{-3}) determined from the volume of sapwood segments (calculated using the equation for volume of a cylinder from measurements of length and diameter of each segment) and sapwood oven-dry weights. Sapwood capacitance can then be calculated from curves of CWR against Ψ_s (see Richards *et al.* 2013 for raw data). Expressing sapwood capacitance in terms of water release per volume of wood ensures that species' differences are due to different biophysical properties of the storage tissues rather than differences in the size of storage compartments (Gartner & Meinzer 2005).

Rather than calculating capacitance as the slope of a straight line fitted to the very steep initial phase of the water release curve [i.e. over phase I in Fig. 1a; (Meinzer *et al.* 2003)], we instead chose to calculate capacitance over the interval in Ψ_s lying between Ψ_{PD} and Ψ_{MD}, what we call the 'native operating range' in Ψ_s. That is, capacitance was calculated as the cumulative water released from Ψ_{PD} to Ψ_{MD} divided by the difference in Ψ_s between Ψ_{PD} and Ψ_{MD} ($\Delta\Psi_{native}$). Since the operating ranges of many species in our study are clearly in phase II rather than phase I of the conceptual CWR – Ψ_s graph (Fig. 1a), this approach far better represents conditions experienced by plants in the field than the more common phase I approach (straight line fitted to the initial, approximately linear and most rapidly changing phase of the water release curve).

Cumulative water release values at Ψ_{PD} and Ψ_{MD} were determined by linear interpolation between the water potential measurement points on either side of the value of interest. Values of Ψ_{PD} and Ψ_{MD} had been measured in a previous study (Lenz, Wright & Westoby 2006) on terminal twigs of all species (except *Beyeria opaca*) in spring (August–September) when weather conditions are suitable for active plant growth.

In a second step, capacitance was also determined for each species across the mean $\Delta\Psi_{native}$ for each rainfall zone (high rainfall or '$\Delta\Psi_{high\ rain}$': −0·54 to −1·03 MPa; low rainfall or '$\Delta\Psi_{low\ rain}$': −2·85 to −3·77 MPa). This approach allowed us to compare species over common ranges in Ψ_s. Most CWR curves for replicates of the low-rainfall species *Eremophila glabra* did not extend to the very low water potential values measured in the field for that species; therefore, this species was only included in analyses using the mean high- and low-rainfall shifts in Ψ_{PD} and Ψ_{MD}.

DATA ANALYSES

Mean differences in capacitance and CWR between sites were tested using linear mixed effects models, where species was included as a random effect (five individuals per species for 32 species), and rainfall (high/low) and soil nutrients (high/low) were treated as fixed effects. Model residuals were checked to ensure assumptions of normality were met, and model variance structures were specified so that a different standard deviation was used for each rainfall regime, ensuring assumptions of homogeneity of variance were met (Zuur *et al.* 2009). As capacitance, CWR and shoot water potentials were strongly right-skewed, we log$_{10}$-transformed them prior to the analysis. Bivariate trait relationships (between capacitance, CWR, wood density, Ψ_{PD}) were described using Pearson correlation and ordinary least squares regression analyses. Differences in regression slopes and elevations were tested by likelihood methods (Warton *et al.* 2006). Phylogenetically independent contrast (PIC) analyses were used to explore whether significant results from the bivariate species-based analyses resulted from repeated evolutionary trait associations spread across the phylogeny (in which case PIC and species-based analyses would yield similar results) or by a few deep divergences between clades (and thus analyses would not be significant when considered as PICs). These analyses were run using the analysis of traits (AOT) module in Phylocom 4.1 (Webb, Ackerly & Kembel 2008), with branch lengths set to one, and phylogenies based on current APG tree topology for deeper clades (families and below; www.mobot.org/mobot/research/apweb) and from Lenz, Wright & Westoby (2006) for more recent divergences. All other statistical analyses were run using the R package 'nlme' (version 2.12.0; R Foundation for Statistical Computing, Vienna, Austria).

Results

CAPACITANCE AT NATIVE OPERATING RANGES

Mean sapwood capacitance across a species' native operating range ('$\Delta\Psi_{native}$') was significantly higher for species growing at high vs. low rainfall (means 42·6 vs. 13·1 kg m^{-3} MPa^{-1}, $P < 0{\cdot}001$; Table 1, Fig. 2a). That is, on average, high-rainfall species released greater than threefold more water than low-rainfall species, per unit change in sapwood water potential. There was also a significant (but notably smaller) difference associated with soil nutrients (higher capacitance at high-nutrient sites; means 35·0 vs. 24·3 kg m^{-3} MPa^{-1}). The interaction between rainfall and nutrients was not significant. In the sections below, we tease apart the underlying causes of these site-related differences, in turn looking at the various components of capacitance (i.e. CWR, $\Delta\Psi_{native}$, Ψ_{PD} and Ψ_{MD}), and finally at the trait relationships involving wood density, a proxy for stem anatomy.

On average, CWR over $\Delta\Psi_{native}$ did not differ with site rainfall or with soil nutrients (Table 1) and thus was not the cause of the observed differences in capacitance. Although site means ranged from 10·1 to 27·6 kg m^{-3} (Fig. 2b), these were not significantly different due to the considerable within-site variability in CWR. Indeed, 55% of total variance in CWR could be ascribed to species within sites and just 7% to differences among sites, with the remaining 38% contributed by within-species variation (i.e. between replicates).

Capacitance was calculated as CWR divided by $\Delta\Psi_{native}$; thus, given the lack of site differences in CWR, presumably the differences among sites in capacitance were largely driven by differences in the width of their native operating ranges. Indeed, species at low-rainfall sites had significantly wider $\Delta\Psi_{native}$ than did high-rainfall species (Fig. 3c: means 0·93 vs. 0·49 MPa; $F_{1,28} = 15{\cdot}11$, $P < 0{\cdot}001$). That is, at low-rainfall stem water potential variation from pre-dawn (Ψ_{PD}) to midday (Ψ_{MD}) was on average twofold greater than at high rainfall, and this

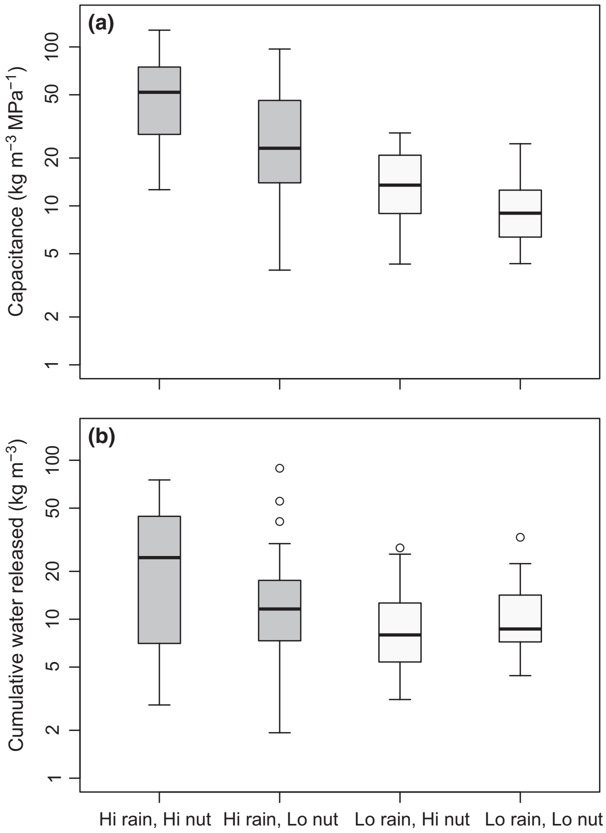

Fig. 2. (a) Sapwood capacitance and (b) cumulative water released for 30 species measured across sites with contrasting rainfall and soil nutrients. Capacitance was measured as the water released across the field determined (native) operating range, ($\Delta\Psi_{native} = \Psi_{PD} - \Psi_{MD}$) measured for each species in spring. Dark line shows median value, box represents interquartile range, whiskers extend to 1·5 times interquartile range and open circles represent outliers (*n* = 23–40). Note log scale of *y*-axes.

Table 1. Summary of the effects of rainfall (high and low) and soil nutrient content (high and low) on sapwood capacitance and cumulative water release (CWR) at species' field measured (native) operating range ($\Delta\Psi_{native} = \Psi_{PD} - \Psi_{MD}$), CWR at common $\Delta\Psi$ (i.e. mean range for species at high rainfall ($\Delta\Psi_{high\ rain}$) and mean range for species at low rainfall ($\Delta\Psi_{low\ rain}$) sites), and wood density. Linear mixed effects models were used to test the significance of fixed site effects, and species were treated as random effects

Response variable	d.f. (treatment)	Nutrients	Rainfall	Nutrients × Rainfall	d.f. (intercept)	Intercept
Capacitance	26	8·20**	42·15***	0·53^{NS}	102	1205***
CWR	26	0·59^{NS}	3·66^{NS}	1·36^{NS}	102	395***
CWR (high rain $\Delta\Psi$)	28	1·56^{NS}	0·004^{NS}	0·09^{NS}	116	1093***
CWR (low rain $\Delta\Psi$)	27	13·64**	7·66*	0·39^{NS}	96	1592***
Wood density	28	4·14^{NS}	6·05*	3·71^{NS}	103	1683***

NS, not significant.
Values reported are denominator degrees of freedom (d.f.), *F*-values and their significance: *$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

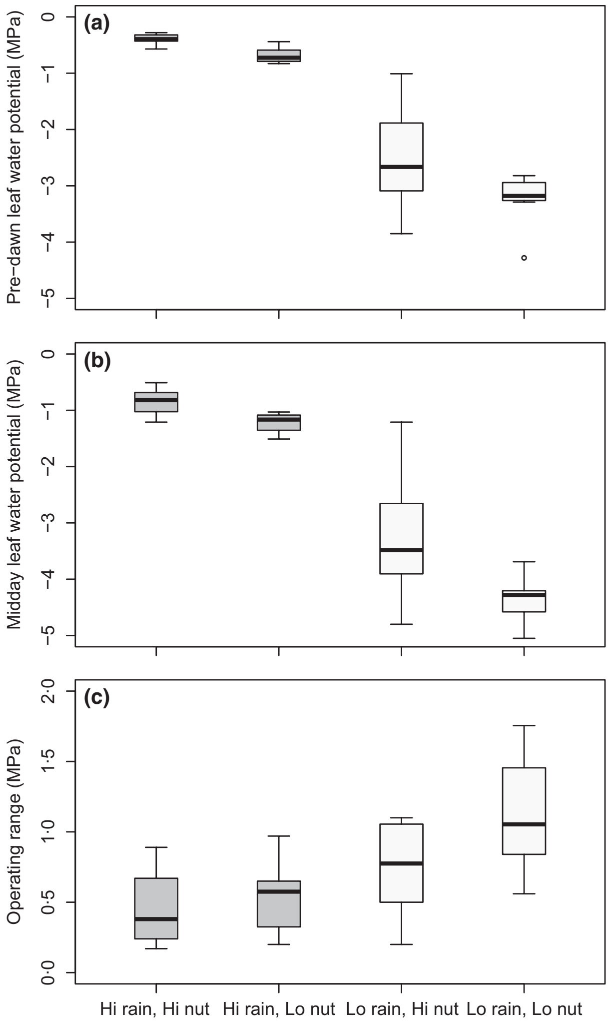

Fig. 3. (a) Pre-dawn (Ψ_{PD}), and (b) midday (Ψ_{MD}) shoot water potentials, and (c) native operating range ($\Delta\Psi_{native} = \Psi_{MD} - \Psi_{PD}$) of 31 species measured across sites with contrasting rainfall and soil nutrients. Dark line shows median value, box represents interquartile range, whiskers extend to 1·5 times interquartile range and open circles represent outliers ($n = 8$). Data are taken from Lenz, Wright & Westoby (2006).

strongly affected measured capacitance. In contrast, no differences were found in $\Delta\Psi_{native}$ under contrasting soil nutrients.

Differences among species in capacitance measured over $\Delta\Psi_{native}$ could be due to their operating over very different regions of their intrinsic water release curves (Fig. 1a). Indeed, the water release curves of high-rainfall species started at far less negative Ψ_{PD} than those of low-rainfall species (Figs 3a and 4; low rainfall: Ψ_{PD}: −2·85 MPa, high rainfall: Ψ_{PD}: −0·54 MPa; $F_{1,28} = 310{\cdot}47$, $P < 0{\cdot}001$). That is, the water release curves for most high-rainfall species started either towards the end of phase I or in early phase II (Fig. 1a), whereas those for low rainfall started in the flatter, phase II section of their curves. Furthermore, across all species (as well as within rainfall zones), capacitance and Ψ_{PD} were positively related, indicating that species that adjust their shoot water potentials overnight to less negative values were also those that showed greater capacitance. This effect was most pronounced at high rainfall, with the capacitance – Ψ_{PD} slope being significantly steeper at these sites, compared to low-rainfall sites ($P = 0{\cdot}013$; Fig. 4). On average, Ψ_{PD} was significantly more negative at low-nutrient sites (Fig. 3a; −1·87 vs. −1·46 MPa at high-nutrient sites; $F_{1,28} = 20{\cdot}75$, $P < 0{\cdot}001$), although this nutrient-related effect was far less pronounced than the rainfall-related effect. Trends in Ψ_{MD} closely mirrored those in Ψ_{PD} (Fig. 3b; −3·68 MPa at low rainfall vs. −1·03 MPa at high rainfall, $F_{1,28} = 175{\cdot}93$, $P < 0{\cdot}001$; −2·52 MPa at low nutrients vs. −2·06 MPa at high nutrients, $F_{1,28} = 16{\cdot}61$, $P < 0{\cdot}001$).

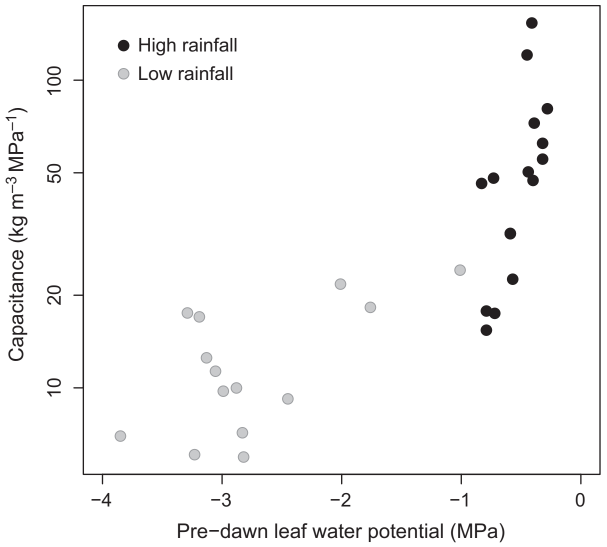

Fig. 4. Relationship between sapwood capacitance and pre-dawn shoot water potentials (Ψ_{PD}) for 30 species measured across sites with contrasting rainfall. Note log scale of *y*-axis. The slope of the linear relationship between capacitance and Ψ_{PD} was significantly steeper ($P = 0{\cdot}013$) for high-rainfall species than that fitted to low-rainfall species (high-rainfall slope: 1·09 (±0·3), $r^2 = 0{\cdot}48$, $P = 0{\cdot}003$; low-rainfall slope: 0·17 (±0·1), $r^2 = 0{\cdot}37$, $P = 0{\cdot}021$; regression lines not shown).

On average, wood density was lower in high-rainfall species (means 0·67 vs. 0·75 g cm^{-3}; Table 1) although this pattern was largely driven by species from the high-rainfall/high-nutrient site, where many species had quite low wood density (Fig. 5a). As expected, species with lower wood density showed significantly higher capacitance, although the explanatory power of this relationship was relatively weak ($r^2 = 0{\cdot}22$ across all species; $P = 0{\cdot}006$; Fig. 5b), and relationships within individual rainfall zones were not significant.

CAPACITANCE AT COMMON OPERATING RANGES

To further explore site-related differences in capacitance, we calculated for each species the estimated water release across the mean $\Delta\Psi_{native}$ for high-rainfall species ($\Delta\Psi_{high\ rain}$), and then the estimated water release across the mean

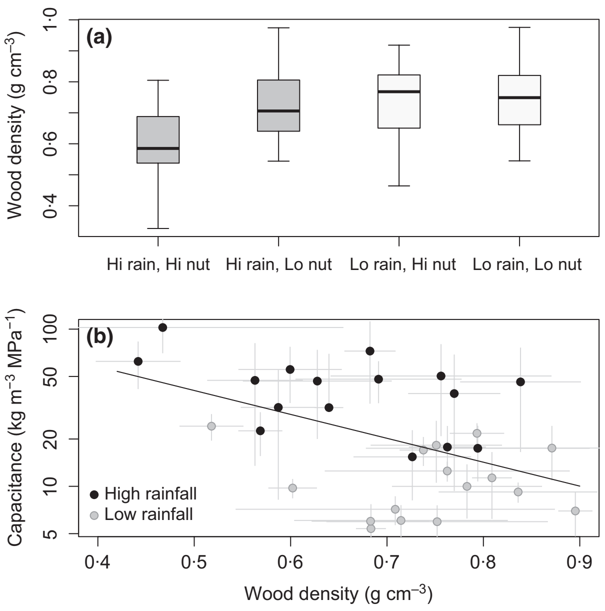

Fig. 5. (a) Wood density of 32 species measured across sites with contrasting rainfall and soil nutrients. Dark line shows median value, box represents interquartile range, whiskers extend to 1·5 times interquartile range and open circles represent outliers (n = 34–40). (b) The relationship between sapwood capacitance and wood density for 32 species measured across sites with contrasting rainfall ($\log_{10}y = -1{\cdot}52x + 2{\cdot}37$, $r^2 = 0{\cdot}223$, $P = 0{\cdot}006$). Points in (b) are means ± standard deviations. Note log scale of *y*-axis.

$\Delta\Psi_{\mathrm{native}}$ for low-rainfall species ($\Delta\Psi_{\mathrm{low\ rain}}$). Since $\Delta\Psi$ is being held constant in these comparisons, quantifying CWR is exactly equivalent to quantifying capacitance. Surprisingly, average CWR calculated across $\Delta\Psi_{\mathrm{high\ rain}}$ did not differ between sites contrasting in either rainfall or soil nutrients (Table 1), with species pooled by rainfall zone depicted in Fig. 6a (high rainfall: 21·9 kg m^{-3}, low rainfall: 23·1 kg m^{-3}, $F_{1,30} = 0{\cdot}004$, $P = 0{\cdot}95$). In contrast, average CWR calculated across $\Delta\Psi_{\mathrm{low\ rain}}$ did differ according to the site. On average, high-rainfall species released *ca.* 38% more water across $\Delta\Psi_{\mathrm{low\ rain}}$ than low-rainfall species (14·9 vs. 10·8 kg m^{-3}, $F_{1,29} = 5{\cdot}36$, $P = 0{\cdot}03$; Table 1, Fig. 6b). There was also a significant negative relationship between wood density and CWR measured across $\Delta\Psi_{\mathrm{low\ rain}}$ (Fig. 7b; $r^2 = 0{\cdot}25$, $P = 0{\cdot}007$), but no relationship between wood density and CWR measured across $\Delta\Psi_{\mathrm{high\ rain}}$ (Fig. 7a).

PHYLOGENETIC ANALYSES MIRROR 'CROSS-SPECIES' ANALYSES

The cross-species correlations described above were, for the most part, also found in evolutionary divergence analyses (see Table S2, Supporting information). This suggests that traits have evolved in coordination with each other repeatedly across the phylogeny and that the cross-species patterns did not simply arise due to differences between a few major clades.

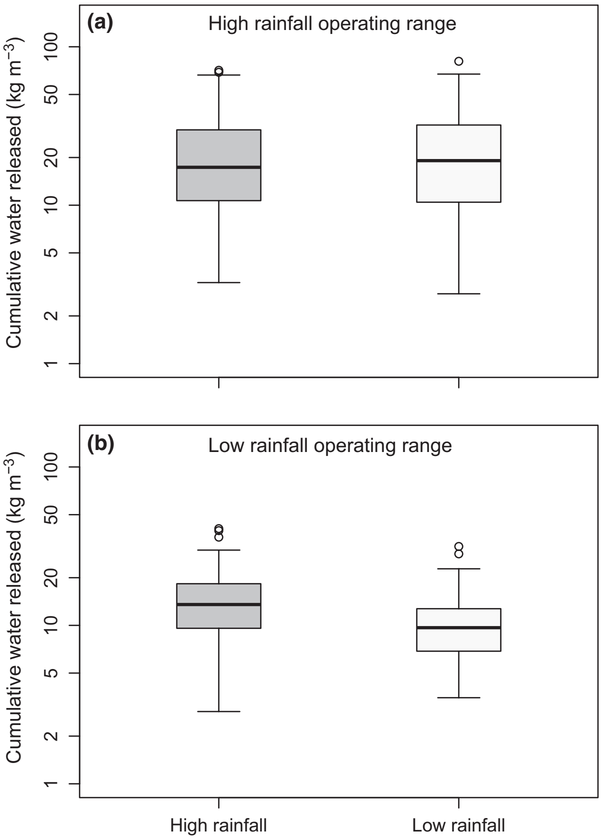

Fig. 6. Cumulative water released from sapwood of species growing at high or low-rainfall sites, measured at common operating ranges, including the mean operating range (Ψ_{PD} –Ψ_{MD}) for (a) high-rainfall species ($\Delta\Psi_{\mathrm{high\ rain}}$: −0·54 to −1·03 MPa, 32 species), and (b) low-rainfall species ($\Delta\Psi_{\mathrm{low\ rain}}$: −2·85 to −3·77 MPa, 31 species). Dark line shows median value, box represents interquartile range, whiskers extend to 1·5 times interquartile range and open circles represent outliers (n = 61–77). Note log scale of *y*-axes.

Discussion

Consistent with our predictions (and see Meinzer *et al.* 2009), measured at $\Delta\Psi_{\mathrm{native}}$, species from high-rainfall sites had higher (*ca.* 3-fold) sapwood capacitance than species from low-rainfall sites. This difference was related to less negative water potentials (both Ψ_{PD} and Ψ_{MD}) in high-rainfall species, such that these species were operating in steeper regions of their CWR curves, and low-rainfall species in flatter regions (with more negative Ψ_{PD} and Ψ_{MD}). Combined with a wider $\Delta\Psi_{\mathrm{native}}$ in low-rainfall species, this resulted in less water release over a given change in water potential and thus lower measured capacitance in low-rainfall species.

The capacitance values measured in this study (6–102 kg m^{-3} MPa^{-1}) occur at the lower end of values reported for tropical and temperate wet forest trees (17–518 kg m^{-3} MPa^{-1}; Tyree *et al.* 1991; Machado & Tyree 1994; Domec & Gartner 2001; Meinzer *et al.* 2003, 2006) or tropical savanna trees (66–186; Scholz *et al.* 2007). This result is probably not surprising given that our study

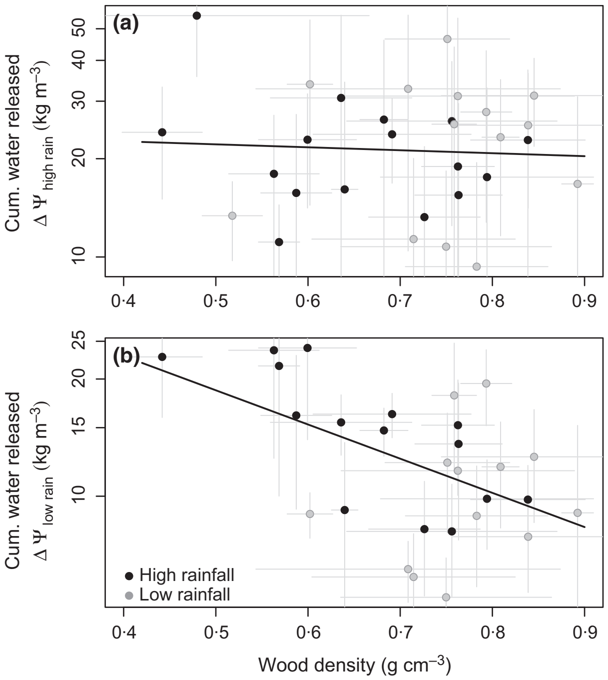

Fig. 7. The relationship between wood density and cumulative water release measured at common operating ranges, including the mean operating range (Ψ_{PD}-Ψ_{MD}) for (a) high-rainfall species ($\Delta\Psi_{\text{high rain}}$: −0·54 to −1·03 MPa) and (b) low-rainfall species ($\Delta\Psi_{\text{low rain}}$: −2·85 to −3·77 MPa), for species from high- and low-rainfall sites. Points are means ± standard deviations and note log scale of *y*-axis. Only the regression line in (b) is significant ($\log_{10}y = -0{\cdot}88x + 1{\cdot}71$, $r^2 = 0{\cdot}25$, $P = 0{\cdot}007$).

species are predominantly sclerophyllous evergreen shrubs and trees, well accustomed to periodic drought (even at high-rainfall sites). Our decision to calculate capacitance over $\Delta\Psi_{\text{native}}$ would also have contributed to the lower capacitance seen here.

As explained earlier, for our species and system using $\Delta\Psi_{\text{native}}$ was a far more logical choice than measuring capacitance within the very steep 'phase I' of species' water release curves, which presumably makes good sense for species occupying more mesic sites. Our measurements of field water potentials were taken during late winter/early spring, a generally benign time of year in this region of eastern Australia, rainfall being relatively aseasonal. Nonetheless, conditions at the low-rainfall sites were quite dry, with many species still exhibiting $\Delta\Psi_{PD}$ of around −3 MPa. Consequently, in order to remove the confounding influence of $\Delta\Psi_{\text{native}}$ on our intersite capacitance comparisons, we also compared all species under a typical low-rainfall $\Delta\Psi_{\text{native}}$ and a typical high-rainfall $\Delta\Psi_{\text{native}}$ (i.e. $\Delta\Psi_{\text{low rain}}$ and $\Delta\Psi_{\text{high rain}}$), as further discussed below.

CAPACITANCE UNDER CONTRASTING RAINFALL REGIMES

There was no difference between sites when species CWR values were compared across the mean operating range of *high-rainfall* species ($\Delta\Psi_{\text{high rain}}$). This suggests that the capacity to release water when soil moisture is abundant is very similar across species from high- and low-rainfall environments, at least in this study system. Water released at $\Delta\Psi_{\text{high rain}}$ is removed in the steeper sections of the water release curve (Fig. 1a), presumably from easily accessible stores, such as intercellular capillary spaces and very elastic storage spaces. However, compared across the mean *low-rainfall* operating range ($\Delta\Psi_{\text{low rain}}$), high-rainfall species released on average 38% more sapwood water than low-rainfall species. This result suggests that at these far more negative water potentials, there is a systematic difference in the slope of water release curves for high-rainfall species (steeper) and low-rainfall species (flatter). These findings are consistent with theory put forward by Meinzer *et al.* (2009) suggesting that species that experience very low stem water potentials, such as those growing in low-rainfall environments, should have wood anatomies conferring greater resistance to embolism (a 'drought tolerance' strategy); but, in so doing, they experience a trade-off with lower capacity for water discharge from living tissues, via elastic cell walls or cavitation. On the other hand, species from high-rainfall environments rely on the transient release of stored water to reduce fluctuations in xylem water potential; a 'drought avoidance' strategy which is effective in regions where only short-term dry periods occur. Modelling suggests that the marginal loss in hydraulic conductivity from sapwood water release via cavitation is more than compensated by the release of tension in the transpiration stream, providing a short-term physiological advantage, in terms of photosynthesis, to plants growing under dry conditions (Hölttä *et al.* 2009). However, under extended droughts experienced in more arid areas, a high capacity to release water through cavitation may lead to dangerous, runaway cavitation, xylem dysfunction and a reduction in long-term carbon gain (Tyree & Zimmermann 2002).

Still, we need to be careful in speculating too much about associations between the proposed phases of water release (cf. Tyree & Yang 1990) and site-related differences among species, as our measurements are based on small sapwood sections that would be unlikely to contain intact vessels. We also acknowledge that branch capacitance measures may not relate directly to whole tree hydraulic functioning under different rainfall regimes (Meinzer *et al.* 2010; Barnard *et al.* 2011), particularly in tall trees with considerable trunk tissue. However, of the 32 species studied here, only five are clearly classified as trees, with all others classed as shrubs or small trees, where our branch samples were generally representative of the majority of plant stems.

CAPACITANCE AND STEM CONSTRUCTION

Previous studies have shown that species with higher wood density have lower sapwood capacitance (Scholz *et al.* 2007; Meinzer *et al.* 2008a). Our data also show this pattern, with species from low-rainfall sites having higher wood density and lower sapwood capacitance (across $\Delta\Psi_{native}$) than those at high-rainfall sites. However, interestingly, when CWR (and thus capacitance) was estimated for all species under typical high-rainfall conditions ($\Delta\Psi_{high\ rain}$), there was no longer any relationship with wood density, while CWR at $\Delta\Psi_{low\ rain}$ and wood density were negatively correlated (albeit somewhat weakly). That is, it seems that (at least among these species) the differences in anatomy best indexed by wood density have the greatest influence on water storage and release at lower water potentials.

Dense wood can be produced through a number of mechanisms including variation in tissue wall thickness, increased concentrations of non-structural compounds (e.g. starch and resin) or differences in the fraction of different sapwood tissue types (e.g. fibres, parenchyma, vessels and rays; Chave *et al.* 2009), all of which may affect wood water storage and capacitance to varying extents. Several recent studies have speculated that wood density may not be a unifying trait for hydraulic functioning in plants, because it describes such a broad range of possible anatomies, even at a given density (Chave *et al.* 2009; Martinez-Cabrera *et al.* 2009; Meinzer *et al.* 2010). More detailed studies of wood anatomical differences, rather than wood density alone, may uncover more relevant correlates of sapwood capacitance.

CAPACITANCE UNDER CONTRASTING SOIL NUTRIENTS

On average, sapwood capacitance was 44% higher at higher-nutrient sites, suggesting (as might be expected) that soil properties can influence plant hydraulic traits. In these systems, the higher-nutrient soils are more finely textured, with a greater percentage of clay rather than sand. The lower capacitance values on sandy, low-nutrient soils were due to a shift to both a lower Ψ_{PD} and Ψ_{MD}, resulting in less water release for a given change in water potential (because calculations were performed from the flatter section of the water release curve). This finding is inconsistent with some previous studies that found plants growing on fine textured (clay) soils had lower shoot water potentials, greater resistance to root and shoot cavitation and shallower rooting depths relative to coarse textured (sandy) soils (Hacke *et al.* 2000; Sperry & Hacke 2002; Xu & Li 2008). Since capacitance is inversely related to cavitation resistance in roots and shoots (Pratt *et al.* 2007; Meinzer *et al.* 2008b; Sperry, Meinzer & McCulloh 2008) and positively correlated with Ψ_{PD} (Fig. 4) and rooting depth (Domec *et al.* 2006), these findings suggest that plants growing on clay soils should have lower capacitance than those growing on sandy soils, opposite to what we observed. Perhaps differences in soil nutrients rather than soil texture are a better explanation for differences in capacitance across contrasting soil textures? For example, higher soil nutrient availability, which is often associated with greater investment in canopy biomass relative to roots (Coomes & Grubb 2000), may increase plant reliance on stem-stored water to maintain transpiration rates during the day and into the dry season, relative to uptake of soil stored water.

Conclusions

Overall, our findings confirmed our prediction that plants from high-rainfall environments would have greater sapwood capacitance than low-rainfall species. This resulted from a combination of lower Ψ_{PD}, wider $\Delta\Psi_{native}$ and flatter water release curves in low compared to high-rainfall species. By contrast, CWR showed considerable species-level variation but did not differ between sites and therefore did not determine site differences in capacitance.

These findings have potential implications for shifts in species traits under climate change. For example, McDowell *et al.* (2008) put forward evidence that prolonged drought could cause hydraulically mediated carbon starvation resulting in differential vegetation mortality and changes to plant community composition, with communities filled by drought tolerant species. In south-east Australia, it has been predicted that mesic environments will experience more frequent or longer dry periods under climate change (Whetton, Moise & Abbs 2011). These climatic shifts could result in decreased abundance of species that have traits associated with high sapwood capacitance (drought avoiders), due to greater incidences of hydraulic failure, compared to those with woody tissues that are less vulnerable to drought-induced embolism and, therefore, have lower capacitance (drought tolerators; Choat *et al.* 2012).

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Data accessibility

Data deposited in the Dryad repository: http://doi.org/10·5061/dryad.hm482 (Richards *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean pre-dawn (Ψ_{PD}) and midday (Ψ_{MD}) shoot water potentials, wood density (ρ), cumulative water released (CWR) and sapwood capacitance for 32 species.

Table S2. Correlations of phylogenetically independent contrasts (PIC) and cross-species values.