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**Hydraulic architecture and water relations of several species at diverse sites
around Sydney**

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Running heading: Hydraulic architecture of Sydney native trees

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Abstract

We made seasonal comparisons of leaf water potentials, root biomass, hydraulic architecture, xylem embolism, and xylem conduit dimensions in eight woody species growing in four diverse habitats common in the Sydney region, namely mangroves, coastal heathland, ridge-top woodland and woodland at the base of the ridge. We assessed these vegetation characteristics in the context of seasonal variation in site microclimate (rainfall, temperature, light flux density and vapour pressure deficit). Some species were common to more than one habitat.

Pre-dawn leaf water potential and minimum leaf water potentials were lowest at all times in the two mangrove species. In the mangrove, leaf water potentials were lower in summer than winter, but in all other habitats, water potentials were generally lower in winter than summer. Root biomass was larger in all habitats in summer than winter.

Huber values were generally smaller in winter than summer for all species in all habitats. In contrast, branch hydraulic conductance (absolute value or expressed per unit leaf or sapwood or branch cross-sectional area) were larger in summer than winter. Similarly branch conductivity (absolute or expressed per unit leaf area, sapwood area or cross-sectional area) were generally larger in summer than winter across all species in all habitats. An inverse relationship between Huber value and conductivity was observed across all four habitats.

In 8 of 11 species comparisons, percentage loss in xylem conductance was larger in summer than winter. Similarly, temperature, rainfall, photosynthetic photon flux density and root biomass tended to be larger in summer than winter. Significant species and habitat differences in xylem dimensions and pit pore membrane diameter were observed.

These results are discussed in relation to patterns and relationships amongst water relations, microclimate and hydraulic architecture.

Introduction

Hydraulic architecture varies in different plant types and can potentially limit the flow of water to the leaves, influencing leaf water potential, stomatal behaviour, gas exchange, and tree height (Tyree and Ewers 1996). Hydraulic conductivities tend to be larger in mesic sites than xeric sites (Van der Willigen and Pammenter 1998; Eamus and Prior 2001), so differences in hydraulic architecture may help to explain species habitat preferences.

Parameters used to describe hydraulic architecture include hydraulic conductance, hydraulic conductivity and Huber value (H_v). Hydraulic conductance and conductivity vary according to soil water status. Drought-stressed plants experience smaller mean conductance and conductivity per leaf area and per sapwood area, lower transpiration rates, lower Huber values, more negative osmotic potentials and a higher degree of xylem embolism, compared with well-watered plants (Tognetti *et al.* 1997).

Other environmental factors that influence water balance, such as water availability, temperature, humidity, solar radiation and wind can affect the efficiency of the hydraulic architecture of a plant. Differences in hydraulic conductivity per sapwood area in desert sites compared to montane sites have been attributed to differences in temperature and evaporative demand between these sites (Maherali and DeLucia 2000). Mencuccini and Grace (1995) note variation in H_v and conductance within a species in response to site differences in VPD and soil water status.

Leaf water potential varies with transpiration and is influenced by evaporative demand and soil moisture availability. The water potential of a tree comes into equilibrium with the soil overnight (Borel *et al.* 1997), hence pre-dawn water potential is indicative of soil moisture content within the root zone (Prior *et al.* 1997). Pre-dawn water potential is therefore an indicator of water status, while minimum leaf water potential experienced in the day is an indicator of the maximum water stress in the plant, on that day.

Xylem embolism occurs when the continuity of the water column in xylem conduits breaks causing cavitation (Tyree and Ewers 1991). Xylem embolism is a function of

hydraulic architecture and soil and atmospheric water content. Xylem embolism reduces hydraulic conductivity, requiring steeper pressure gradients between roots and leaves to maintain transpiration. Different functional plant groups have varied vulnerability to xylem embolism (Eamus and Prior 2001) and seasonal and site factors can influence xylem embolism within one species (Van der Willigen and Pammenter 1998). Vulnerability to embolism induced by water stress is similar in deciduous and evergreen plants, but higher in tropical plants compared with temperate forest species (Machado and Tyree 1994; Sobrado 1997). As leaf water potential declines, plants growing in humid environments experience a much higher percentage embolism compared with plants growing in semi-arid environments (Franks *et al.* 1995). Xylem embolism can be prevented through regulation of stomatal conductance by limiting the change in water potential across the whole plant (Cochard *et al.* 1994).

Most comparative studies of hydraulic architecture have focused on American and European species (e.g. Chiu and Ewer 1992; Patiño *et al.* 1995; Hubbard *et al.* 1999; Brooks *et al.* 2002) although there have been some tropical studies (Tyree and Ewers 1996; Prior and Eamus 2000), the latter study in Australia. However, we know very little about the comparative hydraulic architecture of trees in contrasting Australian habitats, the significance of different architectural systems and their contribution to competition among species (Tyree and Ewers 1991). The present study is the first to compare hydraulic characteristics in species from different temperate ecosystems in Australia. Australian ecosystems generally experience drier soil and atmospheric conditions and lower nutrient levels in comparison to northern hemisphere environments, and hence present a unique challenge for plant water relations. Understanding hydraulic architecture of different species will provide insight into plant adaptations to particular ecosystems. It may also allow us to predict the impacts of global climate change or breed more stress-resistant trees (Tyree and Ewers 1991).

In the present study, we examined microclimate, leaf water potential and hydraulic architecture of several species in four diverse habitats: mangroves, coastal heathland, and eucalypt woodland sites on a sandstone ridge (ridge-top woodland) and at the base of the ridge (river-flat woodland). The four habitats were chosen because (a) they represent significant habitats in temperate Australia; (b) they differ substantially in vegetation structure and composition; (c) some species can be found in more than one

habitat; (d) the water balance of each habitat is likely to differ significantly, but gross climatological factors (average temperature, rainfall, solar radiation receipt at the top of the canopy) are likely to show only small variation between habitats.

The aims of the work described in this study were to answer the following questions:

- 1) How does microclimate differ between four diverse habitats located within a small geographical range?
- 2) How does leaf water potential and soil moisture content vary between species within a single habitat and how do average habitat differences vary between the four habitats?
- 3) How does the hydraulic architecture vary between species and between habitats?
- 4) Do xylem cell dimensions differ between species and between habitats?

Materials and Methods

Study sites

Mangroves, heathlands and woodlands are common in the Sydney region, particularly on Sydney sandstone soils. Stands of mangroves consist of two species, *Avicennia marina* (Avicenniaceae) which grows to 6 m and the less-common *Aegiceras corniculatum* (Myrsinaceae) which grows to 4 m.

Heathlands in Sydney are dominated by a number of species. The heathland used in this study was dominated by *Leucopogon microphyllus*, *Epacris microphylla*, *Darwinia fascicularis*, *Conospermum longifolium*, *Sprengelia incarnata*, *Allocasuarina distyla*, *Isopogon anethifolius*, *Angophora hispida*, *Banksia oblongifolia* and *Petrophile pulchella*, interspersed with a *Xanthorrhoea* sp. Vegetation is mostly less than 1 m high, growing to 2 m in isolated patches.

Woodlands in Sydney are dominated by different species according to their elevation, aspect, slope and microclimate. In this study, two adjacent woodlands were assessed. The first, at the top of a ridge, is 150 m above sea level and is dominated by *Eucalyptus haemostoma*, growing to a height of 10 m. The understorey consists of a number of shrubs including *Gompholobium grandiflorum*, *Acacia suaveolens*, *Grevillea buxifolia*, *Petrophile pulchella*, *Xanthorrhoea* sp., *Bossiaea scolopendria*, *Angophora hispida*, *Banksia oblongifolia* and *Dianella revoluta*.

The second woodland site is 10 m above sea level, on the river flat below the ridge site. The canopy, consisting of a number of *Eucalyptus*, *Angophora*, *Casuarina* and *Banksia* species reaches 20-25 m but averages 13 m. There are a number of dominant vines in the canopy (*Pandorea pandorana*, *Smilax glycopylla* and *Cissus hypoglauca*) and understorey species include, *Pteridium esculentum*, *Trema aspera*, *Istrotricha floccosa*, *Bursaria spinosa*, *Dodonaea triquetra*, *Grevillea linearis*, *Glochidion ferdinandi*, *Lomandra longifolia*, *Adiantum aethiopicum*, *Dianella revoluta* and *Ziera smithii*.

The mangrove, and both woodland communities are in Crosslands Reserve, 30 km north of Sydney (33°40'S 151°10'E). Both woodland communities are on Sydney sandstone soil.

The coastal heathland site is in Royal National Park (34°10'S 151°10'E), 30 km south of Sydney. The site is on the Walumarra track, 15 km from the park entrance, on Sydney sandstone soil.

Vegetation attributes, microclimate and soil moisture

Each 1 ha site in each habitat was divided into two plots to provide replication at each site. Tree height was determined for 15-20 randomly chosen trees in each plot in each habitat using a clinometer. Diameter at breast height (DBH) was determined for each of these trees (only trees over 2 m high were measured). DBH was not determined in the heathland as all vegetation was below 2 m. Foliage Projective Cover (FPC) was calculated for each site by holding a mirror at 45° and recording whether the sky or foliage covered the central point of the mirror whilst walking a series of transects at each location. Data were recorded every meter along four transects of 25 m in length. As the canopy was not overhead in the heathland a downward facing mirror was used to measure the frequency of leaves or bare soil along the transect.

Root biomass of the upper soil profile was determined in each habitat by collecting three random samples in each plot (a total of six samples per habitat). A volume of 8000 cm³ of soil was collected to a depth of 20 cm. Roots were extracted from each sample and washed thoroughly before being placed in an oven at 70 °C for three days and then weighed.

Wet and dry bulb temperatures were recorded with a whirling hydrometer every ninety minutes starting at 6 am and finishing at 5 pm. From the wet and dry bulb temperatures relative humidity and vapor pressure deficit (VPD) were calculated. Air temperature was recorded with a thermometer every 90 minutes in the shade and sun at each site, where possible. Photosynthetically active radiation (PAR, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was determined using a LI – 1400 datalogger with a LI-COR Quantum light sensor (LI-COR Inc. USA). Every 90 minutes ten samples were recorded along a 10

m transect. Relative humidity, VPD, air temperature and PAR were measured for each day of leaf water potential sampling (see below).

Soil moisture was measured using a Theta Probe Soil Moisture Sensor (Delta-T Devices Ltd, ML2x). Ten measurements were randomly made per plot every 90 minutes and soil content recorded in volts. These measurements were calibrated by collecting soil samples from each site with a range of water contents and determining their gravimetric water content and soil moisture content with the theta probe.

Mean monthly rainfall and temperature data for Sydney airport and Marsfield/Macquarie University were obtained from the Bureau of Meteorology. These are the closest meteorological stations to Royal National Park and Crosslands Reserve, respectively.

Leaf water potential

Pre-dawn and diurnal leaf water potentials were determined for each species in each habitat for each of the study species using a pressure bomb (Model 3000, Soil Moisture Equipment Corp. USA). Measurements were taken every ninety minutes throughout the day between 6:30 am and 4:00 pm.

Leaf water potential from randomly selected trees was determined for one leaf from each of two branches, from three trees of each species, in each of the two plots in each habitat. Mean pre-dawn water potential and mean minimum water potential (generally the mid-day sample) was calculated for each species and habitat in summer (January) and winter (June). Two-way ANOVA was used to determine whether there were significant differences between season and species and season and habitat. Tukey's *post hoc* comparison was used to determine where the differences lay (STATISTICA v. 2).

Hydraulic conductance, conductivity and Huber values

Hydraulic conductance was determined using the method described by Prior and Eamus (2000). Branches were collected before 9:00 am to avoid the diurnal period of

most stress. Two terminal branches were cut under water from each of three plants in each of the two plots, for the determination of hydraulic conductance. These branches were then placed upright in a container of water and covered with a black plastic bag to reduce transpiration during the 60-90 minute trip to the laboratory. Once in the laboratory all leaves and petioles were removed under water with a razor blade. Basal and distal ends of the branch were both re-cut under water. Branches were then connected to graduated 1 ml pipettes via tubing filled with degassed, filtered (0.22 μm), acidified (pH 2, HCl; Sperry *et al.* 1994) water.

Hydraulic conductance was determined using two vacuum systems approximately 2 m long and 30 cm wide, each of which could accommodate three branches. The solution was pulled through the branch in the normal direction of the transpiration stream by applying a vacuum to the chamber. Flow rate of the acidified de-gassed water was measured at four levels of vacuum (pressure difference (ΔP) = 20, 30, 40 and 50 kPa), which was measured with a vacuum gauge (Leybold, Germany). Branches were allowed to reach an equilibrium flow rate before measurements of flow rate.

Hydraulic conductance ($\text{mg s}^{-1} \text{MPa}^{-1}$) was calculated as the slope of the relationship between flow rate and pressure difference using linear regression. Hydraulic conductance was also expressed per leaf area, branch transverse area and sapwood area of the branch at the proximal end of the cut. Hydraulic conductivity ($\text{mg cm s}^{-1} \text{MPa}^{-1}$) was calculated by multiplying the conductance by the branch length and was also expressed in terms of leaf area, sapwood area and branch transverse area.

Huber values were calculated as the branch transverse area per leaf area. The diameter of the basal end of each branch was measured using a micrometer and the length of each branch was measured with a ruler. Leaf area attached to each branch was determined using a WinDIAS (Type WDIGC-2 Delta-T Devices Ltd, UK) leaf area meter. Sapwood cross-sectional area was determined by soaking thin sections of branch in 0.5% toluidine blue solution. The stained sapwood area was measured with a calibrated eyepiece micrometer.

Hydraulic characteristics are reported as species and habitat means. Two two-way ANOVAs were used to find differences between species and season and habitat and

season. Tukey's *post hoc* comparisons were used to determine where the differences lay (STATISTICA v.2).

The relationship between Huber value and conductivity was investigated by taking the natural logarithm of both (to normalise distribution) and then conducting a Pearson's correlation with SPSS for windows.

Xylem embolism

The initial determination of hydraulic conductance was followed by a 30 minute perfusion of acidified, filtered, degassed water at a positive pressure of 175 kPa to remove any air emboli, where present (Williams *et al.* 1997). Compressed nitrogen was used to pressurize a reservoir of water to 175 kPa. After perfusion, each branch was removed from the vacuum system and approximately 2-3 mm was cut from the basal end before hydraulic conductance measurements were repeated. To allow tubing and xylem vessels to relax measurements were resumed approximately 10 minutes after perfusion (Prior and Eamus 2000). The percentage difference in conductance was calculated from the initial and final readings and this value represents the percentage loss in conductance due to embolism (Williams *et al.* 1997; Sperry *et al.* 1988) *in vivo*.

Some branches experienced a slightly reduced conductance after perfusion. Wang *et al.* (1992) experienced the same phenomenon and attributed it to plugging of the vessels by particles or micro-organisms already in the vessels and not easily flushed out. In these cases the percentage loss of conductance due to embolism was taken as zero.

Loss of conductance data were arcsine transformed and the relationship between loss of conductance and minimum leaf water potential was assessed with a Pearson's correlation (SPSS for windows).

Xylem dimensions

Branches between 0.5 and 1 cm diameter were cut to 1 cm lengths and placed in approximately 10 ml maceration fluid (1 part hydrogen peroxide, 4 parts distilled water and 5 parts glacial acetic acid). The mixture was placed in the oven for five days at 56°C, longer for hardwood species. Stems were removed from the maceration fluid and shaken in small vials with about 5 times as much water as tissue. Two drops of this solution was placed on a slide with one drop of 0.5% toluidine blue. Cell length and diameter of spiral, reticular and pitted xylem vessels and pit pore dimensions were measured with a calibrated eyepiece micrometer.

The relationship between loss of conductance due to xylem embolism and pit pore length and pitted cell length was assessed with Pearson's a correlation (SPSS for windows). Pitted cell length was log-transformed to normalise the distribution of data.

Results

Site microclimate and soil water content

Mean monthly rainfall did not show a strong seasonal pattern for any of the sites. Rainfall was similar during January and June (the sample months) (Fig. 1). Temperature differences were more seasonal, with a monthly average of approximately 17°C in June at both locations and a monthly average above 25°C throughout the summer months (Fig. 1).

VPD and PAR values were much higher in summer than in winter at each site (Table 1). The highest winter VPD was recorded at the heathland site, while the highest summer VPD values were recorded at the two woodland sites. Summer PAR was highest at the heathland site and lowest at the woodland ridge-top site. Winter PAR was very low at the mangrove and woodland (below ridge) sites and higher at the woodland (ridge-top) site. Soil moisture was more uniform between seasons except at the heathland, where there was approximately half as much water in the soil in summer than in winter (Table 1).

DBH was largest at the woodland (ridge-top) site and the woodland (below-ridge) site had the tallest canopy. The largest FPC was observed at the mangrove site (Table 2).

Root biomass was largest in the summer in all habitats. Similar root biomass was observed in the mangrove and heathland in the summer and these habitats exhibited the largest root biomass of all habitats.

Leaf water potentials

Pre-dawn leaf water potential (Ψ_{pd}) was lower in summer than winter for both mangrove species (Fig. 2a). *A. corniculatum* and *A. marina* had different Ψ_{pd} values in the winter but similar values in the summer. The minimum leaf water potential for these species also occurred in the summer for both species (Fig. 2b). Similarly, winter values of minimum leaf water potential were also different between the two species (Fig. 2b) in the mangrove.

All woodland species at the top of the ridge had similar pre-dawn leaf water potentials within both seasons but all species were different between seasons (Fig. 2a). Ψ_{pd} (Fig 2a) and minimum leaf water potentials (Fig 2b) were lower in winter than in summer for all species at the top of the woodland.

A similar trend to that observed in the ridge-top site was observed in Ψ_{pd} values for species growing at the woodland site below the ridge, except for *B. integrifolia* in summer, when Ψ_{pd} was significantly lower than for all other species (Fig. 2a). *B. integrifolia* showed seasonal differences in minimum leaf water potential, as did *C. hypoglauca* (Fig. 2b). Minimum water potential of these two species was significantly different but this parameter was the same in winter for *C. hypoglauca* as *G. ferdinandi* in both seasons (Fig. 2b).

Pre-dawn leaf water potentials were the same for all species in the summer in the heathland (Fig. 2a). At this site, winter Ψ_{pd} values were all significantly lower than the summer values and Ψ_{pd} was similar for *A. hispida* and *P. lanceolata* but was higher in *B. oblongifolia* (Fig. 2a). Minimum leaf water potentials were lower in the

winter than in the summer for the three heathland species and were lower in *A. hispida* and *B. oblongifolia* than *P. lanceolata* in both seasons (Fig. 2b).

Ecosystem means show that the lowest pre-dawn leaf water potential occurred in summer in the mangroves (Fig. 3a). The mangrove mean winter pre-dawn leaf water potential was also lower than in the other three habitats in both winter and summer. Mean winter pre-dawn leaf water potentials in the woodland (ridge-top) and in the heathland were similar and both were lower than their respective summer means. There was no difference in Ψ_{pd} between seasons in the woodland (below-ridge) species and these values were the highest for any habitat (Fig. 3a).

Minimum leaf water potentials were lowest in the summer for both mangrove species, followed by winter mangrove and woodland (ridge-top) species (Fig. 3b). Woodland (ridge-top) and heathland species had significantly lower leaf water potentials in winter than summer, while woodland (below-ridge) values were similar between seasons (Fig. 3b). Leaf water potentials in the woodland (below ridge) site were not significantly different from those at the heathland site.

Hydraulic architecture – comparisons within habitats

Both mangrove species had higher Huber values in winter than in summer (Table 3). In contrast, hydraulic conductance, conductance per branch transverse area and conductance per sapwood area were all higher in summer for both species but hydraulic conductance per leaf area was the same across seasons and both mangrove species. All hydraulic conductivity values were higher in summer than winter and there was no significant difference between species within a season (Table 3), in the mangrove.

For woodland (ridge-top) species, season influenced Huber values, but species did not (Table 4). Thus, Huber values were larger in winter than summer. Hydraulic conductance and conductance per branch transverse area were similar across species and seasons, except for *A. hispida* in summer (Table 4). Hydraulic conductance per leaf area varied between species but not seasons, with *A. hispida* intermediary

between *E. haemostoma* and *B. oblongifolia*. Hydraulic conductance per sapwood area was seasonally different in *A. hispida* with most values for other species at this site falling within the seasonal range exhibited by *A. hispida* (Table 4). Hydraulic conductivity, conductivity per leaf area, conductivity per branch transverse area and conductivity per sapwood area were similar across species for winter and in most cases, were significantly larger in summer than winter within species (Table 4). There were some differences between species in summer hydraulic conductance and conductivity values; hydraulic conductivity and conductivity per sapwood area were larger in *A. hispida* than in *E. haemostoma* and *B. oblongifolia*, while hydraulic conductivity per branch transverse area was larger in *A. hispida* than *B. oblongifolia*.

Of the woodland (below ridge) species, *C. hypoglauca* was the only one to have a significant difference in seasonal Huber values (Table 5). Hydraulic conductance and conductance per branch transverse area were largest in *C. hypoglauca* and lowest in *B. integrifolia*. Hydraulic conductance per leaf area within the three species was larger in winter than summer. Summer conductance per sapwood area was significantly larger in *C. hypoglauca* than in *B. integrifolia* (Table 5). Values of hydraulic conductivity, conductivity per branch transverse area and conductivity per sapwood area were similar across species and seasons, except for *C. hypoglauca* in summer, in which they were significantly larger than for all other species (Table 5).

Huber values at the heathland site varied seasonally for *A. hispida* and *P. lanceolata* but not for *B. oblongifolia* (Table 6). Complex interactions between season and species factors meant that no one species had a higher Huber value overall than any other. Hydraulic conductance was larger in summer than winter for *P. lanceolata*. Hydraulic conductance per leaf area was larger in *P. lanceolata* than *A. hispida*, while differences in conductance per branch transverse area and conductance per sapwood area were dominated more by differences between seasons than species differences. Hydraulic conductivity and conductivity per leaf area were similar across species and seasons except for *P. lanceolata* in summer. Conductivity per branch transverse area and conductivity per sapwood area were larger in summer for *A. hispida* and *P. lanceolata* (Table 6).

There was an inverse linear relationship between the log-transformed branch conductivity and log-transformed Huber value (Fig. 4; Pearson's correlation coefficient = -0.73, $p = 0.000$).

Hydraulic architecture – comparison among habitats and seasons

Huber values were larger in winter than summer for all habitats (Table 7). Huber values were more similar in summer than winter for all habitats, with the woodland (ridge-top) values larger than all other values (Table 7). In most comparisons all measures of hydraulic conductance (per unit leaf area, per sapwood area, per transverse area) were larger in summer than winter in the four habitats (Table 7). Similarly, for most comparison, all expressions of hydraulic conductivity were larger in summer than in winter for all four habitats (Table 7).

Xylem embolism

In mangroves and woodlands (ridge top), the habitat mean percentage embolism was larger in summer than in winter. In contrast, the habitat mean for percentage embolism was larger in winter than in summer for the heathland and woodland (below ridge) sites.

Investigations of xylem cell structure and size revealed that only the *Banksia* species had reticular xylem cells and *B. integrifolia* had no spiral cells (Table 9). *G. ferdinandi* and *C. hypoglauca* had the widest and longest pitted cells and *A. corniculatum* and *A. marina* had the thinnest, shortest xylem cells.

The relationship between percentage loss of conductance and minimum leaf water potential gave Pearson's correlation coefficients of -0.62 ($p = 0.012$) and -0.54 ($p = 0.045$) for winter and summer respectively (Fig. 5). The seasons were treated separately because there was an interaction between the effect of season and minimum leaf water potential on the loss of conductance ($F = 6.492$, $p = 0.007$; General Linear Model, SPSS for windows).

Seasons were also treated differently for comparisons of pit pore length ($F = 6.603$, $p = 0.008$, GLM) and pitted cell length ($F = 12.772$, $p = 0.000$) with loss of conductance due to xylem embolism. Pearson's correlation coefficients for winter were -0.418 ($p = 0.115$) and -0.591 ($p = 0.036$) for pit pore length and log-transformed pitted cell length respectively and values for summer were -0.610 ($p = 0.031$) and -0.781 ($p = 0.004$) for pit pore length and log-transformed pitted cell length respectively.

Discussion

The amount of light (PAR), the vapour pressure deficits and temperature all increased in the summer, compared to the winter (Table 1, Fig 1). In addition, rainfall was slightly higher in the summer than in the winter (Fig 1). The increase in evaporative demand (that is, increased temperature, VPD and solar radiation input) are likely to cause the significant decline in pre-dawn and minimum leaf water potential expressed by both mangrove species in the summer compared to the winter. Such responses of leaf water potential to evaporative demand are well-documented (Eamus and Prior 2001). The much lower absolute values for the two mangrove species are a result of the influences of salinity in the root environment. A much lower leaf water potential is required to maintain water uptake from saline soils compared to non-saline soils.

The three non-mangrove habitats (heathland and woodlands) showed either lower pre-dawn and minimum leaf water potentials in the winter compared to the summer, or a non-significant difference (Figs 2,3). Clearly this can not be explained by seasonal changes in evaporative demand, and is discussed below.

In the winter pre-dawn water potentials, and to a less pronounced extent, minimum leaf water potentials, were lower in the woodland at the top of the ridge and in the heathland, than in the woodland at the base of the ridge. In winter the reduced rainfall (compared to summer) and the higher degree of exposure to wind, high levels of light and, in the case of the heathland, salt spray) probably explained this result.

Furthermore the significance of enhanced run-off of rainfall to the below-ridge woodland site (as reflected in the higher soil moisture at this site compared to the ridge-top) also exacerbated this result. In the summer the trend was less pronounced because of the interaction of increased rain, the very large increase in average light

levels that occurred predominantly in the below-ridge woodland, and the largest absolute value in VPD that was experienced in the summer in the below-ridge woodland.

How do we account for the increase in pre-dawn and minimum water potential observed in summer for the three terrestrial ecosystems despite the larger evaporative demand (higher VPD, temperature and solar radiation input)? First, rainfall was larger in the summer than the winter. In contrast to the mangroves, rainfall is the principal source of water to the roots. In mangroves, daily inundation by tidal water is the principal source of water. Consequently the impact of a large rainfall in the summer will be expressed in the predawn and minimum leaf water potentials of terrestrial plants more than species of mangrove. Two additional features may also contribute to the generally higher water potential observed in the summer compared to the winter. First, root biomass (and hence presumably increased capacity for water uptake) was always larger in summer than winter. Second, hydraulic conductance and conductivity were generally larger in summer than winter for all habitats. Of 36 seasonal comparisons (8 hydraulic measures x 4 habitats; Table 4), 30 show an increase in summer and two show no change. During the spring and summer months when new leaf tissue has been produced and is expanding, new xylem is also produced. Domec and Gartner (2002) showed that early wood (new xylem) is more conductive than latewood due to larger tracheid diameter in the early wood, possibly because of an enhanced water status during earlywood formation (Nardini and Tyree 1999). Because of the higher conductance/conductivity, the gradient in water potential required to cause a given rate of water flow is reduced (Patino *et al.* 1995) and hence leaf water potential can be higher (closer to zero) as was observed in the present study.

A trade-off exists between large diameter vessels, which have a larger conductivity, and a greater chance of embolism (Domec and Gartner 2002). Consistent with this is the observation that of eleven pair-wise comparisons of percentage embolism, eight showed an increased embolism in the summer compared to the winter (Table 8) despite minimum leaf water potentials being higher in summer than in winter. Therefore we must conclude that the vulnerability of xylem to embolism is higher in summer than winter (Prior and Eamus 2000). High hydraulic conductance and conductivity in *C. hypoglauca* compared to all other species in the present study

agrees with previous findings that liannas have higher conductivity than, for example, trees, due to the reduced role of mechanical support of xylem vessels (Tyree and Ewers 1991). Liannas generally have narrow stems but have wide vessels to promote transport (Patiño *et al.* 1995), as was observed in the present study (Table 9). Furthermore, xylem cell length and width and pit pore membrane dimensions of *C. hypoglauca* were larger than for all other species (Table 9) which further facilitates the higher conductance and conductivity values compared to other species (Tyree and Ewers 1996; Eamus and Prior 2001).

Higher conductance and conductivity in *C. hypoglauca* are also related to site characteristics. Soil moisture availability was high, evaporative demand was low, and pre-dawn water potentials were high, at the below-ridge woodland site (Table 1) compared to the ridge-top site. Mesophytic species growing in wetter sites have higher shoot conductance than drought-adapted species (van der Willigen and Pammenter 1998; Nardini and Tyree 1999; Engelbrecht *et al.* 2000). Similarly, although soil moisture was very high in the mangrove habitat, this site was xeric due to daily inundation with seawater. Hence the low hydraulic conductance and conductivity values seen in the mangrove habitat (particularly in summer) are consistent with these conclusions (van der Willigen and Pammenter 1998).

Xylem embolism

The relationship between loss of hydraulic conductance to xylem embolism and minimum water potential (Fig 5) shows that patterns in xylem vulnerability previously observed within a single species may hold across species and habitats. Most vulnerability curves consist of a single species (Tyree and Ewers 1991; Thomas and Eamus 1999) rather than a variety of species from different habitats. Our data suggest that the relationship can apply across species.

Weak inverse relationships between xylem cell diameter or pit pore dimensions and loss of conductance were observed in the present study. Previous studies suggest that larger xylem vessels are more vulnerable to embolism (Eamus and Prior 2001). Therefore other factors independent of vessel dimensions were determining the degree of xylem embolism in the present study. For instance, despite having large xylem cells

and pit pore membranes, *C. hypoglauca* had a low loss of conductance in summer, suggesting that other mechanisms such as stomatal regulation (Cochard *et al.* 1994) were preventing the formation of xylem emboli. Similarly, both mangrove species had relatively small xylem cells and pit pore membranes but their percent loss in conductance was high in comparison to the other species. Pit membrane diameter and pit membrane properties (which also influence cavitation vulnerability) are not necessarily associated. Hacke and Sperry (2001) found no relationship between conduit width and susceptibility to cavitation across 38 angiosperms. They concluded that differences in the properties of pit membranes were overriding any size-associated relationship.

Assessing diurnal changes in xylem embolism may further clarify patterns. Xylem conductance can recover from embolism at pressures slightly below atmospheric in some species, while others rely on production of new vessels each spring (Eamus and Prior, 2001). Collection of branch material in the morning in the present study would reflect the lowest daily loss of conductance due to embolism. *In situ* assessment of diurnal changes in xylem embolism would indicate the capacity of each of these species to recover from embolism and the relationship between ψ_w and xylem cavitation could be further investigated.

Assessing diurnal changes in xylem embolism may further clarify any potential relationships between pit membrane dimensions and susceptibility to embolism. Xylem conductance can recover overnight, in some species, while others rely on production of new vessels each spring for recovery (Eamus and Prior 2001). The routine collection of branch material in the morning in the present study will reflect the lowest daily loss of conductance due to embolism, if any refilling occurred overnight. Therefore an *in situ* assessment of diurnal changes in embolism would indicate the capacity of each of these species to recover from embolism and the relationship and the relationship between Ψ_w and xylem cavitation could be further investigated.

Conclusions

In conclusion, we found that microclimate is highly variable across the four habitats. We found seasonal and site differences in VPD, PAR and soil moisture. Leaf water potentials were mostly consistent within a season within a habitat and most habitats had different leaf water potentials for summer and winter. Mangroves had the lowest leaf water potential, followed by the woodland (ridge-top), heathland and woodland (below ridge) habitats.

Seasonality had a greater influence on hydraulic architecture characteristics than species or habitats, due to seasonal variation in microclimate. The inverse relationship between Huber value and hydraulic conductance shows that this pattern in hydraulic architecture is universal across these species and habitats. Similarly the inverse relationship between loss of conductance and minimum leaf water potential is another inter-species and inter-habitat pattern.

Xylem cell and pit pore dimensions were related to habitat (such as small values for mangroves) and species (such as large values for the vine, *C. hypoglauca*). The inverse relationships between cell and pit pore length and xylem embolism suggest that another mechanism such as stomatal conductance is governing the formation of emboli.

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References

Borel C, Simonneau T, This D, Tardieu F (1997) Stomatal conductance and ABA concentration in the xylem sap of barley lines of contrasting origins. *Australian Journal of Plant Physiology* **24**, 607-615.

Brooks JR, Meinzer FC, Coulombe R, Gregg J (2002) Hydraulic redistribution of soil

water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* **22**, 1107-1117.

Chiu ST, Ewers FW (1992) Xylem structure and water transport in a twiner, a scrambler, and a shrub of *Lonicera* (Caprifoliaceae). *Trees* **6**, 216-224.

Cochard H, Ewers FW, Tyree MT (1994) Water relations of tropical vine-like bamboo (*Rhipidocladum racemiflorum*): root pressures, vulnerability to cavitation and seasonal changes in embolism. *Journal of Experimental Botany* **45**, 1085-1089.

Domec J-C, Gartner BL (2002) How do water transport and water storage differ in coniferous earlywood and latewood? *Journal of Experimental Botany* **53**, 2369-2379.

Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Advances in Ecological Research* **32**, 113-197.

Engelbrecht BMJ, Velez V, Tyree MT (2000) Hydraulic conductance of two co-occurring neotropical understorey shrubs with different habitat preferences. *Annals of Forest Science* **57**, 201-208.

Franks PJ, Gibson A, Bachelard EP (1995) Xylem permeability and embolism susceptibility in seedlings of *Eucalyptus camaldulensis* Dehnh. from two different climatic zones. *Australian Journal of Plant Physiology* **22**, 15-21.

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics* **4**, 97-115.

Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* **19**, 165-172.

Machado J, Tyree M (1994) Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax sepenatum*. *Tree Physiology* **14**, 219-240.

Maherali H, De Lucia EH (2000) Xylem conductivity and vulnerability to cavitation

of ponderosa pine growing in contrasting climates. *Tree Physiology* **20**, 859-867.

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology* **15**,1-10.

Nardini A, Tyree MT (1999) Root and shoot hydraulic conductance of seven *Quercus* species. *Annals of Forest Science* **56**, 371-377.

Patiño S, Tyree MT, Herre EA (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic *Ficus* species from Panama. *New Phytologist* **129**, 125-134.

Prior LD, Eamus D (2000) Seasonal changes in hydraulic conductance, xylem embolism and leaf area in *Eucalyptus tetradonta* and *Eucalyptus miniata* saplings in a north Australian savanna. *Plant, Cell and Environment*, **23**, 955-965.

Prior LD, Eamus D, Duff GA (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetradonta* saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* **45**, 241-258.

Sobrado MA (1997) Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest. *Acta Oecologica* **18**, 383-391.

Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**, 35-40.

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous and coniferous trees of northern Utah and interior Alaska. *Ecology* **75**, 1736-1752.

Thomas DS, Eamus D (1999) The influence of predawn leaf water potential on stomatal responses to atmospheric water content at constant C_i and on stem hydraulic conductance and foliar ABA concentrations. *Journal of Experimental Botany* **50**, 243-

251.

Tognetti R, Michelozzi M, Giovannelli A (1997) Geographical variation in water relations, hydraulic architecture and terpene comparison of Aleppo pine seedlings from Italian provenances. *Tree Physiology* **17**, 241-250

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**, 345-360.

Tyree MT, Ewers FW (1996) Hydraulic architecture of woody tropical plants. In 'Tropical Forest Plant Ecophysiology'. (Eds S. S. Mulkey, R. L. Chazdon and A. P. Smith.) pp. 217-243. (Chapman and Hall: New York.)

Van der Willigen C, Pammenter NW (1998) Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites. *Tree Physiology* **18**, 595-600.

Wang J, Ives NE, Lechowicz MJ (1992) The relation of foliar phenology to xylem embolism in trees. *Functional Ecology* **6**, 469-475.

Williams JE, Davis SD, Portwood K (1997) Xylem embolism in seedlings and resprouts of *Adenostoma fasciculatum* after fire. *Australian Journal of Botany* **45**, 291-300.

Tables

Table 1. Site climate data

Daily average vapour pressure deficit (VPD), photosynthetically active radiation (PAR) and soil moisture. Values are mean \pm standard error of the mean.

Habitat	Season	VPD (kPa)	PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	Soil moisture (% weight/weight)
Mangrove	winter	0.31 \pm 0.14	25.9 \pm 4.4	31.1 \pm 6.7
	summer	1.46 \pm 0.13	697.0 \pm 63.8	31.7 \pm 5.1
Woodland (ridge-top)	winter	0.37 \pm 0.11	337.3 \pm 50.8	2.3 \pm 0.1
	summer	1.60 \pm 0.13	538.3 \pm 52.2	3.3 \pm 0.3
Woodland (below ridge)	winter	0.55 \pm 0.11	11.3 \pm 2.4	5.2 \pm 0.2
	summer	1.69 \pm 0.12	663.2 \pm 38.7	5.0 \pm 0.5
Heathland	winter	0.73 \pm 0.13	135.7 \pm 10.7	7.3 \pm 0.2
	summer	1.18 \pm 0.04	854.7 \pm 34.3	3.6 \pm 0.1

Table 2. Vegetation properties at each site

Average diameter at breast height (DBH), canopy height, foliage projective cover (FPC) and root biomass (calculated as grams of dried root material in 8000 cm³ soil). Values are mean \pm standard error of the mean.

Habitat	Season	DBH (cm)	Height (m)	FPC (%)	Root biomass (g)
Mangrove	winter	21.6 \pm 2.2	9.3 \pm 0.8	77%	36.6 \pm 6.6
	summer				42.9 \pm 12.8
Woodland (ridge-top)	winter	38.5 \pm 5.0	9.8 \pm 0.6	60%	27.6 \pm 1.5
	summer				33.7 \pm 3.9
Woodland (below ridge)	winter	29.7 \pm 3.9	11.8 \pm 0.8	70%	13.3 \pm 2.1
	summer				22.9 \pm 6.1
Heathland	winter	na	1.2 \pm 0.1	76%	18.2 \pm 2.3
	summer				47.7 \pm 6.2

Table 3. Size and hydraulic characteristics of mangrove species *Aegiceras corniculatum* and *Avicennia marina*

All values are means \pm standard error for six branches. Values marked with the same letter are not significantly different (Tukey's *post hoc* comparison, $p < 0.05$).

	<i>A. corniculatum</i>		<i>A. marina</i>	
	Winter	Summer	Winter	Summer
Branch length (cm)	11.6 \pm 0.2a	20.5 \pm 1.9b	9.6 \pm 0.3a	30.9 \pm 3.4c
Diameter at base (mm)	3.34 \pm 0.14a	3.90 \pm 0.17ab	3.69 \pm 0.08ab	4.17 \pm 0.18b
Leaf area (cm ²)	92.4 \pm 13.3a	193.3 \pm 16.1b	108.7 \pm 13.0a	237.5 \pm 26.1b
Huber value ($\times 10^{-4}$)	10.31 \pm 1.16a	6.28 \pm 0.37b	10.73 \pm 1.86a	6.17 \pm 0.97b
Hydraulic conductance (mg s ⁻¹ MPa ⁻¹)	3.30 \pm 0.26a	12.92 \pm 1.76b	7.43 \pm 0.90a	16.25 \pm 4.22b
Hydraulic conductance per leaf area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	0.41 \pm 0.08a	0.70 \pm 0.13a	0.71 \pm 0.76a	0.66 \pm 0.11a
Hydraulic conductance per branch transverse area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	39.2 \pm 5.0a	110.8 \pm 17.4b	69.5 \pm 7.7a	120.9 \pm 29.7b
Hydraulic conductance per sapwood area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	40.4 \pm 5.0a	148.1 \pm 18.2b	71.1 \pm 7.4a	111.5 \pm 26.3b
Hydraulic conductivity (mg cm ⁻¹ s ⁻¹ MPa ⁻¹)	38 \pm 3a	254 \pm 26b	72 \pm 10a	487 \pm 111b
Hydraulic conductivity per leaf area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	4.8 \pm 1.0a	13.9 \pm 2.3b	6.8 \pm 0.6a	19.5 \pm 2.7b
Hydraulic conductivity per branch transverse area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	456 \pm 60a	2205 \pm 330b	678 \pm 90a	3652 \pm 802b
Hydraulic conductivity per sapwood area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	469 \pm 61a	881 \pm 59a	693 \pm 88a	3312 \pm 668b

Table 4. Size and hydraulic characteristics of woodland (ridge-top) species, *Eucalyptus haemostoma*, *Angophora hispida* and *Banksia oblongifolia*. All values are means \pm standard error for six branches. Values marked with the same letter are not significantly different (Tukey's *post hoc* comparison, $p < 0.05$).

	<i>E. haemostoma</i>		<i>A. hispida</i>		<i>B. oblongifolia</i>	
	Winter	Summer	Winter	Summer	Winter	Summer
Branch length (cm)	10.0 \pm 2.7a	55.0 \pm 6.1c	13.4 \pm 0.4a	38.5 \pm 4.0b	12.3 \pm 0.3a	35.6 \pm 1.8b
Diameter at base (mm)	3.35 \pm 0.09a	5.15 \pm 0.21c	3.76 \pm 0.10ab	5.18 \pm 0.19c	3.77 \pm 0.16ab	4.42 \pm 0.19b
Leaf area (cm ²)	71.6 \pm 21.2a	767.2 \pm 131.3 b	162.9 \pm 22.4a	1007.8 \pm 152. 4b	140.5 \pm 6.0a	292.6 \pm 36.2a
Huber value (x 10 ⁻⁴)	20.43 \pm 6.72a	3.21 \pm 0.65b	13.92 \pm 2.90a	2.51 \pm 0.58b	14.15 \pm 1.22a	5.97 \pm 1.26b
Hydraulic conductance (mg s ⁻¹ MPa ⁻¹)	12.91 \pm 3.64a	39.72 \pm 11.42a	16.45 \pm 3.12a	85.56 \pm 15.94 b	9.36 \pm 2.23a	28.19 \pm 6.79a
Hydraulic conductance per leaf area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	0.32 \pm 0.20a	0.59 \pm 0.17a	0.84 \pm 0.24ab	0.90 \pm 0.21ab	1.24 \pm 0.33b	1.01 \pm 0.22b
Hydraulic conductance per branch transverse area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	14.6 \pm 3.7a	202.3 \pm 63.3a	153.2 \pm 37.9a	422.6 \pm 80.2b	83.1 \pm 18.7a	176.0 \pm 38.3a
Hydraulic conductance per sapwood area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	218.7 \pm 137.2a b	184.4 \pm 55.6ab	110.4 \pm 25.0a	510.0 \pm 100.8 b	76.9 \pm 17.9a	228.7 \pm 48.5ab
Hydraulic conductivity (mg cm ⁻¹ s ⁻¹ MPa ⁻¹)	93 \pm 31a	1848 \pm 253b	165 \pm 34a	3235 \pm 559c	118 \pm 30a	1024 \pm 249ab
Hydraulic conductivity per leaf area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	16.0 \pm 4.3a	28.3 \pm 6.1b	24.7 \pm 8.8a	32.6 \pm 6.2b	15.7 \pm 4.4a	37.2 \pm 8.5b
Hydraulic conductivity per branch transverse area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	1067 \pm 368a	9287 \pm 1636bc	1740 \pm 472a	16426 \pm 3390c	1043 \pm 246a	6369 \pm 1400ab
Hydraulic conductivity per sapwood area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	1259 \pm 816a	8509 \pm 1475a	1462 \pm 302a	19300 \pm 3658 b	969 \pm 239a	8301 \pm 1797a

Table 5. Size and hydraulic characteristics of woodland (below ridge) species, *Glochidion ferdinandi*, *Banksia integrifolia* and *Cissus hypoglauca*. All values are means \pm standard error for six branches. Values marked with the same letter are not significantly different (Tukey's *post hoc* comparison, $p < 0.05$).

	<i>G. ferdinandi</i>		<i>B. integrifolia</i>		<i>C. hypoglauca</i>	
	Winter	Summer	Winter	Summer	Winter	Summer
Branch length (cm)	16.3 \pm 0.2a	32.6 \pm 2.0b	13.9 \pm 0.2a	41.0 \pm 4.4b	16.8 \pm 0.1a	61.8 \pm 6.8c
Diameter at base (mm)	2.88 \pm 0.14a	5.02 \pm 0.05c	3.81 \pm 0.16b	4.34 \pm 0.23b	4.07 \pm 0.10b	4.45 \pm 0.15bc
Leaf area (cm ²)	195.2 \pm 21.7a	573.9 \pm 25.7c	173.2 \pm 30.3a	309.6 \pm 32.9ab	137.4 \pm 15.0a	483.6 \pm 86.4bc
Huber value (x 10 ⁻⁴)	3.43 \pm 0.27a	3.48 \pm 0.18a	8.17 \pm 2.06bc	5.14 \pm 0.71ab	9.98 \pm 0.97c	3.87 \pm 0.80ab
Hydraulic conductance (mg s ⁻¹ MPa ⁻¹)	25.33 \pm 4.10ab	37.22 \pm 2.20ab	21.07 \pm 3.65a	19.44 \pm 4.19a	34.22 \pm 11.75b	58.47 \pm 16.80b
Hydraulic conductance per leaf area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	1.30 \pm 0.19a	0.66 \pm 0.06b	1.45 \pm 0.48a	0.66 \pm 0.13b	2.52 \pm 0.87a	1.23 \pm 0.37b
Hydraulic conductance per branch transverse area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	381.8 \pm 51.2ab	188.7 \pm 12.1ab	180.2 \pm 25.0a	124.0 \pm 15.5a	263.1 \pm 99.3b	391.4 \pm 110.1b
Hydraulic conductance per sapwood area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	389.6 \pm 51.3ab	189.3 \pm 12.9ab	191.9 \pm 27.3ab	141.7 \pm 18.7a	293.3 \pm 93.4ab	443.4 \pm 118.7b
Hydraulic conductivity (mg cm ⁻¹ s ⁻¹ MPa ⁻¹)	411 \pm 66a	1203 \pm 77a	19 \pm 3a	780 \pm 147a	572 \pm 196a	3125 \pm 774b
Hydraulic conductivity per leaf area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	21.0 \pm 2.9ab	21.1 \pm 1.6ab	1.3 \pm 0.3a	27.5 \pm 6.3abc	42.0 \pm 14.4bc	65.8 \pm 16.5c
Hydraulic conductivity per branch transverse area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	6184 \pm 801a	6100 \pm 422a	168 \pm 25a	5088 \pm 803a	4396 \pm 1657a	20815 \pm 5191b
Hydraulic conductivity per sapwood area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	6311 \pm 803a	6110 \pm 447a	178 \pm 26a	5882 \pm 1075a	4898 \pm 1554a	23747 \pm 5657b

Table 6. Size and hydraulic characteristics of heathland species, *Angophora hispida*, *Banksia oblongifolia*, and *Persoonia lanceolata*
 All values are means \pm standard error for six branches. Values marked with the same letter are not significantly different (Tukey's *post hoc* comparison, $p < 0.05$).

	<i>A. hispida</i>		<i>B. oblongifolia</i>		<i>P. lanceolata</i>	
	Winter	Summer	Winter	Summer	Winter	Summer
Branch length (cm)	13.3 \pm 0.2a	28.4 \pm 1.0b	13.4 \pm 0.2a	16.0 \pm 1.0a	16.6 \pm 0.1a	38.6 \pm 3.6c
Diameter at base (mm)	3.78 \pm 0.07a	3.74 \pm 0.17a	4.06 \pm 0.12ab	4.00 \pm 0.23ab	3.54 \pm 0.09a	4.61 \pm 0.19b
Leaf area (cm ²)	179.7 \pm 18.5a	575.9 \pm 68.1a	138.6 \pm 12.3a	184.0 \pm 24.7c	66.9 \pm 5.39a	365.6 \pm 62.4b
Huber value ($\times 10^{-4}$)	6.51 \pm 0.54bc	2.04 \pm 0.30a	10.13 \pm 0.80c	7.18 \pm 0.71bc	15.24 \pm 1.61d	5.38 \pm 1.10ab
Hydraulic conductance (mg s ⁻¹ MPa ⁻¹)	17.66 \pm 4.56ab	45.83 \pm 8.57bc	12.61 \pm 3.45a	34.03 \pm 9.32ab	11.20 \pm 2.65a	75.83 \pm 11.64c
Hydraulic conductance per leaf area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	1.11 \pm 0.31a	0.77 \pm 0.06a	0.88 \pm 0.23ab	1.82 \pm 0.30ab	1.60 \pm 0.29b	2.25 \pm 0.35b
Hydraulic conductance per branch transverse area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	165.3 \pm 45.5a	414.8 \pm 62.9b	95.8 \pm 24.0a	266.9 \pm 56.2ab	109.9 \pm 22.9a	442.8 \pm 41.8b
Hydraulic conductance per sapwood area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	171.2 \pm 46.0a	377.2 \pm 58.0b	100.4 \pm 25.2a	335.3 \pm 38.9b	110.3 \pm 23.8a	373.8 \pm 38.8b
Hydraulic conductivity (mg cm ⁻¹ s ⁻¹ MPa ⁻¹)	236 \pm 62a	1308 \pm 260a	166 \pm 45a	570 \pm 189a	186 \pm 44a	3037 \pm 682b
Hydraulic conductivity per leaf area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	14.8 \pm 4.2a	21.9 \pm 1.7a	11.7 \pm 3.0a	29.3 \pm 5.7a	26.6 \pm 4.9a	90.9 \pm 20.9b
Hydraulic conductivity per branch transverse area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	2209 \pm 617a	11788 \pm 1845 b	1264 \pm 315a	4326 \pm 1099a	1823 \pm 383a	17174 \pm 2436 b
Hydraulic conductivity per sapwood area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	2289 \pm 624a	10653 \pm 1640 bc	1323 \pm 330a	5419 \pm 840ab	1830 \pm 398a	14589 \pm 2402c

Table 7. Size and hydraulic characteristics of four ecosystems, Mangroves, Woodland (ridge-top), Woodland (below ridge) and Heathland. All values are ecosystem means \pm standard error. Values marked with the same letter are not significantly different (Tukey's *post hoc* comparison, $p < 0.05$).

	Mangrove		Woodland (ridge-top)		Woodland (below ridge)		Heathland	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Branch length (cm)	10.6 \pm 0.3a	25.7 \pm 2.5bc	11.9 \pm 0.9a	43.0 \pm 3.1d	15.6 \pm 0.3ab	45.1 \pm 4.0d	14.4 \pm 0.4a	27.7 \pm 2.5c
Diameter at base (mm)	3.51 \pm 0.09a	4.03 \pm 0.12ab	3.63 \pm 0.08a	4.92 \pm 0.14d	3.59 \pm 0.14a	4.60 \pm 0.11cd	3.79 \pm 0.07ab	4.12 \pm 0.14bc
Leaf area (cm ²)	100.6 \pm 9.2a	215.4 \pm 16.1a	125.0 \pm 13.6a	689.2 \pm 96.4d	168.6 \pm 13.9a	455.7 \pm 40.1c	128.4 \pm 13.4a	375.2 \pm 49.0b
Huber value (x 10 ⁻⁴)	10.52 \pm 1.05	6.23 \pm 0.49a	16.17 \pm 2.44c	3.89 \pm 0.60a	7.19 \pm 0.98b	4.16 \pm 0.38a	10.63 \pm 1.05b	4.87 \pm 0.67a
Hydraulic conductance (mg s ⁻¹ MPa ⁻¹)	5.37 \pm 0.77a	14.58 \pm 2.24a	12.90 \pm 1.80a	51.16 \pm 8.85c	26.88 \pm 4.27a	38.38 \pm 6.70b	13.82 \pm 2.08a	51.90 \pm 6.87c
Hydraulic conductance per leaf area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	0.56 \pm 0.07a	0.68 \pm 0.08a	0.80 \pm 0.17a	0.83 \pm 0.12ab	1.76 \pm 0.34c	0.85 \pm 0.14ab	1.20 \pm 0.17ab	1.61 \pm 0.21bc
Hydraulic conductance per branch transverse area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	54.4 \pm 6.3a	115.8 \pm 16.5a	83.6 \pm 19.1a	266.7 \pm 43.4c	275.0 \pm 41.1d	234.7 \pm 44.6b	123.7 \pm 19.1a	374.8 \pm 34.9e
Hydraulic conductance per sapwood area (mg s ⁻¹ MPa ⁻¹ cm ⁻²)	55.8 \pm 6.3a	129.8 \pm 16.2a	135.3 \pm 46.4a	307.7 \pm 52.5d	291.6 \pm 39.6c	258.1 \pm 49.6b	127.3 \pm 19.6a	362.1 \pm 25.4e
Hydraulic conductivity (mg cm ⁻¹ s ⁻¹ MPa ⁻¹)	55 \pm 7a	370 \pm 64a	125 \pm 18a	2036 \pm 303b	334 \pm 86a	1703 \pm 350b	196 \pm 29a	1638 \pm 344b
Hydraulic conductivity per leaf area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	5.8 \pm 0.6a	16.7 \pm 1.9ab	18.8 \pm 3.5ab	32.7 \pm 3.9abc	21.4 \pm 6.1ab	38.1 \pm 7.3bc	17.7 \pm 2.7ab	47.4 \pm 10.1c
Hydraulic conductivity per branch transverse area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	567 \pm 62a	2929 \pm 467a	1283 \pm 217a	10693 \pm 1622	3582 \pm 840a	10668 \pm 2400	1765 \pm 265a	11096 \pm 1633
Hydraulic conductivity per sapwood area (mg cm ⁻¹ s ⁻¹ MPa ⁻¹ cm ⁻²)	581 \pm 61a	2069 \pm 487a	1230 \pm 287a	12037 \pm 1842	3796 \pm 839a	11912 \pm 2718	1815 \pm 271a	10220 \pm 1315

Table 8. Xylem embolism

Species mean % loss in conductance in four contrasting habitats in NSW, Australia

Habitat	Species	% loss in conductance	
		Winter	Summer
Mangrove	<i>A. corniculatum</i>	19	40
	<i>A. marina</i>	12	28
Woodland (ridge-top)	<i>E. haemostoma</i>	18	35
	<i>A. hispida</i>	12	15
	<i>B. oblongifolia</i>	33	57
Woodland (below ridge)	<i>G. ferdinandi</i>	0	12
	<i>B. integrifolia</i>	11	36
	<i>C. hypoglauca</i>	44	4
Heathland	<i>A. hispida</i>	47	20
	<i>B. oblongifolia</i>	13	32
	<i>P. lanceolata</i>	33	7

Table 9. Xylem cell dimensions and pit pore dimensions for each speciesAll values are means \pm standard error of the mean (n = 20)

Species	Pitted cells		Spiral cells		Reticular cells		Pit pore size (μm)
	Width (mm)	Length (mm)	Width (mm)	Length (mm)	Width (mm)	Length (mm)	
<i>E. haemostoma</i>	0.038 \pm 0.009	0.334 \pm 0.011	0.019 \pm 0.001	0.462 \pm 0.020			5.83 x 2.08 \pm 0.89
<i>B. oblongifolia</i>	0.036 \pm 0.003	0.328 \pm 0.008	0.020 \pm 0.001	0.414 \pm 0.018	0.029 \pm 0.001	0.301 \pm 0.006	2.97 x 0.67 \pm 0.23
<i>A. hispida</i>	0.035 \pm 0.002	0.356 \pm 0.006	0.024 \pm 0.001	0.402 \pm 0.013			4.40 x 2.26 \pm 0.09
<i>B. integrifolia</i>	0.036 \pm 0.002	0.311 \pm 0.013			0.019 \pm 0.001	0.335 \pm 0.018	3.87 x 1.16 \pm 0.25
<i>G. ferdinandi</i>	0.047 \pm 0.002	0.637 \pm 0.049	0.023 \pm 0.001	0.403 \pm 0.009			4.29 x 1.96 \pm 0.26
<i>C. hypoglauca</i>	0.054 \pm 0.008	0.502 \pm 0.065	0.038 \pm 0.003	0.639 \pm 0.088			5.91 x 1.99 \pm 0.21
<i>A. corniculatum</i>	0.029 \pm 0.003	0.209 \pm 0.002	0.019 \pm 0.001	0.270 \pm 0.010			1.18 x 0.49 \pm 0.11
<i>A. marina</i>	0.033 \pm 0.006	0.255 \pm 0.007	0.020 \pm 0.001	0.476 \pm 0.060			2.87 x 0.78 \pm 0.27