Convergence in hydraulic architecture and water relations amongst habitats and across seasons in Sydney

Catriona Macinnis-Ng, Kate McClenahan and Derek Eamus[*]

Institute for Water and Environmental Resource Management, Department of Environmental Sciences, University of Technology, Sydney. Westbourne Street, Gore Hill NSW 2065 Australia

Running heading: Hydraulic architecture of Sydney natives

[*] Corresponding author: Derek.Eamus@uts.edu.au

Abstract

We investigated minimum leaf water potential (Ψ_{min}), conductivity per sapwood area (k_s), Huber value (Hv) and xylem embolism in four habitats across two seasons (summer and winter) in the Sydney region: heathland, woodland (ridge-top), woodland (below-ridge) and mangrove. Seasonality strongly influenced all parameters in all habitats. Winter Ψ_{min} values were lower than those for summer in the heathland and both woodland habitats but summer Ψ_{min} values were lower than those for winter in the mangrove. Summer k_s values were higher than winter values in all habitats, while Hv was higher in winter than summer for all habitats. Loss of conductance due to xylem embolism was larger in summer than winter in 8 of 11 species.

We also investigated relationships between the hydraulic parameters across habitats. There was a strong, significant inverse correlation between log-transformed Hv and log-transformed k_s which held across the seasons. There were significant inverse correlations between Ψ_{min} and xylem embolism which held within seasons but not across seasons. We found a strong, significant positive correlation between k_s and Ψ_{min} also within seasons but not across seasons and a significant negative correlation between xylem embolism and k_s for winter but only a weak negative correlation between xylem embolism and k_s for summer.

We believe the seasonal patterns and relationships in hydraulic architecture and water relations are driven by the cost of efficient sapwood. This is demonstrated by the negative correlation between photosynthetic rate and k_s in winter.

Keywords: branch conductivity, hydraulic architecture, leaf water potential, vulnerability to xylem embolism, water relations.

Abbreviations: Ψ, leaf water potential; Ψ_{min}, minimum leaf water potential; A_{mass}, mass-based rate of carbon assimilation; A_{max}, maximum rate of carbon assimilation; DBH, Diameter at Breast Height; FPC, Foliage Projected Cover; Hv, Huber value; k_s, conductivity per sapwood area; LAVPD, Leaf to Air Vapour Pressure Deficit; PAR, Photosyntheticly Active Radiation; VPD, Vapour Pressure Deficit.

Introduction

Leaf water potential (Ψ) varies with transpiration and is influenced by evaporative demand and soil moisture availability. Pre-dawn leaf water potential is an indicator of leaf water status, while minimum leaf water potential (Ψ_{min}) experienced during the day is an indicator of the maximum water stress experienced by the plant, on that day (Borel *et al.* 1997; Prior *et al.* 1997).

Hydraulic architecture can potentially limit the flow of water to the leaves, thereby influencing Ψ, stomatal behaviour, gas exchange, and tree height (Tyree and Ewers 1996). Changes in hydraulic architecture may therefore be reflected in changes in Ψ. Furthermore, 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 plant hydraulic architecture include hydraulic conductance, hydraulic conductivity (k) and Huber value (Hv). Hydraulic conductance and conductivity can vary according to soil water status. Drought-stressed plants experience smaller mean conductance and conductivity per leaf area (k_l) and per sapwood area (k_s), lower transpiration rates, lower Hv, 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 a plant's 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 k_s in desert sites compared to

montane sites have been attributed to differences in temperature and evaporative demand between these sites (Maherali and DeLucia 2000). Similarly, Mencuccini and Grace (1995) noted variation in Hv and conductance within a species in response to site differences in VPD and soil water status.

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 contents. 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 thereby 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 temperate 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 northern 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 look at relationships among hydraulic architecture, Ψ_{min} and xylem embolism in species from different ecosystems in temperate 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, minimum 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 aim of the work described in this study was to determine if there are there any relationships between hydraulic architecture and water status across habitats. We

examined variation in Ψ_{min}, Hv, k_s and xylem embolism across habitats and assessed relationships among these parameters.

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 glycophylla* 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 cm^3 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 ºC 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, µmol photons m^{-2} 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

Diurnal leaf water potentials were determined at approximately ninety minute

intervals throughout the day between 6:30 am and 4:00 pm in each habitat for each of

the study species a using a pressure bomb (Model 3000, Soil Moisture Equipment

Corp. USA).

We used one leaf from each of two branches, from three randomly selected trees of

each species, in each of the two plots in each habitat. Mean minimum leaf water

potential (generally the mid-day sample) was calculated for each species and habitat

in summer (January) and winter (July). Two-way ANOVA was used to determine

whether there were significant differences between season and habitat. Tukey's *post

hoc* comparison was used to determine where the differences lay (SPSS for windows).

Hydraulic 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 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. 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). The laboratory was maintained at 20°C.

Hydraulic conductance (mg s^{-1} MPa^{-1}) was calculated as the slope of the relationship between flow rate and pressure difference using linear regression. Hydraulic conductivity (mg cm s^{-1} MPa^{-1}) was calculated by multiplying the conductance by the branch length and was also expressed in terms of sapwood area (k_s, following Tyree and Ewers 1996). Huber values (Hv) were calculated as the branch sapwood area per leaf area.

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. 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.

Species means were reported for k_s. A two factor ANOVA was used to find differences between species and season. Tukey's *post hoc* comparisons were used to determine where the differences lay (SPSS for windows).

The relationship between Hv and k_s was investigated by taking the natural logarithm of both (to normalise distribution) and then conducting a Pearson's correlation with SPSS for windows. The relationship between minimum leaf water potential and log conductivity per sapwood area was also investigated with 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 (to normalise the distribution) and the relationship between loss of conductance and minimum leaf water potential was assessed with a Pearson's correlation, as was the relationship between loss of conductance and conductivity per sapwood area (SPSS for windows).

Photosynthetic rate

Photosynthetic rate, measured as mass-based rate of carbon assimilation (A_{mass}), was obtained from McPherson (2001) for all habitats except the below-ridge woodland habitat. The relationship between A_{mass} and log-transformed k_s for summer and winter was assessed with Pearson's correlation.

Results

Site microclimate and soil water content

Rainfall and temperature were higher in summer than winter at all sites (Table 1). Vapour pressure deficit (VPD) and photosyntheticly active radiation (PAR) values were much higher in summer than in winter at each site (Table 2). 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 2).

Diameter at breast height (DBH) was largest at the woodland (ridge-top) site and the woodland (below-ridge) site had the tallest canopy. The largest foliage projected cover (FPC) was observed at the mangrove site (Table 3). 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 measurements (Table 3).

Leaf water potentials

Minimum leaf water potentials were more negative in the summer for mangrove species, but more negative in winter for the other three habitats (Fig. 1). 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. 1). Seasonal differences aside, minimum leaf water potentials were lowest in the mangrove habitat, then the woodland (ridge-top) and then the woodland (below ridge) habitat which was not significantly different from the heathland habitat.

Huber value and conductivity

The Hv was significantly larger in winter than summer for all species, with the exception of *Glochidion ferdinandi* (Fig. 2). Conversely, the k_s was significantly larger in summer than winter for all species besides *G. ferdinandi* (Fig. 3). There were

no clear patterns in habitat differences in Hv or k_s (Figs. 2 and 3). There was an inverse linear relationship between log-transformed k_s and log-transformed Hv across seasons (r = -0.698, $P < 0.01$; Fig. 4).

Minimum leaf water potential and log-transformed k_s were significantly related in summer (Pearson's correlation coefficient r = 0.811, $P < 0.01$) and winter (r = 0.657, $P = 0.039$; Fig. 5). Seasonal data were treated separately because there was a significant interaction between the effect of season and log k_s on Ψ_{min} (F = 6.503, $P < 0.01$).

Xylem embolism

Xylem embolism was highly variable within seasons and within species. For simplification of interpretation, xylem embolism is presented as mean values for each species in each season (Fig. 6). Of the 11 species examined, 8 suffered a larger loss in conductance due to xylem embolism in summer than winter.

A linear decline in percentage loss of conductance and Ψ_{min} was observed in both seasons. The relationship between percentage loss of conductance and Ψ_{min} gave Pearson's correlation coefficients of –0.624 ($P = 0.012$) and –0.543 ($P = 0.045$) for winter and summer respectively (Fig. 7). The seasons were treated separately because there was an interaction between the effect of season and Ψ_{min} on the loss of conductance (F = 6.492, $P < 0.01$).

The relationship between loss of conductance due to xylem embolism and k_s gave a Pearson's correlation coefficients of –0.691 ($P = 0.027$) and –0.577 ($P = 0.063$) for

winter and summer respectively (Fig. 8). The clear outlier, *B. integrifolia* was omitted from the winter analysis. The seasons were treated separately because there was an interaction between the effect of season and k_s on the loss of conductance (F = 6.933, $P < 0.01$).

Photosynthetic rate

The correlation between A_{mass} and log-transformed k_s was weakly inverse but not significant in summer (r = -0.489, P = 0.219), while there was a strong, significant inverse correlation between A_{mass} and log-transformed k_s in summer (r = -0.825, P = 0.012; Fig. 9). The Pearson's correlation coefficient, r was 0.596 (P = 0.157).

Water relations in four habitats

Mechanisms of interactions between environmental conditions and plant water relations with respect to seasonal variation are presented in a conceptual model (Fig. 10) showing summer conditions. Increased summer rainfall, temperature and solar radiation increase root and shoot growth, in turn, these factors lead to lower Hv, higher k_s and more embolism (Fig. 10a). Higher summer VPD, temperature and PAR and lower Hv also contribute to higher embolism. Additional summer growth, increased rainfall and higher k_s lead to higher Ψ_{min} values in summer compared to winter (Fig. 10a).

The main difference between the habitats is tidal inundation by saline water in the mangroves (Fig. 10b). Tidal inundation reduces the influence of rainfall, k_s and root biomass on Ψ_{min}, allowing increased summer PAR, temperature and VPD to have a greater impact on plant water stress, resulting in lower summer Ψ_{min} values, in

comparison to winter mangrove values. Seasonal differences in Hv, k_s and embolism are the same as the terrestrial habitats.

Discussion

More negative Ψ_{min} in winter compared to summer in the three terrestrial habitats (Fig. 1) was attributed to increased root biomass (Table 3) and greater rainfall (Table 1) in summer. Greater conductivity per sapwood area in summer (Fig. 3) may have also contributed to amelioration of water stress since a greater conductivity reduces the gradient in water potential required to achieve a given rate of flow (Patino *et al.* 1995) and hence the Ψ_{min} can be less negative when conductivity is larger. The mangrove habitat did not show the same seasonal pattern in Ψ_{min} (Fig. 1) because the twice-daily tidal inundation reduced the impact of more rainfall and root biomass in summer. Thus the higher VPD, PAR (Table 2) and temperature (Table 1) in summer and saline conditions throughout the year were more pivotal to mangrove water stress (van der Willigen and Pammenter 1998).

A larger Huber value (Hv) indicates less leaf surface area is being supported per unit sapwood area (Fig. 2). Thus the growth of new leaf material in summer logically leads to a decreased Hv in summer. This new tissue also had a greater conductivity per sapwood area (Fig. 3), consistent with Domec and Gartner's (2002) finding that early wood (new xylem) is more conductive than latewood because of larger xylem vessel diameters and enhanced water status during earlywood formation (Nardini and Tyree 1999).

Larger xylem vessel diameters encourage conductivity but can also can lead to a greater chance of xylem embolism (Eamus and Prior 2001; Domec and Gartner 2002). In eleven pair-wise (winter versus summer) comparisons of percentage loss of conductance, eight showed enhanced embolism in summer compared to winter (Fig. 6). This trend suggests that vulnerability to xylem embolism is higher in summer than winter (consistent with Prior and Eamus 2000) despite the occurrence of higher Ψ_{min} values in summer compared to winter. Despite this perceived influence of conductivity on xylem embolism, there was only a very weak inverse correlation between loss of conductance and log-transformed conductivity per sapwood area in summer in contrast to the strong inverse correlation in winter (Fig. 8). Rather than conductivity influencing xylem embolism, Tyree and Ewers (1991) suggested xylem embolism reduces hydraulic conductivity, requiring steeper pressure gradients between roots and leaves to maintain transpiration. Engelbrecht *et al.* (2000) suggested that a trade-off between hydraulic conductivity and xylem embolism exists. The outcome of the trade-off reflects the ecology of a plant where plants in mesic environments optimise conductance while water deprived plants or plants in xeric environments optimise avoidance of embolism (Eamus et al. 2000). The relationship between k_s and severity of xylem embolism was steeper for the winter data, possibly reflecting the different relative contribution of early and late wood in branch conductivity in summer and winter.

There was a significant correlation between Ψ_{min} and loss of conductance for both seasons (Fig. 7), suggesting that lower Ψ_{min} values lead to a larger loss of xylem embolism. This has been observed previously in single-species vulnerability curves (Tyree and Ewers 1991; Thomas and Eamus 1999; Prior and Eamus 2000) but the

present data suggest the relationship may apply across species. This relationship does not explain seasonal differences in loss of conductance, however, because it only holds within a season and not across seasons.

Only weak inverse relationships between xylem cell diameter or pit pore dimensions and xylem embolism were observed in the present study (data not shown), in contrast to Eamus and Prior (2001) and Domec and Gartner (2002) who observed positive relationships between vessel dimensions and xylem embolism. Cell dimensions are not necessarily related to vulnerability to cavitation and properties of pit membranes may override size associated relationships (Hacke and Sperry 2001). The roles of stomatal conductance and root pressure were not considered here but they may provide further insight into management of water stress (Cochard *et al.* 1994) in these habitats.

The inverse linear relationship between log-transformed k_s and log-transformed Hv (Fig. 4) is the only instance in the present study where a relationship between parameters shows a consistent pattern across seasons. Plants may compensate for a low k_s by having a higher Hv (Pallardy 1989; Tyree and Ewers 1991; Eamus and Prior 2001). This has been seen within functional plant groups such as lianas (Tyree and Ewers 1996) and was inferred across lianas and shrubs by Tyree and Ewers (1991) but has not been previously quantified over such a diverse group of species from different habitats. The presence of a single linear relationship across four habitats, nine species and two seasons argues strongly for a convergence of strategies linking low k_s to high Hv.

The significant and strong correlation between log-transformed k_s and Ψ_{min} during both seasons (Fig. 5) is also a first for between-habitat comparisons. The positive relationship between hydraulic conductivity and Ψ has been seen in several tree species (Eamus and Prior 2001). Similarly, Nardini and Tyree (1999) postulated that a higher hydraulic conductance would lead to a less negative Ψ, reducing the water stress suffered by the plant, but has not been reported across species and habitats. The presence of a single linear relationship across nine species and four habitats (within a singe season) argues strongly for a convergence of behavioural strategies linking k_s and Ψ_{min}. The shift to the left in the relationship, when comparing summer and winter may reflect a change in the relative contribution of early and late season sapwood to branch conductivity.

The principle driving these convergences in strategies for hydraulic architecture and water relations is highlighted by the cost-benefit relationship shown in Fig. 9. During winter when root biomass and rainfall are lower, conductivity limits carbon assimilation, seen as a linear relationship between A_{mass} and log-transformed k_s (Fig. 9). This relationship is in conflict with several published comparisons between conductivity and photosynthesis (Brodribb and Field, 2000; Hubbard et al. 2001; Rust and Roloff 2002) but we explain our results as follows. Species with lower k_s have a higher Hv (Fig. 4) and therefore have more sapwood per unit leaf area. Since more sapwood requires a larger carbon investment, the leaves associated with a higher Hv (and hence a lower k_s) need to be more efficient in fixing carbon per unit leaf mass to produce sufficient return (i.e. fixed carbon) on their carbon invested in sapwood. Hence a larger A_{mass} is associated with a higher Hv and hence a lower k_s (as seen in

Fig. 9). Therefore, the negative correlation between k_s and A_{mass} (Fig. 9) reflects more efficient leaves required to support carbon-expensive sapwood.

There is a second potential mechanism underlying the log-linear decline in A_{mass} as conductivity declines. Stomata of evergreen species may be more sensitive to LAVPD than deciduous species (Duff et al. 1997). Evergreen species generally have lower conductivities than deciduous species (Eamus and Prior 2001). Therefore, if species with lower conductivities have stomata more sensitive to LAVPD than species with higher conductivities (in order for stomata to tightly regulate transpiration, Ψ and occurrence of embolism), then A_{mass} of species with low conductivities needs to be higher to ensure maximum carbon fixation during the more restricted periods of open stomata.

Other authors looking at relationships between photosynthesis and conductivity have considered slightly different functional groups. Age-related changes in A_{max} and k_s in *Quercus robur* lead to a positive relationship between these parameters (Rust and Roloff, 2002), while manipulations of conductivity in ponderosa pine in controlled conditions caused a positive relationship between A_{max} and conductivity (Hubbard et al. 2001). Both of these studies assessed relatively limited ranges of photosynthesis and conductivity in single-species experiments so it is possible that while a positive relationship holds within a species, comparisons across seasons, species and habitats may reverse that relationship.

The only previous study assessing photosynthesis and conductivity across species (Brodribb and Field, 2000) used quantum yield of photosystem II electron transport as

a surrogate for photosynthetic rate which may not be directly comparable to assimilation rate, particularly in high light conditions (Krall and Edwards 1991; Edwards and Baker, 1993). Furthermore, Brodribb and Field (2000) worked in rainforest habitats where water may not have been a limiting factor, so the plants were not exposed to the same constraints. Clearly more work is required to understand the broad-scale functional relationships between hydraulic architecture and photosynthesis, since there has been very little work comparing different habitats.

There was no correlation of A_{mass} with conductivity, and hence no limitation of A_{mass} in summer (Fig. 9), as water was not as limiting in these habitats due to higher summer rainfall, more conductive shoots and higher root biomass (Fig. 1, Fig. 10). Marked differences in field values of summer and winter conductivity can also be attributed to the influence of temperature on water viscosity, in addition to structural changes outlined above. As temperature increases from 10 to 30°C, viscosity decreases by 39 % (Meiner, 2002). Increasing temperature therefore diminishes hydraulic resistance, increasing stem and root hydraulic conductance (Cochard et al. 2000). In the present study winter daytime maximum temperatures reached about 15°C while summer daytime maximum temperatures reached about 30°C, resulting in a substantial difference in water viscosity in the field. In turn, this will further reduce the influence of water limitation on summer-time assimilation, loosening the correlation between k_s and A_{mass} (Fig. 9).

In conclusion, we found that seasonality had a strong influence on Ψ_{min}, k_s, Hv and xylem embolism. Winter Ψ_{min} values were lower in the three terrestrial habitats due to higher summer rainfall and root biomass and greater k_s values. Mangrove species had

lower Ψ_{min} values in summer due to daily tidal inundation reducing the influence of rainfall and root biomass, thereby amplifying the influence of higher summer temperature, VPD and PAR. Summer k_s values were higher than those for winter, while Hv was higher in winter than summer, a phenomenon attributed to new summer growth producing more conductive vessels.

The trade-off between Hv and k_s held over all habitats and seasons. Loss of conductance due to xylem embolism and Ψ_{min} were negatively correlated but there was a different relationship in summer and winter. There was a strong positive correlation between Ψ_{min} and k_s in summer and winter and there was a weak correlation between loss of conductance due to xylem embolism and k_s also within but not across seasons. These across-habitat relationships support the view that there is convergence in hydraulic architecture and water relations in Sydney natives across a range of habitats. The negative correlation between k_s and A_{mass} in winter provides a possible explanation for this convergence and may be driving the patterns seen in this study.

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.

Brodribb TJ, Field, TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence form New Caledonian and Tasmanian rainforests. *Plant, Cell and Environment* **23**, 1381-1388.

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.

Cochard H, Martin R, Gross P, Bogeat-Triboulot MB (2000) Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. *Journal of Experimental Botany* **51**, 1255-1259.

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.

Duff GA, Myers BA, Williams RJ, Eamus D, O'Grady A, Fordyce IR (1997) Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a northern Australian savanna. *Australian Journal of Botany*, **45**, 211-224.

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

Edwards GE, Baker NR (1993) Can CO_2 assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? *Photosynthesis Research* **37**, 89-102.

Engelbrecht BMJ, Velez V, Tyree MT (2000) Hydraulic conductance of two co-occuring 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.

Hubbard RM, Ryan MG, Stiller V, Sperry JS (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell and Environment* **24**, 113-121.

Krall JP, Edwards GE (1991) Environmental effects on the relationship between the quantum yields of carbon assimilation and *in vivo* PSII electron transport in maize. *Australian Journal of Plant Physiology* **18**, 267-78.

Machado J, Tyree M (1994) Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phonologies: *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.

McPherson, S (2001) Leaf attributes of several plant species growing in the Sydney region. Honours Thesis, University of Technology, Sydney.

Meinzer FC (2002) Co-ordination of vapour and liquid phase water transport properties in plants. *Plant, Cell and Environment* **25**, 265-274.

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 differeing 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 tetrodonta* 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 tetrodonta*

saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* **45**, 241-258.

Rust S, Roloff A (2002) Reduced photosynthesis in old oak (*Quercus robur*): the impact of crown and hydraulic architecture. *Tree Physiology* **22**, 597-601.

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

Sperry JS, Donelly 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 Ci 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. Rainfall and temperature

Mean monthly averages for rainfall and temperature at the closest weather stations, Marsfield (for mangrove and woodland habitats) and Sydney Airport (for heathland habitat). Data source: Australian Bureau of Meteorology website, www.bom.gov.au

	Marsfield		Sydney Airport	
	Rainfall (mm)	Temperature (°C)	Rainfall (mm)	Temperature (°C)
Summer (January)	129.3	27.4	100.4	26.3
Winter (July)	53.0	17.0	69.3	16.9

Table 2. Site micro-climate data

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

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

Table 3. 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 cm^3 soil).

Values are mean ± standard error of the mean.

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

Figures
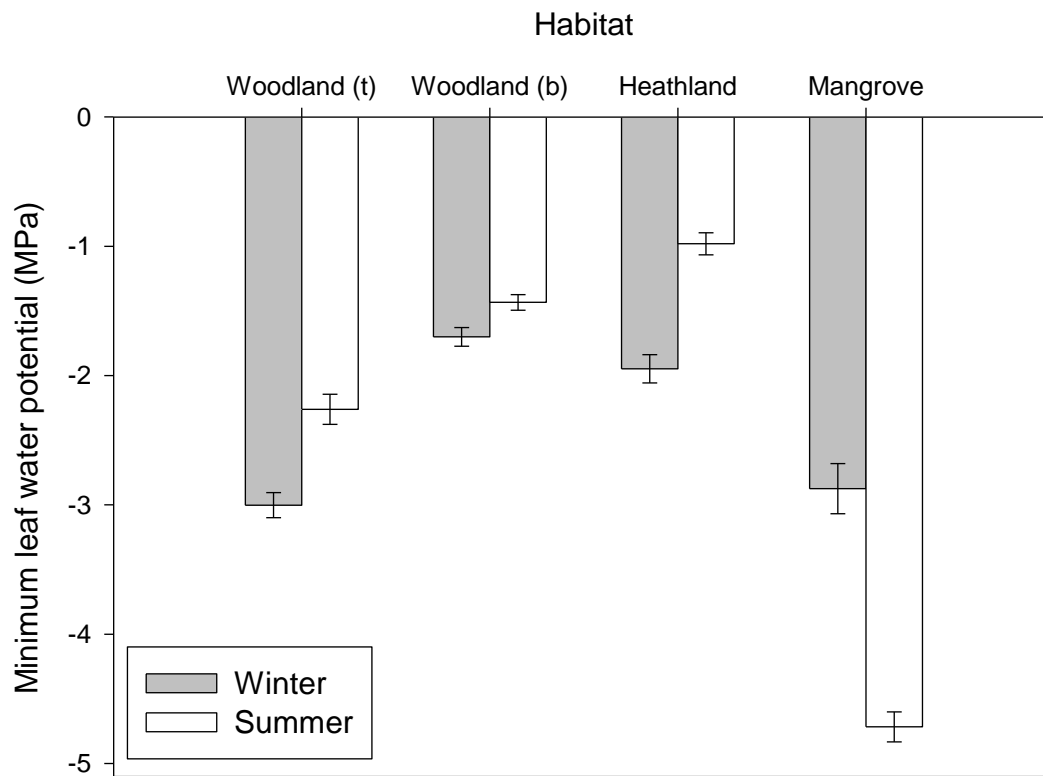
Fig. 1. Mean minimum leaf water potentials for summer and winter at the four habitats. Different letters represent significantly different leaf water potentials (*P*<0.05) determined with Tukey's HSD post hoc comparison. Error bars are standard error of the mean.
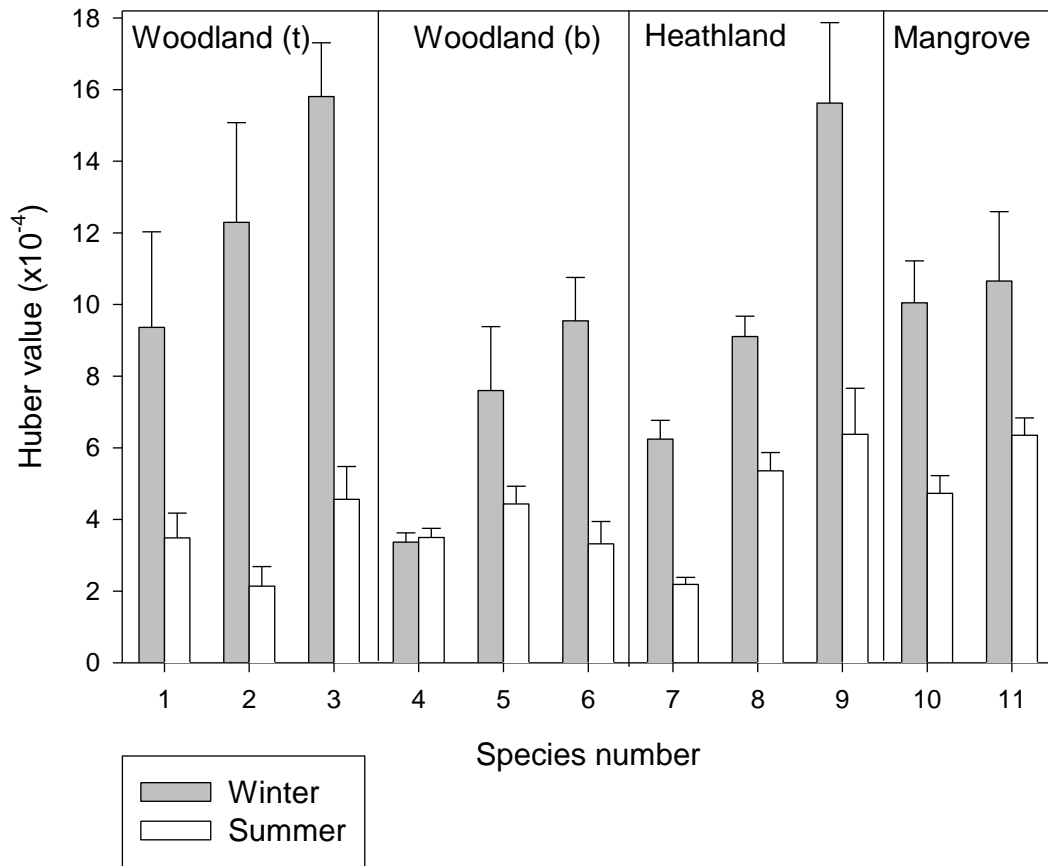
Fig. 2. Mean Huber values (x 10^{-4}) for summer and winter for each species in each habitat. Species numbers were 1= *Eucalyptus haemostoma*, 2= *Angophora hispida*, 3= *Banksia oblongifolia*, 4= *Glochidion ferdinandi*, 5= *Banksia integrifolia*, 6= *Cissus hypoglauca*, 7= *Angophora hispida*, 8= *Banksia oblongifolia*, 9= *Persoonia lanceolata*, 10= *Aegicerus corniculatum*, 11= *Avicennia marina*. Note that sp. 2 = sp. 7; sp. 3 = sp. 8. Error bars are standard error of the mean. Significant seasonal differences were found in all species except *G. ferdinandi*.
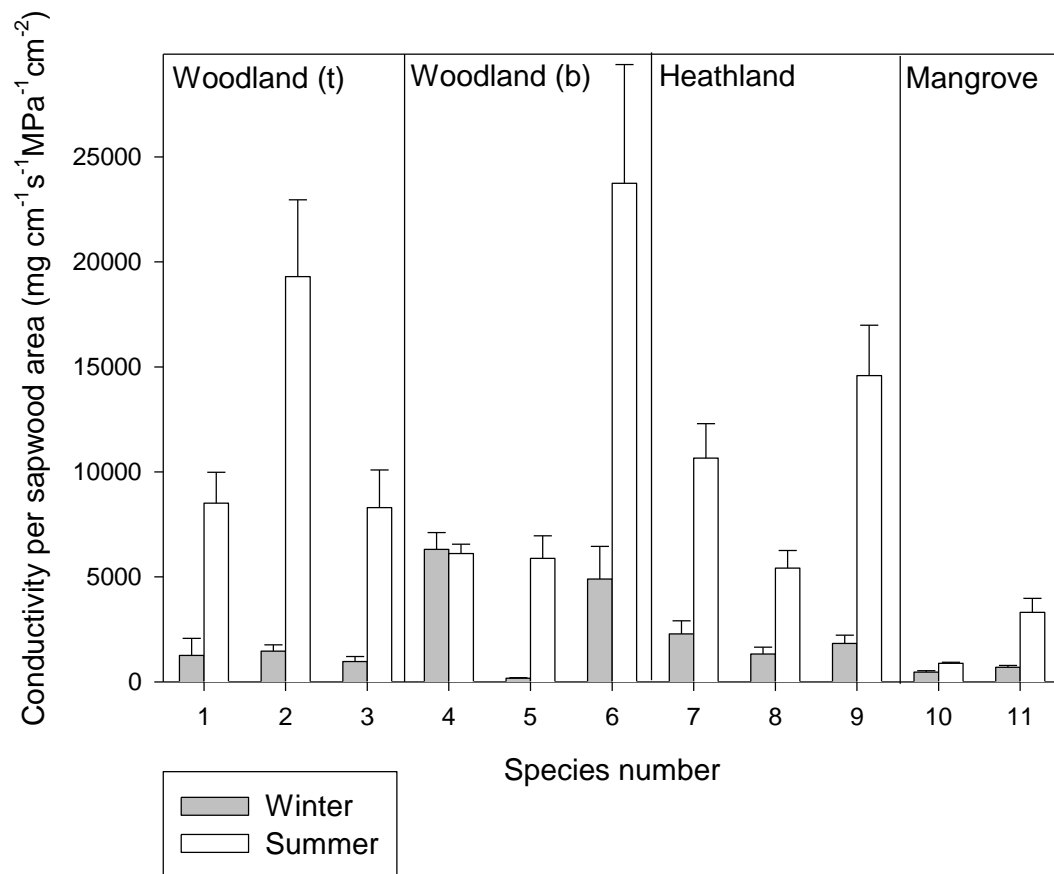
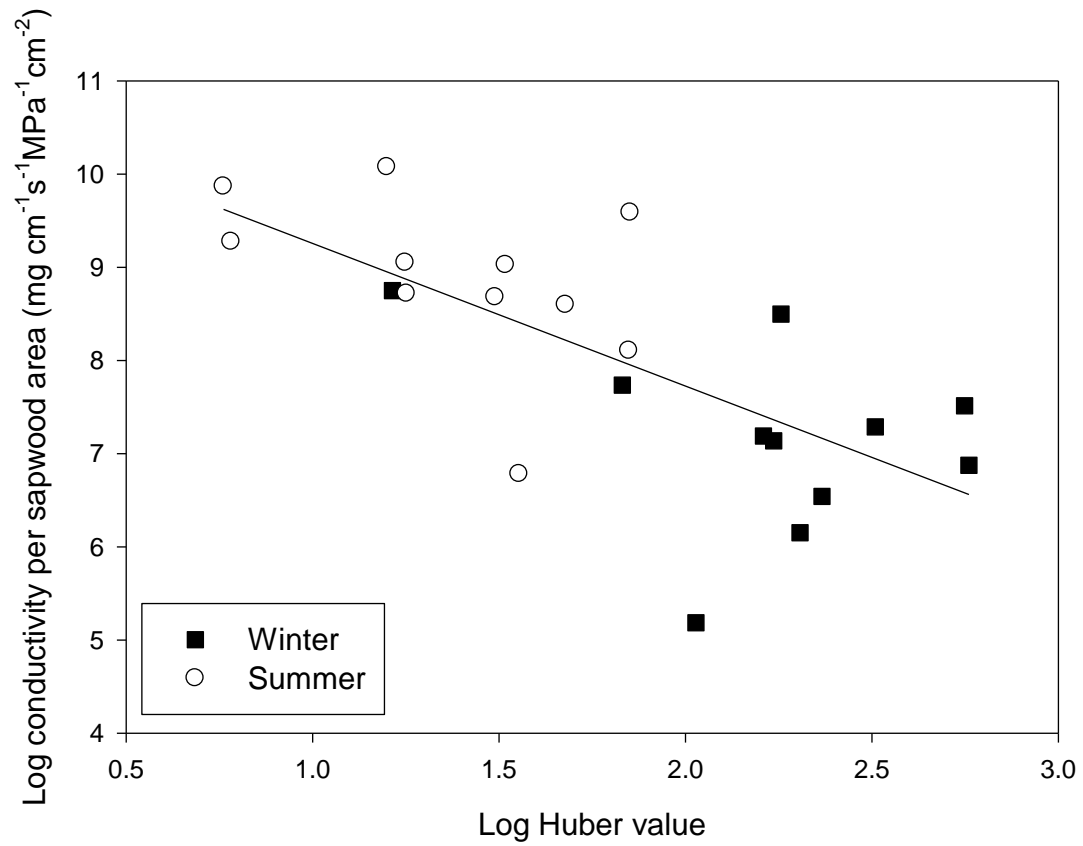**Fig. 3.** Mean conductivity per sapwood area for summer and winter for each species in each habitat. Species numbers were 1= *Eucalyptus haemostoma*, 2= *Angophora hispida*, 3= *Banksia oblongifolia*, 4= *Glochidion ferdinandi*, 5= *Banksia integrifolia*, 6= *Cissus hypoglauca*, 7= *Angophora hispida*, 8= *Banksia oblongifolia*, 9= *Persoonia lanceolata*, 10= *Aegicerus corniculatum*, 11= *Avicennia marina*. Error bars are standard error of the mean. Significant seasonal differences were found in all species except *G. ferdinandi.*

Fig. 4. Log-transformed conductivity per sapwood area plotted against log-transformed Huber value. There was a significant negative correlation (r = -0.698, *P*<0.01) for pooled summer and winter data.
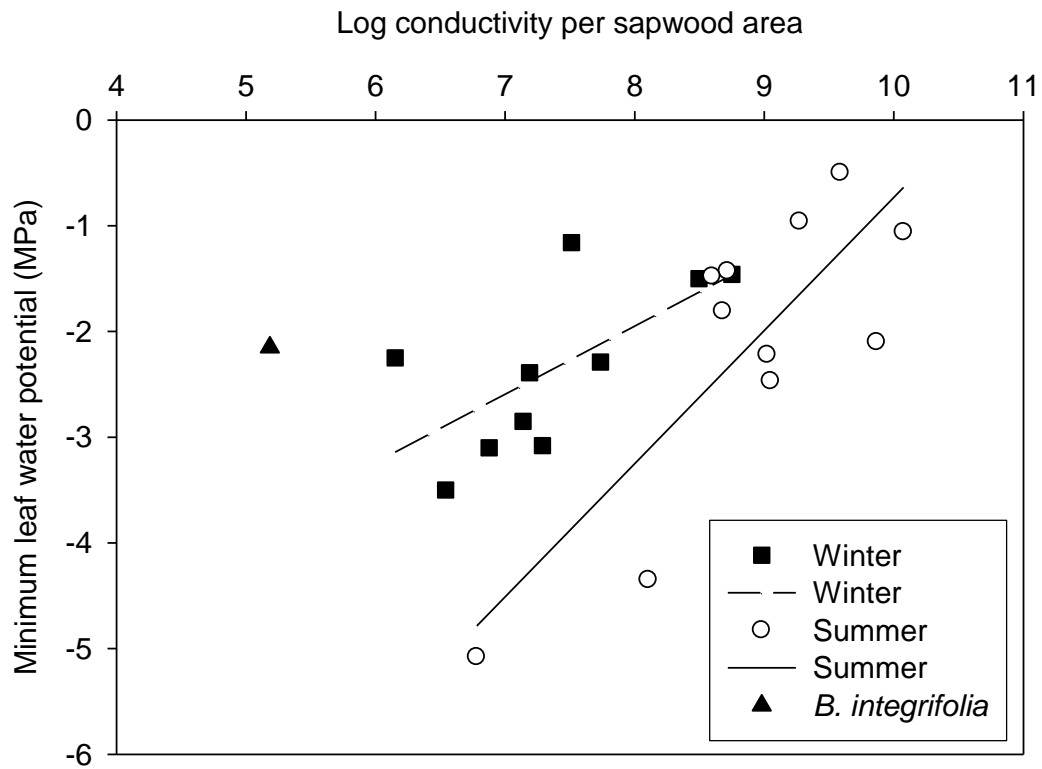
Fig. 5. Minimum leaf water potential plotted against log-transformed conductivity per

sapwood area for summer and winter. There were significant correlations in both

seasons; in winter (r = 0.657, P = 0.039) and in summer (r = 0.811, P<0.01). *B.*

integrifolia (closed triangle) was removed from the winter analysis because it was an

outlier, consistent with Fig. 8. Each point represents the species average in each

season.
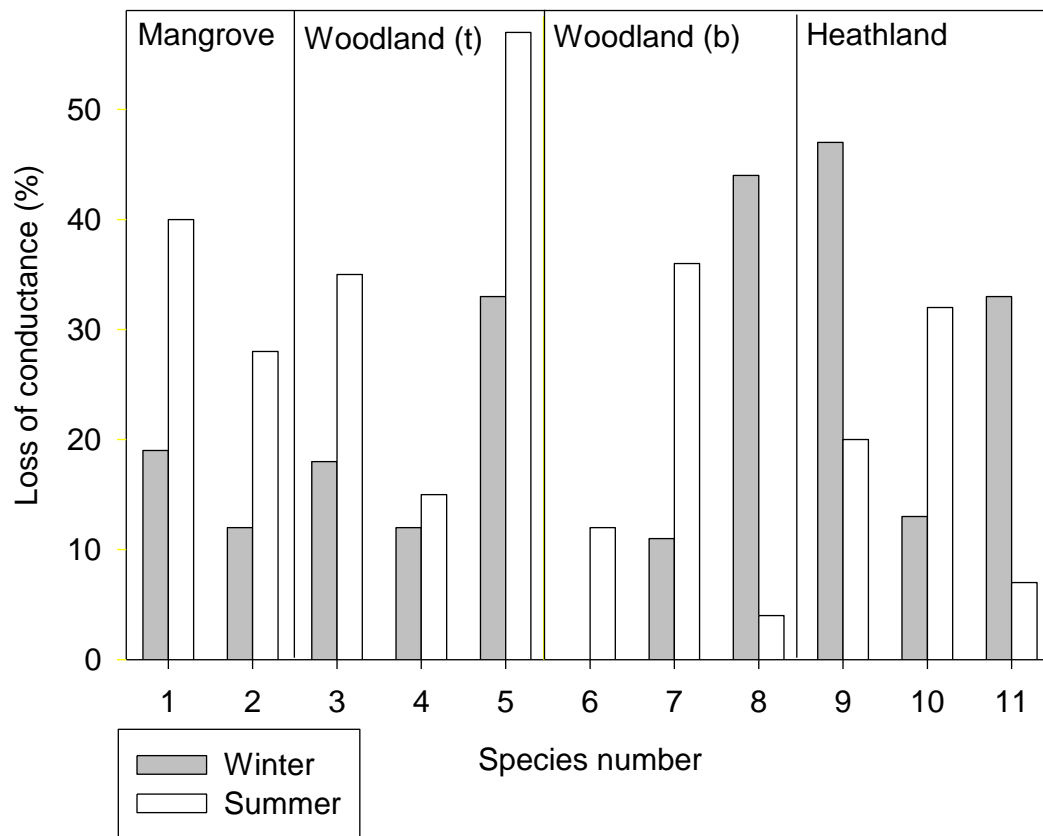
Fig. 6. Mean loss of conductance due to xylem embolism in summer and winter for each species in the four habitats. Species numbers were 1= *Eucalyptus haemostoma*, 2= *Angophora hispida*, 3= *Banksia oblongifolia*, 4= *Glochidion ferdinandi*, 5= *Banksia integrifolia*, 6= *Cissus hypoglauca*, 7= *Angophora hispida*, 8= *Banksia oblongifolia*, 9= *Persoonia lanceolata*, 10= *Aegicerus corniculatum*, 11= *Avicennia marina*.
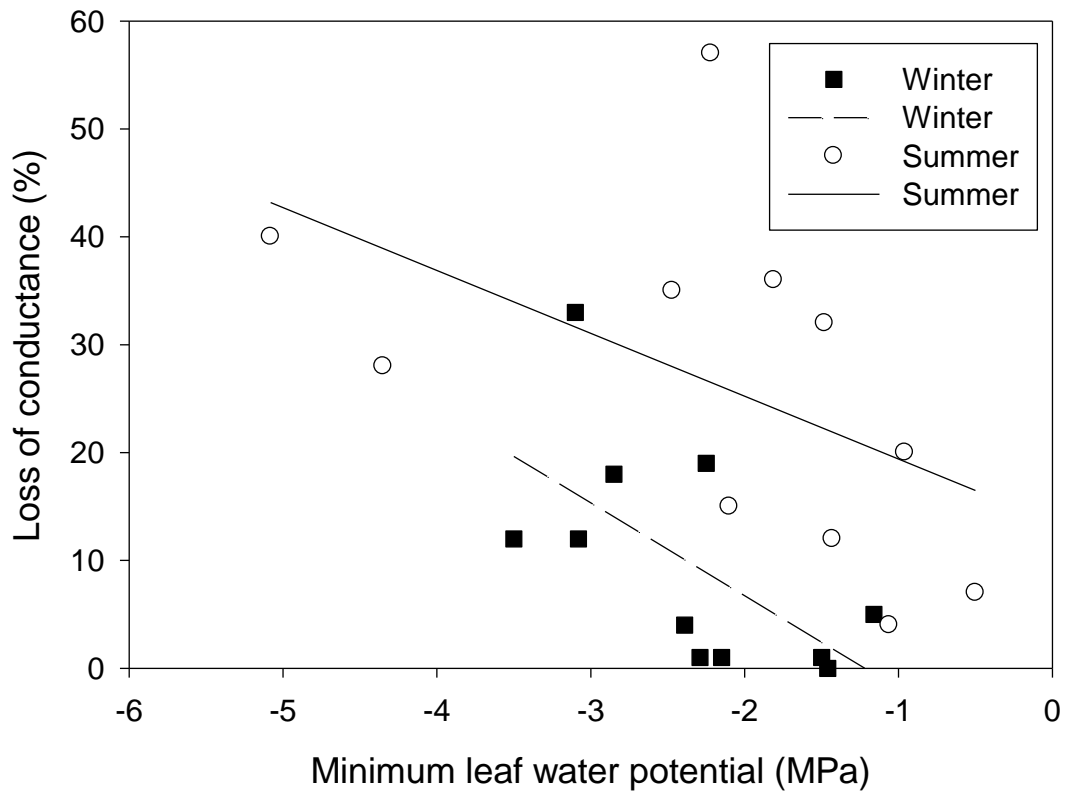
Fig. 7. Loss of conductance due to xylem embolism plotted against minimum leaf water potential. Each point represents the species average in each season. Pearson's correlation coefficients (r) were -0.624 ($P = 0.012$) and -0.543 ($P = 0.045$) for winter and summer respectively.
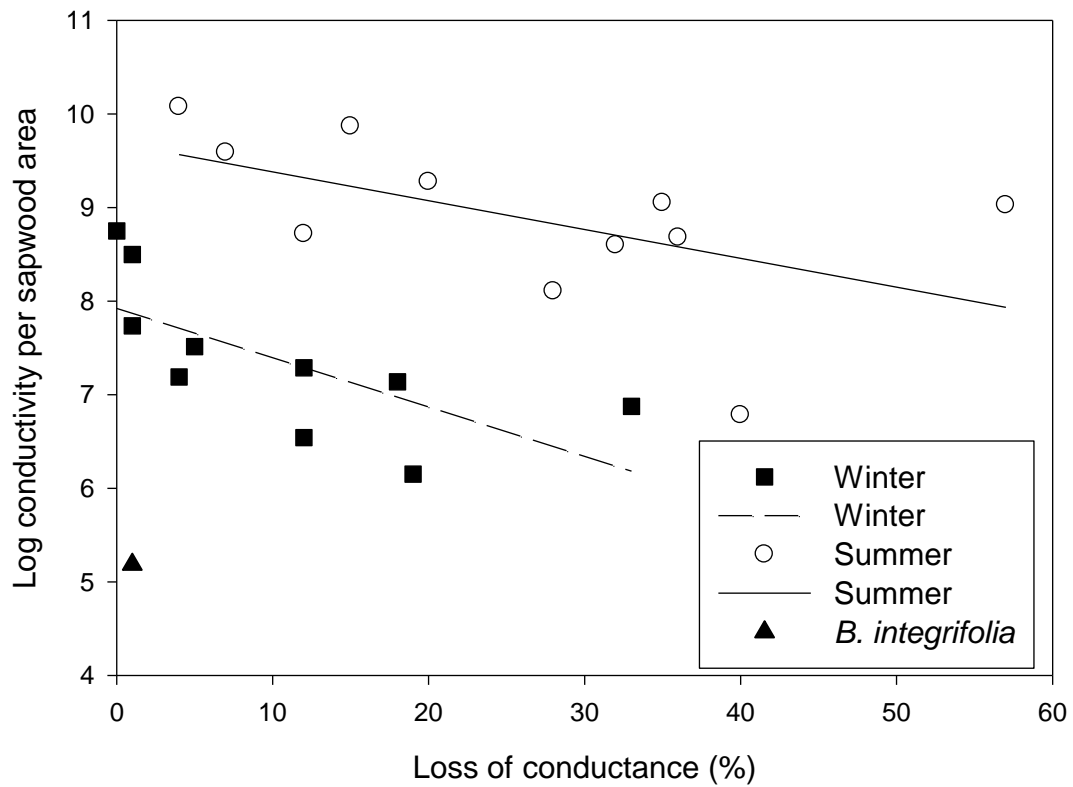
Fig. 8. Log-transformed conductivity per sapwood area plotted against loss of conductance. Each point represents the species average in each season. *B. integrifolia* (closed triangle) was removed from the winter analysis because it was an outlier, consistent with Fig. 5. Pearson's correlation coefficients (r) were –0.691 ($P = 0.027$) and –0.583 ($P = 0.063$) for winter and summer respectively.
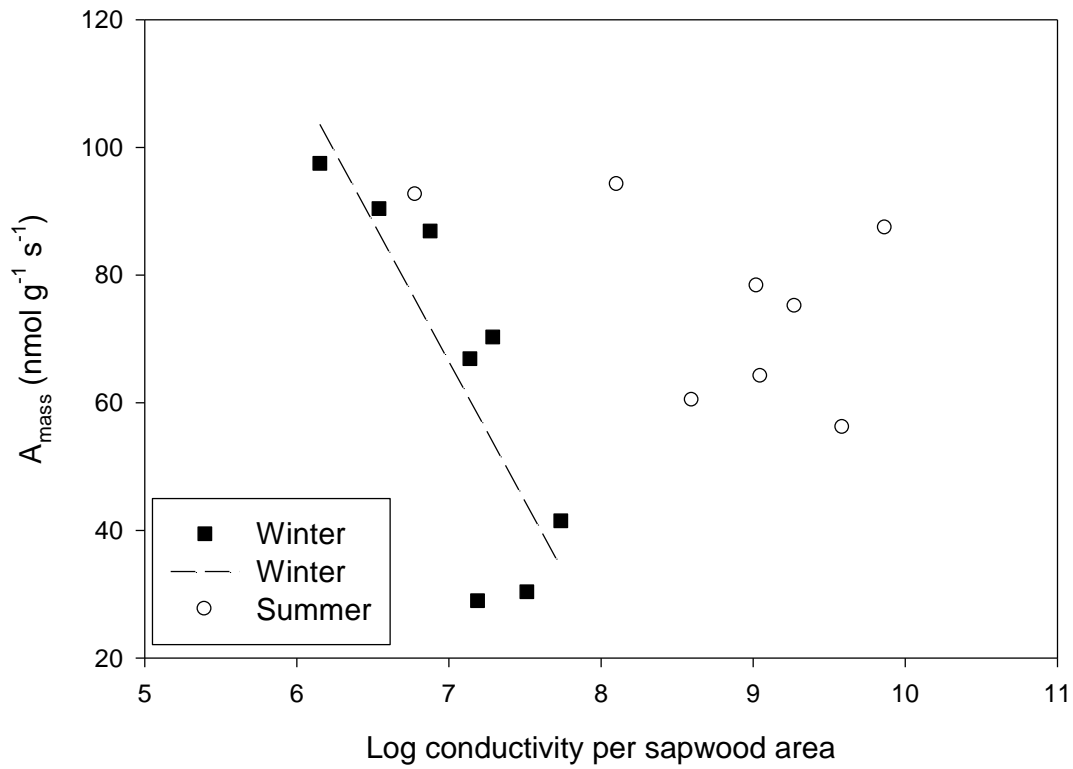
Fig. 9. Mass-based photosynthetic rate (A_{mass}) plotted against log-transformed conductivity per sapwood area for summer and winter for heathland, mangrove and woodland (ridge-top) habitats. Pearson's correlation coefficients (r) were –0.489 ($P = 0.219$) and –0.825 ($P = 0.012$) for summer and winter respectively.
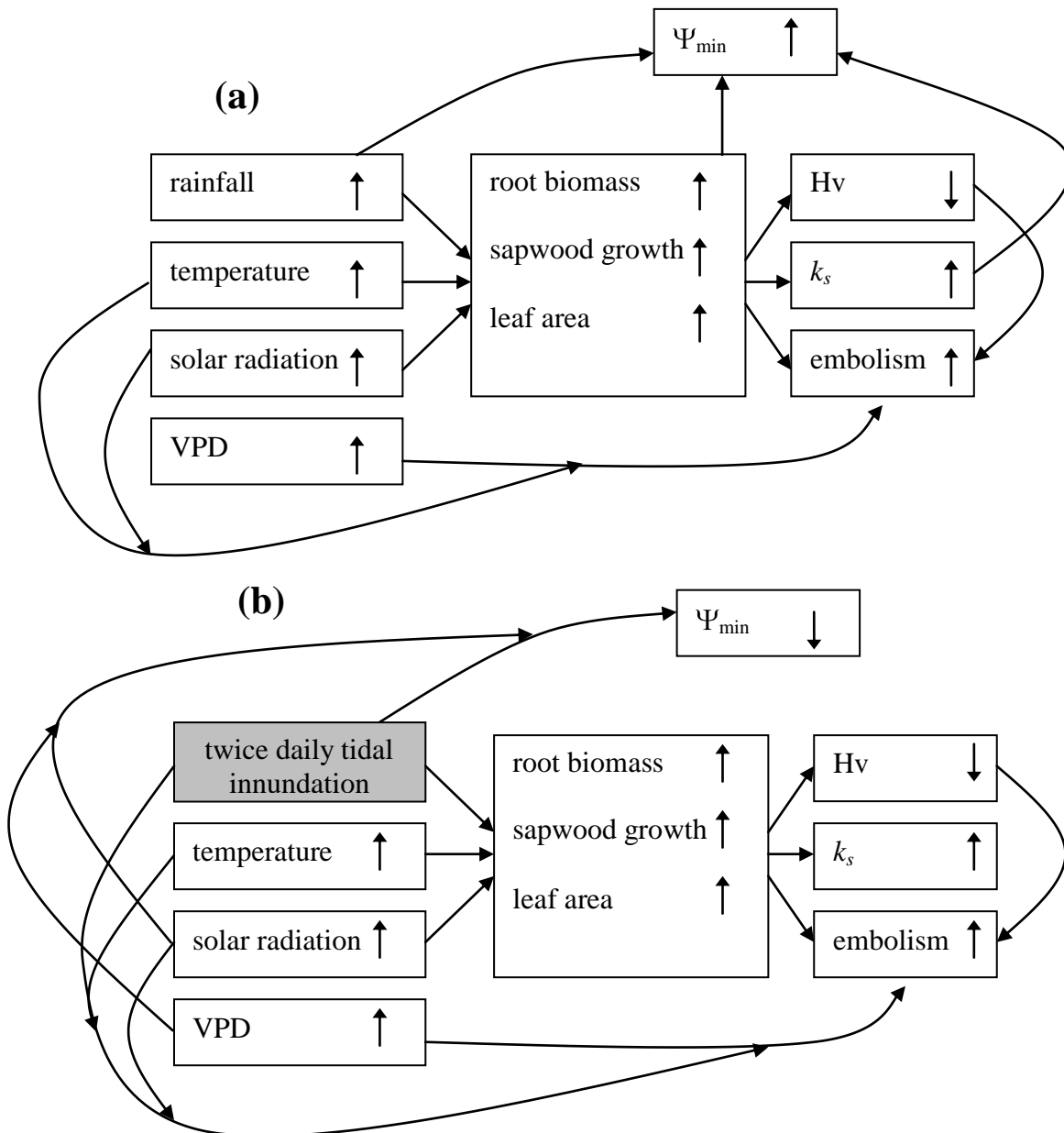
Fig. 10: Conceptual model of summer environmental conditions and their impacts on plant water relations for a) terrestrial habitats (woodlands and heathlands) and b) mangrove habitat. Arrows in boxes represent increase or decline in characteristics relative to winter conditions. All arrows are reversed for winter conditions. The main difference between terrestrial and mangrove habitats is tidal inundation. In mangroves the occurrence of twice daily tidal inundation by saline water reduces the influence of higher root biomass and higher rainfall, allowing direct impacts of solar radiation and VPD to lead to a more negative Ψ_{min} in summer.