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SHIFTS IN LEAF AND STEM HYDRAULIC TRAITS ACROSS ARIDITY GRADIENTS IN EASTERN AUSTRALIA

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Premise of research. Plants are faced with a challenge across all climates they inhabit—they must transport water to their leaves so that photosynthesis can take place. Although this is simple in concept, it can be achieved by different arrangements of root, stem, and leaf traits. The hydraulic functioning of species across aridity gradients is determined by the coordination of these traits. Nevertheless, we have an imperfect understanding of which trait shifts are favored across aridity gradients as well as the alignment of trait shifts with climate.

Methodology. We measured hydraulic traits relating to Darcy's law for 120 angiosperm species across a broad range of climates in eastern Australia; nearly one-third of all biome space on Earth was represented. We then determined which hydraulic trait shifts have been favored across aridity gradients and which climate characteristics these trait shifts aligned with.

Pivotal results. Increasing aridity, from climates with similar precipitation and evaporation to climates where precipitation was only a third of evaporation, was associated with a 4.8-fold decrease in plant height, a 3.0-fold decrease in leaf area–to–sapwood area ratio, and a 3.3-fold decrease in leaf water potential. However, sapwood-specific conductivity decreased by 5.9-fold, more than any other hydraulic trait. Greater sapwood-specific conductivity (decreasing resistance) at wet sites compensated for increasing resistance and hydraulic demand that was associated with taller plants and leafier shoots. All hydraulic traits were strongly correlated with growth season aridity ($r > 0.82$; $P < 0.05$) but were not correlated with maximum aridity. This suggests that plant hydraulic traits are most responsive to water availability and evaporative demand present during the most suitable months for growth rather than the driest months.

Conclusions. We suggest that evolution has equipped plants with various mechanisms to avoid desiccation during the dry season while optimizing hydraulic traits for carbon gain during the growth season.

Keywords: Darcy's law, water balance, aridity, evaporation, cavitation, seasonal precipitation.

Online enhancement: appendix.

Introduction

Plant stems are the organs through which water is delivered from the roots to the leaves, where most evaporates back into the atmosphere. The rate of water transfer is controlled by soil water availability and by the evaporative energy present to pull that water through plant conductive tissue as well as by the physiology and structure of the plants themselves. Considering that the number of possible physiological and structural solutions to achieve water transport are markedly limited (Meinzer 2003), we might expect common patterns of hydraulic trait coordination across environmental gradients. This study addresses the question of how the physical environment relates to the coordination of hydraulic traits across species, in particular leaf, stem, and sapwood traits.

We can more closely examine how climate and hydraulic traits relate to one another using the Whitehead-Jarvis application of Darcy's law (Whitehead et al. 1984), modified to the proportionality (hereafter referred to as "the hydraulic proportionality") shown in figure 1. Sapwood-specific conductivity measures the "ease" with which water can be pulled through wood; it is the rate of water transport through a given area and length of sapwood, across a given pressure gradient. The left side of this proportionality (sapwood-specific conductivity/leaf area–to–sapwood area ratio) is equal to stem conductance per unit leaf area, i.e., the leaf-specific conductivity. This proportionality incorporates several assumptions (see the appendix, available online) that should be viewed as a useful but qualitative representation of how climate (e.g., soil water potential and evaporative demand) and hydraulic

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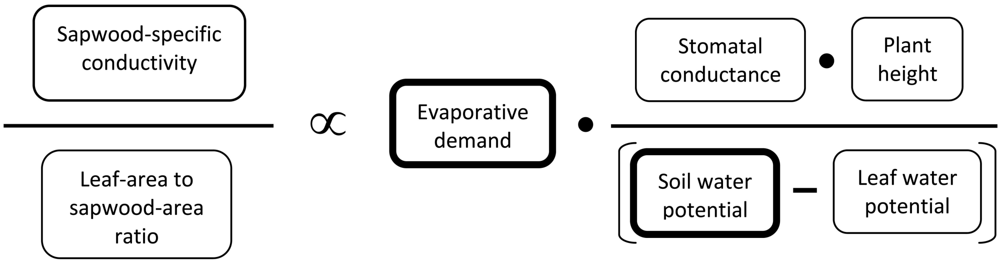

Fig. 1 Whitehead-Jarvis application of Darcy's law (Whitehead et al. 1984) modified to the shown proportionality.

traits might vary in relation to one another. For example, one limitation of the proportionality is that it does not include leaf and root resistance. Although root and leaf resistance are significant proportions of whole-plant resistance, conductance of whole plants and individual organs (e.g., sapwood) are often correlated (Nardini and Salleo 2000; Brodribb et al. 2002; Fichot et al. 2011) and suggest close coordination among water transport tissues.

As evaporative demand and water availability (i.e., soil water potential) vary across habitats, proportional adjustments to other traits in the hydraulic proportionality must be made to achieve water balance (i.e., to maintain proportionality). For example, shorter plants generally have less path-length resistance than tall plants, and as such short stature would help balance an increase in evaporative demand or a decrease in soil water availability. However, being short may also incur a costly decrease in exposure to photosynthetically active radiation, i.e., short plants can be shaded by taller neighbors. Alternatively, plants might "choose" to reduce stomatal conductance in response to increasing aridity, but if they do so their photosynthesis may be constrained by a lack of intracellular CO_2 (but see Wright et al. 2001). Similarly, if plants reduce their leaf water potentials (e.g., leaf osmotic adjustment) in response to increasing aridity, they might then require dense, embolism-resistant sapwood (Hacke et al. 2001). On the face of it, it appears as if the only plant trait in the hydraulic proportionality that can be adjusted to meet increasing aridity without obvious construction costs or decline in net photosynthesis is sapwood-specific conductivity. This is not to say that increasing sapwood-specific conductivity can be achieved without cost or risk.

Sapwood-specific conductivity can be increased by increasing the number of vessels without changing vessel width (i.e., changing vessel lumen fraction; Zanne et al. 2010), but this may result in weaker wood or higher stem maintenance costs (Anten and Schieving 2010; Larjavaara and Muller-Landau 2010). Alternatively, sapwood-specific conductivity can be increased by increasing the width of vessels but without changing vessel lumen fraction, i.e., changing S, the ratio of vessel cross-sectional area to the number of vessels present in a given area of sapwood cross section. Increasing S (wider vessels at a given vessel lumen fraction) appears to be the "preferred" means to achieve higher sapwood-specific conductivity across species (Sperry et al. 2006; Zanne et al. 2010).

Regardless of how high sapwood-specific conductivity is achieved, it is known that across a large subset of the world's angiosperms, species with high sapwood-specific conductivity are largely restricted from arid habitats, with ~98% of these species (sapwood-specific conductivity >2 kg m^{-1} MPa^{-1} s^{-1}) occurring in wet habitats where average predawn water potentials are greater than −2 MPa (Choat et al. 2012). Although it is unclear why species with highly conductive sapwood should be restricted from arid habitats, it may be because sapwood conductivity is often thought to trade off against embolism resistance. However, evidence for this trade-off is inconsistent (Fichot et al. 2010; Zhu et al. 2013) or difficult to interpret because embolism resistance appears to be correlated not only with sapwood conductivity but also with different components of vessel anatomy (Hacke et al. 2006; Lens et al. 2010). Nevertheless, highly conductive xylem does appear to be linked to several vessel and pit characteristics that are associated with reduced embolism resistance (Hacke et al. 2006; Lens et al. 2010). An additional consequence of highly conductive sapwood is that refilling/repair costs following cavitation events are likely significant and costly (Zwieniecki and Holbrook 2009; Brodersen et al. 2010).

As the atmosphere or soil becomes more arid, we might expect a decrease in sapwood conductivity across species to avoid cavitation risk. It is important to remember that these increases in aridity and decreases in sapwood conductivity still need to be balanced by proportional shifts in the other traits in the hydraulic proportionality, e.g., the "expensive" ones: height, leaf area–to–sapwood area ratio, stomatal conductance, and leaf water potential. Thus, as plant height, leaf area–to–sapwood area ratio, and stomatal conductance increase across species (within sites and across climate gradients), it is logical to assume that evolution should favor increasing sapwood-specific conductivity to balance the hydraulic proportionality, but only where the risk of doing so is acceptable—where soil aridity is low.

This study measured plant traits relating to the hydraulic proportionality across three water availability gradients nested within a large latitude gradient in eastern Australia (table 1). We asked the following questions: (1) What are the most common shifts in plant traits as site aridity increases? (2) Are plant hydraulic traits aligned with climate variables, and, if so, what variables and seasons are they particularly aligned with? (3) Is increasing aridity associated with shifts in plant traits that would lead to a reduction in whole-plant resistance and water use, i.e., shorter plants, less leafy shoots, lower leaf water potentials, and more conductive sapwood?

Table 1

Climate Characteristics for All Sites

	Site							
Climate variables	Hot-wet	Hot-dry	Hot-arid	Warm-wet	Warm-dry	Warm-arid	Cool-wet	Cool-dry
Mean annual precipitation (mm)	2117	960	747	1353	843	422	936	544
Summer precipitation (mm mo^{-1})	453	184	202	103	90.2	35.4	86.0	50.8
Winter precipitation (mm mo^{-1})	30.2	24.8	3.30	71.6	37.1	33.8	89.8	46.6
Summer vapor pressure deficit (kPa)	1.58	1.50	2.81	1.40	2.27	3.23	1.02	1.08
Winter vapor pressure deficit (kPa)	1.24	1.16	3.24	.94	1.03	.89	.46	.41
Summer precipitation/vapor pressure deficit[a]	288	125	71.8	73.8	39.6	11.0	85.2	47.6
Winter precipitation/vapor pressure deficit[a]	24.6	21.8	1.04	76.8	35.7	38.5	195	114
Frost days (events yr^{-1})	0	12	0	0	12	36	48	48
Mean annual temperature (°C)	24.1	21.3	26.9	17.0	16.6	17.9	11.3	10.0
Latitude (°S)	18.4	18.3	18.7	33.7	32.8	33.0	43.0	42.4
Longitude (°E)	146.1	145.5	141.8	151.1	150.9	146.2	147.2	147.0

Note. "Summer" refers to the summer months most optimum for plant growth: November and December at the "cool" and "warm" sites and the peak of the wet season at the "hot" sites (January and February). "Winter" refers to the coldest months of the year at the cool and warm sites (July and August) and the peak of the dry season at the hot sites (also July and August).

[a] Growth season (summer) and nongrowth season (winter) aridity values are represented by the ratio of precipitation to vapor pressure deficit measured during these seasons.

Material and Methods

Site, Species Collection, and Replication

Eight sites were chosen across a broad aridity and temperature range (fig. A1; figs. A1–A5 are available online). We chose the commonly used aridity index (AI), the ratio of precipitation to potential evapotranspiration, to choose sites for sampling (Thornthwaite 1948). This index has been found to agree well with plant water availability in Australia (Walker and Langridge 1997; Eamus et al. 2000) and globally (Oudin et al. 2005; Tsakiris and Vangelis 2005). Three water availability gradients were established in eastern Australia in tropical, subtropical, and temperate latitudes (~18.5°, 33.0°, and 42.5°S; fig. A1). Three sites of contrasting water availability ($AI \approx 1.1, 0.60, 0.35$) were chosen within each latitude, except at the temperate latitude, where arid climates ($AI \approx 0.35$) do not occur. Thus, only two sites ("wet" and "dry") were established within the temperate latitude. We denote these sites by their relative temperature and water availability, e.g., "cold-wet," "warm-dry," "hot-arid," etc. (table 1). Seasonal climate plots of monthly precipitation, maximum temperature, and vapor pressure deficit as well as the time of year when sampling was carried out are provided for each site in figures A2–A4.

The tropical sites differ from the subtropical and temperate sites in that more than half of the total annual precipitation falls during summer months (December, January, February, and March) in the tropics, whereas precipitation is spread fairly uniformly throughout the year at the other sites (table 1; fig. A3). Additionally, although the arid sites at both tropical and temperate latitudes have similar annual aridity (precipitation relative to potential evaporation), rainfall at the temperate site (warm-arid) is markedly unpredictable, whereas rainfall in the tropics is monsoonal and falls regularly between December and March nearly every year. We identify times of peak growth at each site, denoted as "summer" in all tables and figures. At temperate and subtropical latitudes (cool and warm sites), peak growth is achieved during early summer (Specht and Brouwer 1975) and is represented by the mean monthly climate values for November and December (table 1). In the tropics (hot sites), peak growth is achieved during the wet season (Prior et al. 2004) and is represented by the mean monthly climate values for January and February (table 1). "Winter" refers to the two months with the lowest growth rates, which are also the coldest months of the year at all sites (July and August; Specht and Brouwer 1975; Prior et al. 2004).

Sites were chosen on soils judged to be oligotrophic on the basis of parent materials (weathered sandstone, granite, or siliceous alluvial/eolian deposits), vegetation characteristics, and soil maps/data, where available. All sites were relatively level (<5% slope) and vegetated with late successional plant communities. Soils profiles were described to a depth of 1.5 m (where possible) from a single pit within each site. Diagnostic horizons were sketched, noting root density, texture, color, and structure as well as redoximorphic and xeric soil features. Total P and N were generally low, ranging from 40 to 157 mg P kg^{-1} and 0.03%–0.26% N, and pH values ranged from 4.0 to 6.3 (Gleason et al. 2012). Aluminum saturation and organic carbon ranged from 2.2% to 47.1% and from 0.3% to 6.1%, respectively (Gleason et al. 2012).

The 16 most common woody dicot species were chosen within each site for analysis (table A1; tables A1–A3 are available online). Sampling was undertaken to avoid seasonal extremes, such as maximum and minimum annual temperatures as well as the peak wet and dry seasons in the tropics. Trait collection times occurred as follows: September 2009 (hot-wet), November 2009 (hot-dry), May 2010 (hot-arid), October 2010 (warm-wet), June 2009 (warm-dry), April 2009 (warm-arid), January 2010 (cool-wet), and March 2010 (cool-dry). As such, trait values represent one-time measurements rather than integrated values across the year. Although it is known that seasonal emboli may result in meaningful changes in sapwood-specific conductivity (Prior and Eamus 2000; Drake and Franks 2003; Macinnis-Ng et al. 2004), our measurements of sapwood-specific conductivity reflect maximum values after flushing emboli from the stems and should more closely represent species-level means rather than seasonal conditions. However, leaf water potential and leaf area–to–sapwood area ratio are markedly plastic across seasons and should be interpreted with some caution.

Unless otherwise mentioned, five individual plants of each species were used to generate mean trait values for all species. For species >5 m in height, individuals ~5 m tall were sampled; otherwise, plants are representative of the average mature height of the species.

Climate Variables

Monthly precipitation, temperature, relative humidity, pan evaporation, and frost days were downloaded as monthly averages (approximately 1970–2011) from the Australian Bureau of Meteorology. Vapor pressure was calculated from daytime relative humidity and temperature (Weiss 1977). We estimate evaporative demand (vapor pressure deficit) as the difference between the leaf vapor pressure at saturation (at air temperature) and the measured vapor pressure of air beyond the leaf boundary layer. However, we note that the Whitehead-Jarvis equation (Whitehead 1998) assumes that evaporative demand is calculated as the saturated vapor pressure (at leaf temperature) minus the measured vapor pressure of the air at the leaf surface. We express "aridity" as the mean monthly precipitation divided by the mean monthly vapor pressure deficit during either the summer or the winter months. However, we present other measures of aridity (e.g., precipitation/pan evaporation) and their relationships with hydraulic traits in table A3 for comparison.

Sapwood-Specific and Leaf-Specific Conductivity

Stem segments 80 cm long were cut from the leading shoot of each plant (5 plants species^{-1} × 16 species site^{-1} × 8 sites = 640 branch segments) and placed in a sealed plastic bag. Shoots were transported back to the laboratory within 4 d of collection and submerged in water for 24 h prior to measurement. Side branches were trimmed and sealed (Loctite 550 adhesive, 779 activator; Henkel, Kilsyth, Australia), recut under water (0.5 cm diameter at the distal end), and connected to a Sperry apparatus (Sperry et al. 1988), and conductivity was measured using filtered (0.02 μm) and pressurized (100 kPa) 0.02 M KCl solution. Conducted solution was collected in a beaker resting on a computer balance (to the nearest 0.00001 g), and changes in mass were logged every 15 s to calculate flow rate. After measuring flow rate, each segment was then submerged in water and pressurized (100 kPa) from the distal end with N_2. Segments were judged to have 100% complete vessel lengths if bubbles were not observed exiting from the proximal end after 5 min. Although ~26 species were judged to have at least some open vessels, these species did not have significantly higher sapwood-specific conductivity rates than closed-vesseled species (fig. A5) and were included in all analyses. We also noted that the outcomes of our hypotheses tests were not influenced by including or excluding these species. Sapwood-specific conductivity was calculated by dividing the flow rate by (1) the pressure gradient (100 kPa), (2) the cross-sectional area of the distal end (~0.5 cm diameter, omitting pith and bark), and (3) the segment length (80 cm; Sperry et al. 1988). This result was then corrected for temperature-dependent changes in viscosity and expressed as conductivity at 25°C. Leaf-specific conductivity was calculated by dividing the segment conductance by the total distal leaf area, as estimated from species-specific allometric equations predicting leaf area from sapwood area (described below).

Leaf Area–to–Sapwood Area Ratio

Leaf area–to–sapwood area ratios were calculated using an allometric approach. Leading shoots were cut along the main stem in the distal to proximal end into 5-, 10-, 20-, 40-, 80-, and 120-cm sections. The inside-bark diameter of each segment was measured at the distal and proximal ends using digital calipers. Leaf mass and stem mass were calculated for each segment after drying to constant mass at 70°C. An ordinary least squares model was then built from these data for each species, predicting leaf mass as a function of sapwood diameter. Leaf area of shoots was calculated by dividing the predicted leaf mass by leaf mass–area relationships (Gleason et al. 2012). Because leaf area–to–sapwood area ratios were relatively similar across species at a given sapwood area (i.e., leaf area scaled similarly with sapwood area across species), we present interpolated leaf area–to–sapwood area ratios at a sapwood diameter of 1 cm.

Midday Leaf Water Potential

Leaf water potentials were measured using a pressure chamber (model 1000; PMS Instruments, Corvallis, OR) during midday hours on sunny days. Leaves or small terminal branches were cut, immediately placed in a sealed plastic bag, placed in the dark, and transferred to the pressure chamber for measurement. For each species, five replicate measurements were made on five different individual plants, with each plant being measured on different but consecutive days. See "Site, Species Collection, and Replication" for the specific month and year when trait data were measured at each site.

Sapwood Anatomy

Vessel anatomy was sampled from a single stem section from each species. Stem segments (~0.5 cm × 10 cm long) were taken from the leading shoots of plants, and cross sections were cut from them using a sledge microtome (Reichert; Vienna, Austria). Each section was then placed in a glycerol drop on a microscope slide, covered with a cover slip, and placed under ×200 magnification (model BH-2; Olympus, Tokyo, Japan). A grid (484 intersections mm^{-2}) was then superimposed over a randomly selected area of the magnified cross section, and intersections were tallied as falling either inside or outside vessel lumen. This procedure was carried out on two more randomly selected areas of the magnified image, yielding three samples per cross section. The percentage of cross-sectional area that is vessel lumen (vessel lumen fraction) was then calculated as the total number of intersections falling within vessel lumen divided by the total number of intersections.

Vessel density (vessels mm^{-2}) was measured by superimposing a 0.25-mm^2 square over the same magnified cross section described above, counting the number of vessels within

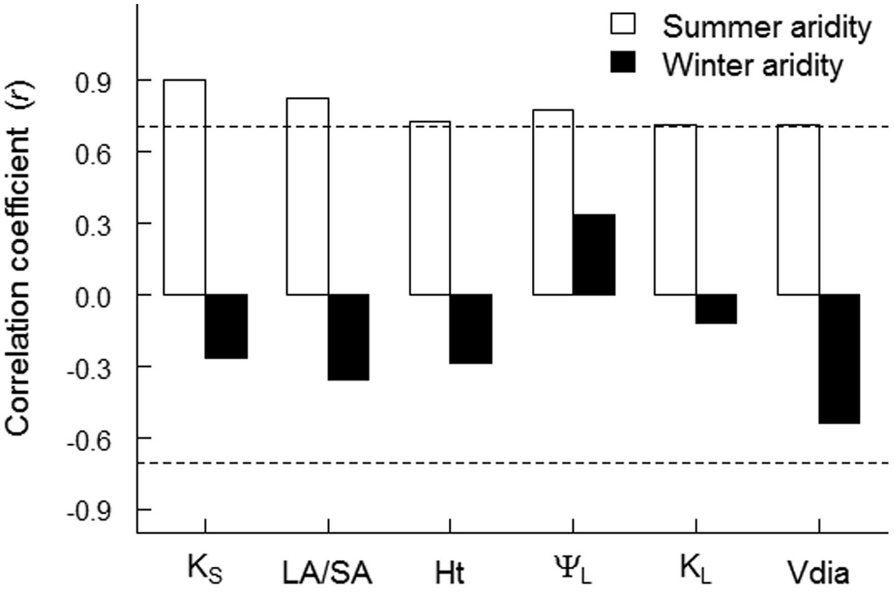

Fig. 2 Correlation coefficients (r) for linear relationships between "aridity" (either summer or winter) and hydraulic traits. Aridity is calculated as the mean monthly precipitation falling during either the summer or the winter months divided by the mean monthly vapor pressure deficit during that time. Dashed lines indicate significant correlation coefficient values ($\alpha = 0.05$). K_S = sapwood-specific conductivity, LA/SA = leaf area divided by sapwood cross-sectional area, Ht = maximum attainable height of the species, Ψ_L = leaf water potential measured at midday, K_L = leaf-specific conductivity, V_{dia} = mean vessel diameter.

the square, and then dividing by 0.25. This procedure was also carried out on three randomly chosen areas of each cross section.

Average vessel area, i.e., the cross-sectional lumen area of an average-sized vessel, was calculated by dividing vessel lumen fraction by vessel density. Average vessel diameter was simply calculated by applying the relationship: average vessel area = $\pi \cdot r^2$ and solving for r (diameter = $2r$). Although this is not the hydraulically weighted average diameter necessary for calculating hydraulic conductivity, average conduit diameter was strongly correlated with hydraulically weighted diameter ($r^2 = 0.92$) across 284 species (B. Choat, S. Jansen, T. J. Brodribb, et al., unpublished data).

Data Analysis

Ordinary least squares regression was used to explore relationships between mean site values ($n = 8$) and climate variables. We used mean trait values rather than all observations (species means) because, at least to some extent, species are not completely independent observations (relative to climate), and our aim was to explain trait shifts across sites, not species. We note that using site means in our regression tests is a more conservative approach than using species means, which arguably overestimates the degrees of freedom. ANOVA (aridity nested within latitude) was used to test mean differences among aridity and latitude treatments. All data were transformed as necessary to meet the assumptions of the analyses.

Results

What Are the Most Common Shifts in Plant Traits as Site Aridity Increases?

As annual aridity (precipitation/evaporation) increased across sites, sapwood-specific conductivity decreased 5.9-fold, maximum height decreased 4.8-fold, leaf area–to–sapwood area ratio decreased 3.0-fold, and midday leaf water potential decreased 3.3-fold (figs. 2, 3). These shifts were evident within individual aridity gradients as well as across latitudes (fig. 3; tables 2, A2). There was a significant increase in hydraulic trait values with decreasing latitude (toward the tropics). These shifts across latitude also appear to have been related mainly to aridity rather than temperature, as the tropical sites receive monsoonal rainfall during the growth season, whereas subtropical and temperate sites do not. This additional rainfall effectively reduces aridity in the tropics during the time of year when plants are actively growing (summer) and appears to engender a shift in hydraulic traits (fig. 4; table 2). Additionally, mean annual temperature was not significantly correlated with any hydraulic trait other than vessel diameter (table A3), suggesting that temperature did not underpin the observed shifts in hydraulic traits other than possibly vessel diameter.

Are Plant Hydraulic Traits Aligned with Climate Variables, and, If So, What Seasons Are They Particularly Aligned With?

All plant traits exhibited much stronger correlations with climate variables measured during months of peak summer

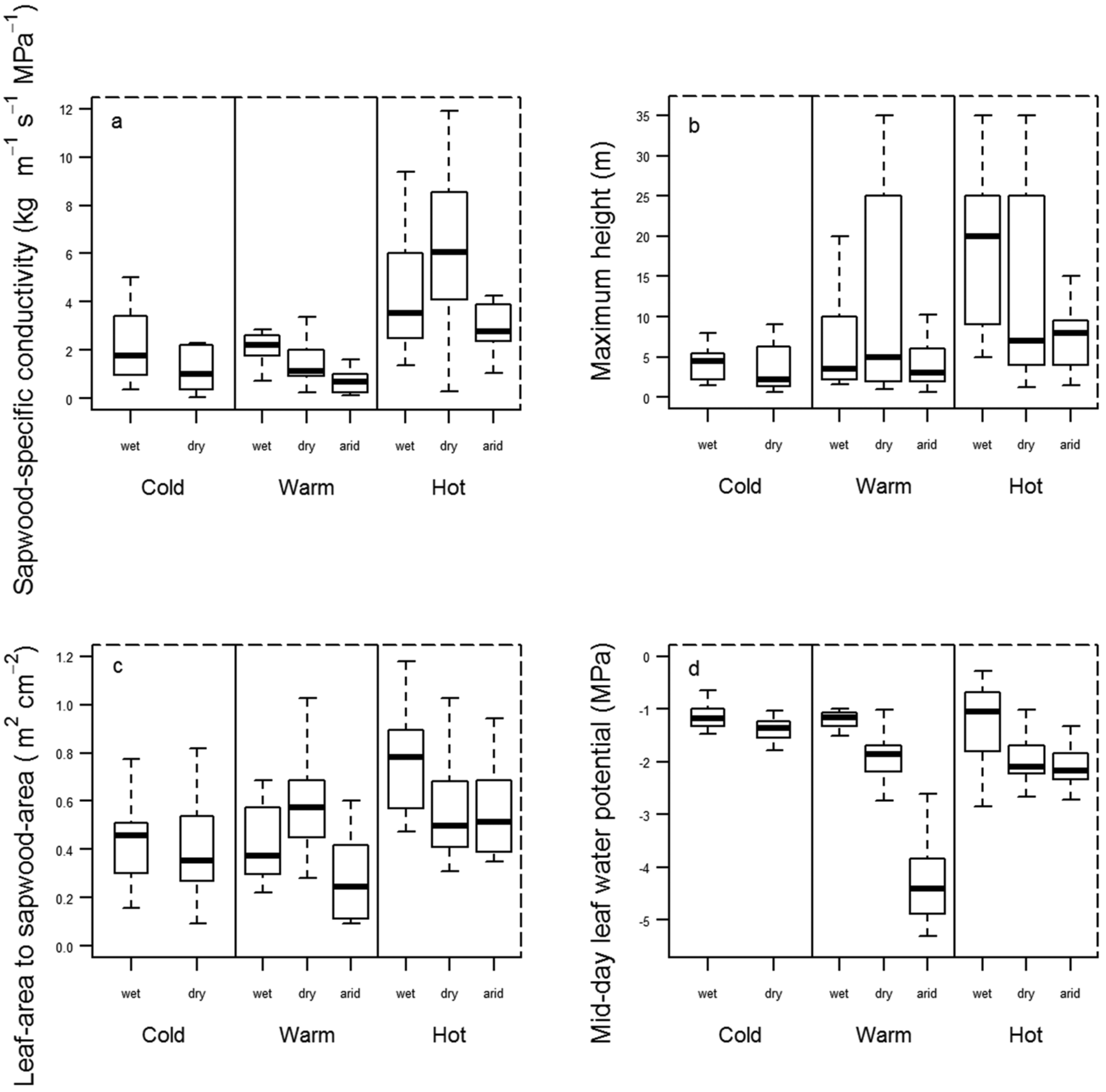

Fig. 3 Box plots of hydraulic traits across aridity gradients (“wet,” “dry,” “arid”), nested within temperate, subtropical, and tropical latitudes (“cool,” “warm,” “hot”). The center of each box represents the medium species value for each site (e.g., the “cool-wet” site). The upper and lower sides of each box represent the upper and lower quartiles for each site, respectively. Maximum and minimum species values are represented by dashed error bars extending out from each box.

growth (fig. 2). In particular, summer precipitation and the ratio of summer precipitation to either vapor pressure deficit or pan evaporation were strong predictors of most plant hydraulic traits (fig. 2; table A3), whereas months of peak aridity or nongrowth months were, in general, not correlated with plant hydraulic traits whatsoever (fig. 2).

Is Increasing Aridity Associated with Shifts in Plant Traits That Would Lead to a Reduction in Whole-Plant Resistance and Water Use, i.e., Shorter Plants, Less Leafy Shoots, Lower Leaf Water Potentials, and More Conductive Sapwood?

Increasing summer aridity (precipitation/vapor pressure deficit) was associated with shorter stature, lower leaf area–to–sapwood area ratio, and lower leaf water potential (fig. 3). Although sapwood-specific conductivity and vessel width decreased with increasing summer aridity (fig. 2), tropical species exhibited markedly higher sapwood-specific conductivity than nontropical species (fig. 4), which may reflect the abundance of precipitation at these sites during the growth season (summer). Thus, increasing evaporative demand in the tropics was offset (i.e., proportionality was maintained in the hydraulic proportionality) by decreasing hydraulic resistance in sapwood (i.e., increasing sapwood-specific conductivity). In contrast, at the subtropical and temperate latitudes, where summer rainfall is less predictable, it is possible that low soil water availability and the need for embolism resistance during the growth season preclude the construction of highly conductive xylem. This may be because highly conductive xylem is often associated with a spectrum of anatomical characteristics in both pit and vessel anatomy likely to precipitate hydraulic failure at low water potentials (Hacke et al. 2006; Lens et al. 2010).

Precipitation during the growth season (summer) was strongly correlated with taller plants, leafier shoots, and more conductive sapwood (fig. 2). Although the amount of precipitation falling during the growth season was the strongest trait predictor of tree height ($r^2 = 0.69$; $P = 0.011$), the predictive power of precipitation was improved for the other plant traits if it was expressed relative to evaporative demand, i.e., either vapor pressure deficit or pan evaporation (table A3). The simple ratio of growth season (summer) precipitation to vapor pressure deficit was a strong predictor of all hydraulic traits, but especially sapwood- and leaf-specific conductivity (fig. 5*a*).

Across the species and sites studied here, high sapwood conductivity was not associated with high aridity habitats and, thus, did not balance aridity via the hydraulic proportionality. Rather, the other plant traits balanced increasing aridity: decreasing height, decreasing leaf area–to–sapwood area ratio, and decreasing leaf water potential. The apparent incompatibility of high sapwood-specific conductivity in dry habitats appeared to be linked with vessel diameter (fig. 5*b*), which also decreased with increasing aridity, but with one important caveat. The two coldest sites (Tasmania) and the most infertile site had more narrow vessels than was predicted by summer aridity or sapwood-specific conductivity (boxed symbols in fig. 5*b*). Additionally, vessel diameter was positively correlated with mean annual temperature, suggesting that vessel diameters may have been restricted at the coldest sites to avoid freeze-thaw embolism.

Discussion

The Role of Sapwood-Specific Conductivity across Aridity Gradients

Sapwood-specific conductivity decreased 5.9-fold as aridity increased across the sites sampled in this study—significantly more than any other hydraulic trait (height, 4.8-fold; leaf area–to–sapwood area ratio, 3.0-fold; leaf water potential, 3.4-fold). Thus, high sapwood-specific conductivity was associated with wetter habitats. However, in the hydraulic proportionality, decreasing aridity (wetter habitats) can be balanced by decreasing sapwood-specific conductivity, not increasing conductivity, as was found. So, why should sapwood-specific conductivity increase in wet habitats?

Plant biomass and net primary productivity increase monotonically across the range of aridity and precipitation sampled in this study (Whittaker and Niering 1975; Gholz 1982). This implies increasing crowding and places a premium on plant traits that maximize light interception—height and leaf area. However, all else being equal, height and leaf area cannot increase without cost. Building long stems to access high-light environments represents a significant carbon cost. Additionally, the increasing path-length resistance and water demand that is associated with taller and leafier plants would result in a proportional decrease in xylem water potential, which could then lead to hydraulic failure. One way to avoid markedly low xylem water potentials and hydraulic failure but still maintain tall and leafy architecture is to reduce the resistance to water transport somewhere else in the plant. The species in this study appear to be accomplishing this task, at least in part, by reducing resistance in the sapwood itself, i.e., increasing sapwood-specific conductivity.

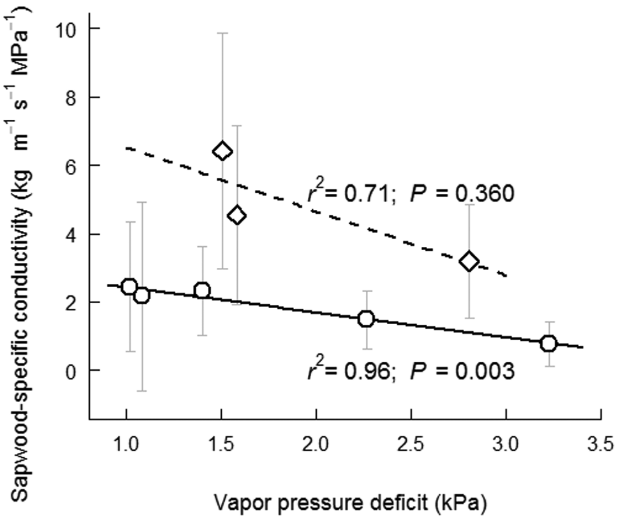

Fig. 4 Relationship between sapwood-specific conductivity and summer vapor pressure deficit. Dashed and solid ordinary least squares regression lines ($n = 8$) respectively represent tropical sites (diamonds), where more than 50% of the annual precipitation occurs during the summer months, and nontropical sites (circles), with nonseasonal precipitation. Error bars represent 1 SD ($n \approx 15$).

Unlike reducing height and leaf area, there is no obvious carbon cost associated with increasing sapwood-specific conductivity. There is a risk that building highly conductive xylem

Table 2

Statistics Summary of Nested ANOVA, with Aridity Gradients Nested with the Latitude Gradient

	Aridity		Latitude		Aridity × latitude	
	F	*P*	*F*	*P*	*F*	*P*
Sapwood conductivity	7.82	.001	27.7	<.001	4.02	.022
Leaf area–to–sapwood area ratio	9.38	<.001	17.4	<.001	9.05	<.001
Maximum height	4.91	.009	17.0	<.001	1.84	.164
Leaf water potential	44.7	<.001	11.4	<.001	33.7	<.001

Note. Interactions were tested using subtropical and tropical gradients only. Aridity = mean annual rainfall/mean annual evaporation.

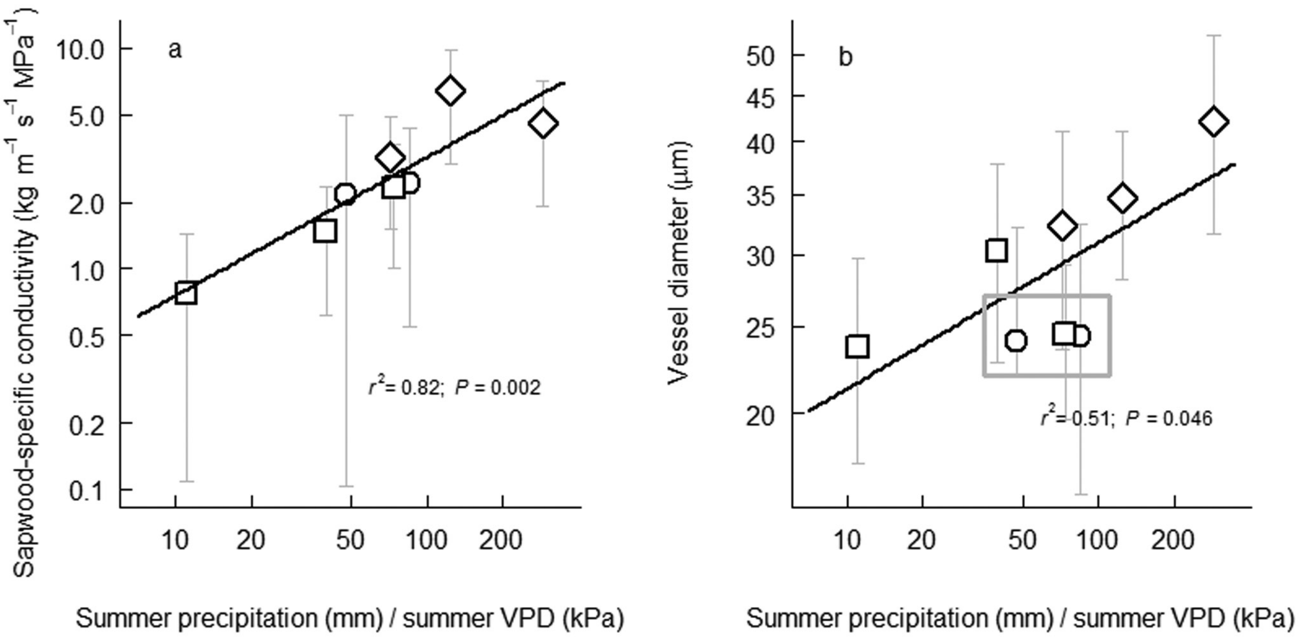

Fig. 5 Relationship between sapwood-specific conductivity and summer aridity (summer precipitation divided by summer vapor pressure deficit [VPD]). Sites located farther on the right of the fitted ordinary least squares regression line ($n = 8$) represent less arid climates (more precipitation relative to evaporative demand). The gray rectangle identifies cold sites (both Tasmanian "cool" sites) and the most infertile site ("warm-wet"). Error bars represent 1 SD ($n \approx 15$). Sites are denoted with the following symbols: tropical (diamonds), subtropical (squares), and temperate (circles).

may result in greater vulnerability to cavitation and hydraulic failure in dry soils, but for species in wet habitats increasing sapwood-specific conductivity may be the ultimate "free lunch" (i.e., species derive benefit without cost). However, highly conductive species are likely to experience much cavitation during periods of low water potential but then also undergo potentially expensive cavitation refilling when the water potential rises (Salleo et al. 2006; Brodersen et al. 2010). Although the cost of cavitation refilling is not presently known, it could potentially rival the costs of reductions in height and leaf area, particularly as soil water availability wanes across habitats. Thus, although increasing sapwood-specific conductivity is likely a carbon-cheap solution for achieving hydraulic balance, it may be a risky strategy in arid habitats.

Risks Associated with High Sapwood-Specific Conductivity

Higher sapwood-specific conductivity may be achieved either by increasing the fraction of conductive tissue in stems (i.e., vessel lumen fraction) or by maintaining the same vessel lumen fraction but building wider vessels (*S*; Zanne et al. 2010). Across angiosperms, species vary markedly more in *S* than in vessel lumen fraction (Sperry et al. 2006; Zanne et al. 2010). Although the trade-off underpinning this relationship is not well understood, it may be related to wood strength (Sperry et al. 2008), vasculature construction costs (Hacke and Sperry 2001), or maintenance costs (Larjavaara and Muller-Landau 2010). Moreover, wide vessels have been associated with other anatomical characteristics (e.g., pit membrane thickness and pit membrane area) thought to be related to embolism resistance (Hacke et al. 2006; Lens et al. 2010), suggesting that highly conducive sapwood is vulnerable to hydraulic failure. It therefore appears that balancing the hydraulic proportionality via sapwood-specific conductivity is not an option for most plants in arid habitats, as the vessel anatomy associated with these species would likely lead to cavitation and hydraulic failure.

Some plants are able to achieve high sapwood-specific conductivity in arid habitats (Maherali and DeLucia 2000; Cornwell et al. 2007), but only where aridity is driven by high evaporative demand rather than low water availability (Whitehead 1998; Maherali and DeLucia 2000; Eamus 2003; Zach et al. 2010), e.g., the shift from the subtropics to the tropics in this study (fig. 4). We suggest that it is these habitats with high evaporative demand and high soil water availability that should favor the use of sapwood-specific conductivity to achieve balance in the hydraulic proportionality. This is because if a plant growing in such a habitat can significantly reduce the resistance in its conductive tissue, the water potential of the plant would then equilibrate to a value near the soil water potential, which in wet habitats would likely be high enough to avoid significant cavitation, regardless of the evaporative demand. As a fictional illustration, if a plant with access to free water could reduce all the resistance in its hydraulic tissue, its leaf water potential would be equal to the soil water potential, regardless of how tall and leafy it was or how fast water evaporated from its canopy.

Hydraulic Traits Are Aligned with the Most Favorable Growth Conditions Rather Than the Most Arid Conditions

All the hydraulic traits measured in this study were strongly associated with precipitation and aridity during the most favorable months for growth but were not correlated at all with these same climate variables during the most arid months of the year (fig. 2). It is possible that because our sampling in the tropics occurred during times of relatively low precipitation (fig. A3) that our data may reflect dry season conditions rather than wet season conditions at these sites. Although this is likely the case for leaf area–to–sapwood area ratio and for leaf water potential, sapwood-specific conductivity measurements would have been relatively insensitive to native emboli because the stems were flushed at high pressure prior to measurement. However, even if our data were influenced by these dry conditions, then it is even more surprising that the hydraulic traits were strongly correlated with wet season aridity rather than dry season aridity. Why should these traits not be aligned with the most arid months of the year, as these are the periods most likely to precipitate hydraulic failure (Eamus et al. 2000)? This question is particularly valid in the tropics, where the dry season can be quite severe (Hutley et al. 2001). If tropical species have hydraulic traits suited to the wet season, how do they survive the dry season?

It is likely that Australian savanna species avoid desiccation during the dry season via several mechanisms. Some of the tropical species sampled in this study (26%) avoid desiccation by dropping their leaves (dry season deciduousness), whereas no temperate or subtropical species in this study were deciduous. Although deciduousness was relatively uncommon in this study, dry season deciduousness is particularly evident among smaller understory species that have little access to deep water (Hutley et al. 2001). It is possible that the larger evergreen species in this study may have access to deep water through the dry season, as has been found in other Australian seasonal forests (Cook et al. 1998; Eamus and Prior 2001; Hutley et al. 2001). It is also possible that the tropical evergreen species in this study, although not obligate deciduous, may reduce their water use by decreasing their leaf area during periods of low water availability (O'Grady et al. 2009) as well as decreasing stomatal conductance and leaf-level CO_2 assimilation (Myers et al. 1997; Prior et al. 2004). Overall, Australian flora has had much opportunity to evolve desiccation-avoiding mechanisms, as seasonal precipitation in Australia has existed at least since the mid-Eocene (~45 Myr; Greenwood 1996). Although this evolutionary scenario is possible, the few species (120) and sites (8) associated with this study make such a generalization tenuous at best.

Conclusions

Plant height, leaf area–to–sapwood area ratio, leaf water potential, and sapwood-specific conductivity all increased significantly as aridity decreased across the sites in this study. Thus, as soil water availability increased, many species exhibited tall and leafy architecture, giving these species greater access to light and, most likely, a competitive advantage over shorter species. Increasing sapwood-specific conductivity was associated with these increases in height and leafiness. It is possible that tall stature and greater leaf area are evolutionarily coordinated with and facilitated by the observed increases in sapwood-specific conductivity. However, we do admit that the correlative nature of this study does not allow for a test of this hypothesis. Nevertheless, it does make sense that evolution should favor shifts in sapwood-specific conductivity to balance the hydraulic proportionality where the risks of doing so are acceptable—in wet habitats. Although the risk of hydraulic failure in arid climates is real, plants may invest resources to avoid hydraulic failure during periods of high aridity to take advantage of precipitation during the wet season. Our study provides some support for this hypothesis, as hydraulic traits were most strongly correlated with aridity during the most suitable months for plant growth. This at least suggests that plants traits related to desiccation avoidance (e.g., deciduousness) may be more important than hydraulic traits for coping with extremes of moisture stress where precipitation is reliable but strongly seasonal, such as tropical Australia.

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