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Below-ground determinants and ecological implications of shrub species' degree of isohydry in subtropical pine plantations

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Summary

- The degree of plant iso/anisohydry is a popular framework for characterising species-specific drought responses. However, we know little about associations between below-ground and above-ground hydraulic traits as well as the broader ecological implications of this framework.
- For 24 understory shrub species in seasonally dry subtropical coniferous plantations, we investigated contributions of the degree of isohydry to species' resource economy strategies, abundance, and importance value, and quantified the hydraulic conductance (K_h) of above-ground and below-ground organs, magnitude of deep water acquisition (WA_{deep}), shallow absorptive root traits (diameter, specific root length, tissue density), and resource-use efficiencies (A_{max}, maximum photosynthesis rate; PNUE, photosynthetic nitrogen-use efficiency).
- The extreme isohydric understory species had lower wood density (a proxy for higher growth rates) because their higher WA_{deep} and whole-plant K_h allowed higher A_{max} and PNUE, and thus did not necessarily show lower abundance and importance values. Although species' K_h was coordinated with their water foraging capacity in shallow soil, the more acquisitive deep roots were more crucial than shallow roots in shaping species' extreme isohydric behaviour.
- Our results provide new insights into the mechanisms through which below-ground hydraulic traits, especially those of deep roots, determine species' degree of isohydry and economic strategies.

Introduction

Under current global change scenarios, the adaptability of different species to drought will determine the structure and function of plant communities (Thuiller *et al.*, 2008; Tylianakis *et al.*, 2008; Anderegg *et al.*, 2012). A continuum of isohydric to anisohydric behaviour provides a framework for characterising whole-plant, species-specific differences in the stringency of stomatal control of transpiration and thus leaf water potential during drought (Klein, 2014; Martínez-Vilalta *et al.*, 2014; Meinzer *et al.*, 2016; Ratzmann *et al.*, 2019). Generally, isohydric species maintain a relatively constant midday minimum leaf water potential (Ψ_{md}) despite changes in soil water potential (Ψ_S), whereas Ψ_{md} of anisohydric species covaries more strongly with Ψ_S (Meinzer *et al.*, 2016, 2017; Hochberg *et al.*, 2018). It is difficult to scale such species-specific iso/anisohydric behaviour to the ecosystem scale (Konings & Gentine, 2017), as coexisting plants can exhibit different hydraulic behaviour and degrees of isohydry (Quero *et al.*, 2011; Roman *et al.*, 2015). However, the relative degree of iso/anisohydry could reflect interspecific or intraspecific differences in the ability to adjust to different environments when the concept is applied either to a single species across environmental gradients or different species under similar environmental conditions (Ratzmann *et al.*, 2019; Novick *et al.*, 2019). Nevertheless, important knowledge gaps persist concerning the broad applicability of this framework and how plant functional traits are integrated to yield a given degree of iso/anisohydry.

One knowledge gap concerns the utility of the iso/anisohydry framework for understanding species-specific economic strategies and community assembly processes. Over the past decade, research on iso/anisohydry directed towards how well this framework predicts species' vulnerability to drought-induced mortality has yielded conflicting results (McDowell *et al.*, 2008, 2011; Kumagai & Porporato, 2012; Gu *et al.*, 2015; Martínez-Vilalta & Garcia-Forner, 2017). The inconsistent results may reflect incompatible, coexisting definitions or misconceptions of iso/anisohydry or may indicate that application of the framework should be restricted to studying relationships among hydraulic strategies, and drought-induced hydraulic damage and recovery processes under nonlethal water stress conditions (Volaire, 2018; Kannenberg *et al.*, 2019). Based on the plant economic spectrum theory, species with lower wood density have faster growth rates

and 'fast' resource acquisition strategies, which would dominate in environments with minimal resource constraints, whereas species with 'slow' resource acquisition strategies would eventually dominate when resources are scarce (Reich, 2014). A recent global meta-analysis showed that species with higher wood density were less isohydric (Fu & Meinzer, 2019), leading to our first hypothesis that less isohydric species may grow slowly and eventually dominate under conditions of lower resource availability, which to our knowledge has never been tested within understory vegetation communities where light is low.

Another knowledge gap concerns the associations between below-ground and above-ground hydraulic traits that determine a species' degree of iso/anisohydry. Studies have shown that where species operate along the isohydric to anisohydric continuum results from the integration of properties of different plant organs (Fu *et al.*, 2019; Li *et al.*, 2019; Mirfenderesgi *et al.*, 2019). At the leaf level, more isohydric species tend to have less negative turgor loss point (Ψ_{TLP}), slower kinetics of stomatal opening and activation of photosynthesis, but higher intrinsic water-use efficiency and are more likely to exhibit drought-induced leaf shedding (Meinzer *et al.*, 2017; Fu & Meinzer, 2019; Li *et al.*, 2019). At the stem level, more isohydric species tend to have higher hydraulic capacitance, conductivity and safety margins, but lower wood density and xylem resistance to embolism (Klein, 2014; Martínez-Vilalta *et al.*, 2014; Fu *et al.*, 2019; Mirfenderesgi *et al.*, 2019). Importantly, plant hydraulic properties could be inversely related across different organs. For example, Fu *et al.* (2019) found that there was a trade-off between hydraulic storage and efficiency in the leaf, but coordination between hydraulic storage and efficiency in the stem along a spectrum of plant iso/anisohydry. The studies cited above have largely focused on the contributions of above-ground functional attributes to the degree of species' isohydry; as a result, little information is known about how below-ground hydraulic attributes shape the degree of isohydry.

It was believed that species with deeper root systems would have greater ability to utilise deep soil water, presumably facilitating maintenance of higher leaf water potentials during periods of soil drying (Bucci *et al.*, 2009; Martínez-Vilalta & Garcia-Forner, 2017). However, some studies have shown that species with deeper root systems did not always maintain higher leaf water potentials than co-occurring species with shallower roots during drought (West *et al.*, 2007; Plaut *et al.*, 2012; Aguadé *et al.*, 2015). In addition to the fact that shallow-rooted plants can benefit from hydraulic redistribution carried out by neighbouring deep-rooted plants during drought and that root presence per se may not be a reliable indicator of actual water uptake dynamics in either time or space (Ehleringer & Dawson, 1992; Yu & D'Odorico, 2015), the conflicting results may also reflect different strategies for utilisation of shallow soil water among co-occurring species. A recent study focused on the evolutionary patterns among plant root systems indicated that the diameter of shallow absorptive roots can be a good indicator of the species-specific strategy for utilisation of shallow resources: species with finer absorptive roots can explore the soil with lower construction costs and less reliance on mycorrhizae, which can benefit plants coping with less predictable environments (e.g. seasonal drought) through rapid root growth (Ma *et al.*, 2018). Studies have shown that species with a large shallow root biomass have greater ability to maintain leaf water potential in drying soil (Houssard *et al.*, 1992; Liu *et al.*, 2015a), and a recent modelling exercise concluded that root hydraulic properties exerted a greater influence on whole-plant hydraulic function than branch hydraulic properties (McCulloh *et al.*, 2019). Based on the preceding findings and observations, our second hypothesis is that the degree of isohydry of coexisting species may be partly determined by coordination between their ability to utilise deep and shallow soil water, and root system hydraulic conductance.

To test the first hypothesis, we quantified the degree of isohydry for 24 understory woody shrub species with a wide range of wood density in subtropical coniferous plantations with a marked dry season (Yang *et al.*, 2015). We then examined the association of the degree of isohydry with species' wood density and abundance. To test the second hypothesis, we investigated the linkage between species' water transport efficiency with below-ground water uptake, and then examined the roles of water transport efficiency and root water uptake in determining species' degree of iso/anisohydry.

Materials and Methods

Site description

This study was conducted at the Qianyanzhou Ecological Station of the Chinese Academy of Sciences, located in a typical hilly red-soil region of subtropical China, which is strongly influenced by the subtropical Eastern-Asian monsoon climate. Due to the unevenly distributed rainfall, seasonal droughts frequently occur from July to October in this region (Yang *et al.*, 2015). The mean annual temperature and precipitation are 18.0°C and 1509.0 mm, respectively. The soil is an iron-rich red soil classified as Typic Dystrudept and Udept Inceptisols of the USDA soil taxonomic system, and the dominant vegetation consists of pure coniferous plantations (*Pinus massoniana* and *P. elliottii*) planted in 1983.

Species selection and abundance

In the pine plantations, we chose 24 coexisting understory shrub species (Table 1) representing a 2.2-fold range of wood density based on our preliminary observations. The phylogenetic tree of these shrub species is shown in Supporting Information Fig. S1. Ten of these 24 shrub species are deciduous and drop their leaves mainly in mid to late November. Leaves of the deciduous species generally flush in the middle of March and are fully mature by early May. For the measurement of wood density, stem segments from at least six individuals of each species were excised at 20–30 cm above-ground level. After removing the bark and cambium with a razor blade, wood density was determined from volumetric displacement and oven-dried mass.

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Table 1 Family, life form, wood density (g cm^{-3} ± SE), and species code of 24 shrub species.

Species	Family	Life form	Code	Wood density
Choerospondias axillaris	Anacardiaceae	DB	CA	0.328 (0.013)
Rhus chinensis	Anacardiaceae	DB	RC	0.381 (0.024)
Clerodendrum cyrtophyllum	Verbenaceae	DB	CC	0.420 (0.007)
Michelia maudiae	Magnoliaceae	EB	MMu	0.420 (0.016)
Phoebe bournei	Lauraceae	EB	PB	0.484 (0.017)
Michelia macclurei	Magnoliaceae	EB	MMc	0.499 (0.020)
Schima superba	Theaceae	EB	SS	0.502 (0.021)
Vaccinium bracteatum	Ericaceae	EB	VB	0.511 (0.018)
Adinandra millettii	Theaceae	EB	AM	0.518 (0.020)
Liquidambar formosana	Hamamelidaceae	DB	LF	0.519 (0.010)
Camellia oleifera	Theaceae	EB	CO	0.556 (0.009)
Ardisia crenata	Myrsinaceae	EB	AC	0.558 (0.010)
Eurya muricata	Theaceae	EB	EM	0.559 (0.012)
Ilex asprella	Aquifoliaceae	DB	IA	0.564 (0.011)
Cyclobalanopsis glauca	Fagaceae	EB	CG	0.581 (0.028)
Loropetalum chinense	Hamamelidaceae	EB	LC	0.582 (0.018)
Rhamnus utilis	Rhamnaceae	DB	RU	0.591 (0.019)
Symplocos paniculata	Symplocaceae	DB	SP	0.607 (0.017)
Vacciniuim mandarinorum	Ericaceae	EB	VM	0.614 (0.009)
Glochidion puberum	Euphorbiaceae	DB	GP	0.627 (0.009)
Gardenia jasminoides	Rubiaceae	EB	GJ	0.639 (0.013)
Viburnum dilatatum	Caprifoliaceae	DB	VD	0.641 (0.012)
Quercus acutissima	Fagaceae	DB	QA	0.681 (0.010)
Rhaphiolepis indica	Rosaceae	EB	RI	0.723 (0.012)

Life form: DB, deciduous broadleaf; EB, evergreen broadleaf.

An understory vegetation survey of 29 pine plantation plots (30 m × 30 m) was conducted in August 2015. In each plot, three representative shrub subplots (5 m × 5 m) were established along the diagonals. In each subplot, the heights, basal diameters, number of stems and crown breadth of all shrubs were recorded. We used individual species' relative occurrence frequency in 87 subplots to represent species abundance (Klanderud & Totland, 2005). Species' importance values were calculated as the sum of the relative coverage, relative density and relative occurrence frequency divided by 3 (Li *et al.*, 2017).

Leaf water potential measurement and iso/anisohydry quantification

'Hydroscape area', a recently developed metric of iso/anisohydry (Meinzer *et al.*, 2016), has been shown to be a comprehensive proxy for species' performance and drought tolerance because it can integrate species' overall water-use strategies (Li *et al.*, 2019). Therefore, in this study we used hydroscape area as the metric of iso/anisohydry based on trajectories of Ψ_{md} vs Ψ_{pd} during soil drying (Meinzer *et al.*, 2016; Fu & Meinzer, 2019):

$$HA = \frac{\alpha^2}{2(1-\beta)}$$

where HA is the hydroscape area (MPa^2) and α and β are the intercept and slope of the regression fitted to phase where stomata play a dominant role in regulating Ψ_{md} (between the point at which the slope of the relationship between Ψ_{md} and Ψ_{pd} abruptly transitions from nearly vertical to <1 and ends when $\Psi_{md} = \Psi_{pd}$). Smaller hydroscape areas indicate more isohydric behaviour.

Predawn (4:30–5:30 h, Ψ_{pd}) and midday (12:00–13:00 h, Ψ_{md}) leaf water potentials were measured on sunny days in seven sampling rounds during the dry seasons of 2017 and 2018. To capture the phase reflecting stomatal regulation of Ψ_{md} during soil drying, each sampling round of 2 or 3 d consecutively was initiated at least 1 wk after rainfall events. On each sampling day, Ψ_{pd} and Ψ_{md} of two replicate individuals of four to six species was measured psychrometrically. For each individual, discs excised from different leaves were sealed inside two cleaned and calibrated thermocouple psychrometer chambers (83-2VC; Merrill, Logan, UT, USA). The chambers were immersed in a water bath and the psychrometers were activated every 30 min and the data recorded by a high-speed data acquisition system (CR6; Campbell Scientific Inc., Logan, UT, USA) until water potential equilibrium had been attained.

The trajectories of Ψ_{md} vs Ψ_{pd} used for quantifying hydroscape areas of the 24 shrub species studied are shown in Fig. S2.

Traits of shallow absorptive roots

Root branches with intact terminal branch orders in topsoil (0–20 cm) were traced back to at least five individuals of each species in May 2018 following the procedure described in Pregitzer *et al.* (2002). The root branches were gently washed with tap water to remove adhering soil, and stored at −20°C until the measurement of root traits. The first two or three order

roots with smaller diameters and higher turnover rates dominate in total root length and surface area and are therefore important in water and nutrient uptake are called absorptive roots (Pregitzer *et al.*, 2002; Guo *et al.*, 2008; Liu *et al.*, 2015b). To reduce the labour requirement, we focused on the traits of first-order absorptive roots.

At least 30 first-order absorptive roots of each individual plant were collected as one subsample. Each subsample was arranged in water with minimal overlap and scanned by an Epson Expression 10000 XL desktop scanner. From the scanned images, the average first-order root diameter and total length were measured using WinRhizo software (Regent Instruments Inc., Quebec City, QC, Canada). Root tissue density (RTD) was calculated as the ratio of root dry mass to its volume assuming that a root was a cylinder. Specific root length (SRL) was calculated as the root length divided by its dry mass.

Magnitude of deep water utilisation and photosynthetic characteristics

The magnitude of deep water utilisation for 18 of the 24 shrub species was previously determined in August 2016 (the dry season). The soil water content throughout the 0–200 cm depth is shown in Fig. S3. The range of wood density of the 18 shrub species covered the entire range of wood density of the 24 shrub species studied (Fig. S4a). After removing the leaves and green tissues, each stem sample (containing two or three individuals) was immediately placed in glass vials sealed with parafilm, and placed in a cooler. Soil samples were collected at depths of 0–20, 20–60, 60–100, 100–150, and > 150 cm (depending on the maximum sampling depth, with the maximum to 200 cm). After extracting water from stem and soil samples, $\delta^{18}O$ of water samples were analysed using a liquid water isotope analyser (912-0050; LGR, San Jose, CA, USA). Plant relative reliance on soil water sources at different depths was calculated using the IsoSource model (the multi-source mass balance approach, http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) (Phillips *et al.*, 2005). Based on root vertical distribution and soil water $\delta^{18}O$ variation along the profile, we defined the deep soil layer as the layer below 60 cm (Jiang *et al.*, 2020). Light-saturated photosynthetic rate (A_{max}) for the 24 study species was measured using a portable photosynthesis system (Li-6400XT; Li-Cor, Lincoln, NE, USA) in August 2016. Procedures for sampling, isotope data analysis for deep water utilisation, and environmental conditions during A_{max} measurements are described in detail by Jiang *et al.* (2020).

For leaf mass per area (LMA, $g\,m^{-2}$) determinations, at least 20 fully expanded sun leaves were collected from at least five individuals per species. After measuring their areas, the leaves were oven dried at 70°C, weighed, and then ground in a ball mill (WS-MM301; Retsch, Haan, Germany). Leaf N was determined on a continuous-flow isotope ratio mass spectrometer (Delta PlusXP; Thermo Finnigan, Bremen, Germany). LMA was calculated as leaf dry weight/leaf area. Area-based leaf nitrogen content (N_{area}, $g\,m^{-2}$) was calculated as the product of leaf N and LMA. Photosynthetic nitrogen-use efficiency (PNUE, $\mu mol\,g^{-1}\,s^{-1}$) was calculated as A_{max}/N_{area} (Field & Mooney, 1986).

Hydraulic conductance of the root system and shoot

The hydraulic conductance (K_h) of entire root systems and shoots was measured with a high-pressure flow meter (HPFM-Gen3; Dynamax, Houston, TX, USA) (Tyree *et al.*, 1994, 1995) during August 2018 (dry season) and April 2019 (wet season). For each species, four to six individuals were selected with their average diameter at 40 mm above ground ranging from 5 to 16 mm to minimise potential effects of plant size on plant hydraulic traits. The average diameter at 40 mm above the soil surface across the 24 species is shown in Fig. S4b. Stem diameter of *Michelia macclurei* was similar to that of five other species, but larger than that of the other 18 species because of its higher growth rates. Shoots were cut about 40 mm above the soil surface and kept covered by a plastic bag with the cut base submerged in water until measurement. The protruding stump was immediately connected to the HPFM without disturbing the soil. Filtered degassed deionised water was forced to flow through the root system under the quasisteady state mode until the curves remained stable. After the measurement of the K_h of the root system, the shoot was connected to the HPFM and measurements were also conducted under the quasisteady state mode. Shoot-specific hydraulic conductance (K_s) was calculated as the ratio of the hydraulic conductance and the stem cross-sectional area at the point where the HPFM was connected (Cohen *et al.*, 2007; Losso *et al.*, 2016). Leaf-specific hydraulic conductance (K_L) was calculated as the ratio of the root system or shoot hydraulic conductance and the total leaf area of each plant.

Data analysis

A hyperbolic decay function ($y = a \times b/(b + x)$) was used to describe the relationships between K_s (or K_L, K_h) and hydroscape area, and exponential decay functions were used to describe the relationships between A_{max} ($y = y_0 + a \times e^{-bx}$) and PNUE ($y = a \times e^{-bx}$) and hydroscape area in SigmaPlot software (v.12.0, San Jose, CA, USA). Confidence intervals of parameters determining the slope (parameter b) of the functions were calculated by the Nonlinear Least Squares (nls) function in R software (v.3.4.3, R Development Core Team, 2017). If the confidence intervals of the parameters b of two models do not overlap, the difference between the two models is significant. Standardised major axis tests (SMA) were used to assess the relations of hydroscape area to wood density, deep water source utilisation parameters, and predawn leaf water potential in R software. The SMA tests were also used to test the relations of K_s (or K_L, K_h) to the deep and shallow water source utilisation parameters, and resource-use efficiencies across species. We used the SMA test instead of a simple linear regression, because we wanted to estimate some underlying line of best fit instead of predicting one variable from another (Warton *et al.*, 2006; Warton *et al.*, 2012). The phylogenetic tree for the 24 species was constructed using Phylomatic online software (http://phylodiversity.net/phylomatic/) with the 'R20120829' megatree.

Highly significant and moderately significant were defined as $P < 0.05$ and 0.10, respectively. Our dataset can be obtained in the supplementary material (Dataset S1).

Results

Relationships between hydroscape area and species' economics strategies, abundance and importance value

Hydroscape areas varied about 14-fold across the 24 shrub species, ranging from 0.15 MPa^2 in *Clerodendrum cyrtophyllum* to 2.13 MPa^2 in *Ardisia crenata* (Fig. 1). Deciduous shrubs generally had smaller hydroscape areas, but higher WA_{deep}, shoot K_L and PNUE, and moderately higher root K_L and A_{max} than the evergreen shrubs (Fig. 1; Table 2). Interestingly, the relatively narrow absolute range of hydroscape area among species captured a wide, 2.2-fold range of interspecific variation in wood density (Fig. 2). Across species, hydroscape area was positively associated with wood density, but negatively associated with A_{max} and PNUE (Figs 2, 3). We detected no significant relationships between the hydroscape area and species' relative abundance ($R^2 = 0.001$, $P = 0.892$) and importance value ($R^2 = 0.023$, $P = 0.485$). Moreover, the hydroscape area of species did not show a significant phylogenetic signal as indicated by Blomberg's K values ($K = 0.489$, $P = 0.171$).

Linking species' water transport efficiency with water uptake capacity

Species' water transport efficiency was associated with traits of their shallow absorptive roots and deep water utilisation (Fig. 4). Shoot K_h was higher in species with larger shallow absorptive root diameter (Fig. 4a). However, there were no significant relationships between root/shoot hydraulic conductance and RTD/SRL of shallow absorptive roots (data not shown). Species with higher shoot K_h had significantly higher magnitude of deep water utilisation in the dry season (Fig. 4b).

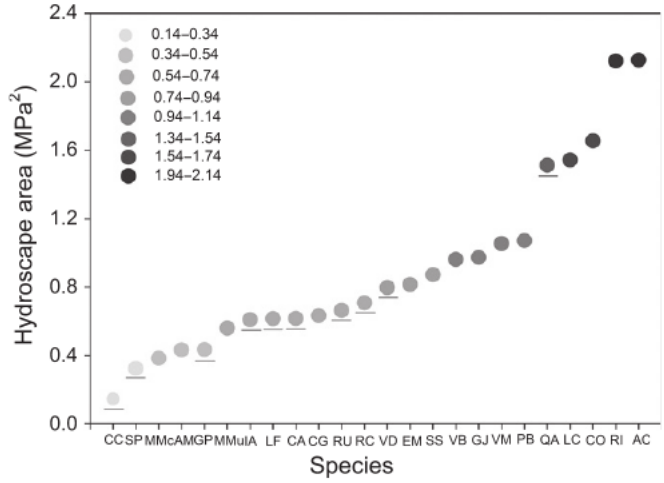

Fig. 1 Hydroscape areas of 24 shrub species. See Table 1 for species codes. Underlined symbols represent deciduous species. Different symbol shades represent different hydroscape area ranges, with lighter shades representing more isohydric species.

Relationships of water transport efficiency and root water uptake with species' hydroscape area

Across the 24 shrub species, there were negative, nonlinear relationships between hydroscape area and root and shoot K_s and K_L (Fig. 5a,b), and between hydroscape area and root K_h (Fig. 5c), indicating higher whole-plant hydraulic transport efficiency was associated with greater isohydry. The higher A_{max} of more isohydric species (Fig. 3) was associated with their higher root and shoot hydraulic transport efficiency (Fig. S5) and PNUE (Fig. S6). However, the extreme isohydric species were differentially affected by organ specific hydraulic conductance relative to the less isohydric species, since there were no overlaps between the confidence intervals of parameter b of the nonlinear model for K_s of root (−0.023, 0.184) against the hydroscape area and that of shoot (0.372, 3.407), and between the confidence intervals of parameter b of the nonlinear model for K_L of roots (−0.045, 0.371) against the hydroscape area and that of shoots (0.624, 20.439).

Across species, hydroscape areas were negatively related to Ψ_{pd} and the magnitude of deep water utilisation during the dry season (Fig. 6). However, the hydroscape area was not related to diameter ($R^2 = 0.003$, $P = 0.794$), RTD ($R^2 = 0.058$, $P = 0.257$), and SRL ($R^2 = 0.028$, $P = 0.436$) of absorptive roots in the shallow soil layer.

Discussion

Hydroscape area variation across species and its implications

Compared with an estimate of the global range of hydroscape area (*c.* 0.7–10 MPa^2) representing a broad range of species and biomes (Fu & Meinzer, 2019), the hydroscape areas in our study (<2.5 MPa^2) were considerably lower, suggesting that the 24 shrub species should be ranked as strongly isohydric along the spectrum of global interspecific variation in iso/anisohydry. The hydroscape area of species did not show a significant phylogenetic signal as indicated by Blomberg's K values and the phylogenetic tree (Figs S1, S2). The isohydric behaviour of the 24 shrubs in our study area is consistent with the expectation that anisohydric species tend to occupy more drought-prone habitats compared with isohydric species (McDowell *et al.*, 2008; Fu & Meinzer, 2019). Considering the relatively wet conditions of our study area and that the iso/anisohydry framework is most commonly brought up in the context of drought (McDowell *et al.*, 2008; Quero *et al.*, 2011; Kannenberg *et al.*, 2019), the applicability of our results under drought conditions needs further study. Moreover, our study also showed that the deciduous species were more isohydric than the evergreen species (Fig. 1; Table 2). The more isohydric behaviours of deciduous species may benefit from their higher WA_{deep}, root and shoot K_L, A_{max} and PNUE (Table 2; Figs 3, 5b), however, the lower shoot hydraulic efficiency and

Table 2 Comparison of root, stem and leaf traits (± SE) between 14 evergreen and 10 deciduous shrub species (linear mixed model).

Trait	Unit	Evergreen	Deciduous	*P*
HA	MPa^2	1.087 (0.153)	0.643 (0.115)	**0.042**
WA_{deep}	%	56.156 (2.914)	62.103 (3.210)	**0.008**
$K_{s\,R}$	$kg\,s^{-1}\,MPa^{-1}\,m^{-2}$	0.508 (0.105)	0.775 (0.193)	0.221
$K_{s\,SH}$	$kg\,s^{-1}\,MPa^{-1}\,m^{-2}$	0.412 (0.051)	0.538 (0.061)	0.127
$K_{L\,R}$	$\times 10^{-5}\ kg\,s^{-1}\,MPa^{-1}\,m^{-2}$	16.887 (2.895)	30.661 (8.269)	0.089
$K_{L\,SH}$	$\times 10^{-5}\ kg\,s^{-1}\,MPa^{-1}\,m^{-2}$	12.982 (1.109)	19.908 (2.603)	**0.013**
WD	$g\,cm^{-3}$	0.553 (0.020)	0.536 (0.038)	0.963
D	Mm	0.238 (0.041)	0.168 (0.011)	0.386
SRL	$g\,m^{-1}$	124.363 (28.596)	135.880 (22.106)	0.698
RTD	$g\,cm^{-3}$	0.410 (0.041)	0.406 (0.033)	0.895
A_{max}	$\mu mol\,m^{-2}\,s^{-1}$	6.687 (0.364)	7.758 (0.384)	0.055
PNUE	$\mu mol\,g^{-1}\,s^{-1}$	4.733 (0.265)	6.587 (0.346)	**0.000**

Bold fonts indicate significant differences between evergreen and deciduous species at the 0.05 level. HA, hydroscape area; WA_{deep}, magnitude of deep water acquisition; $K_{s\,R}$, shoot-specific hydraulic conductance of root system; $K_{s\,SH}$, shoot-specific hydraulic conductance of shoot; $K_{L\,R}$, leaf-specific hydraulic conductance of root; $K_{L\,SH}$, leaf-specific hydraulic conductance of shoot; WD, wood density of stem; D, shallow absorptive root diameter; SRL, specific root length of shallow absorptive roots; RTD, shallow absorptive root tissue density; A_{max}, maximum photosynthesis rate; PNUE, photosynthetic nitrogen-use efficiency.

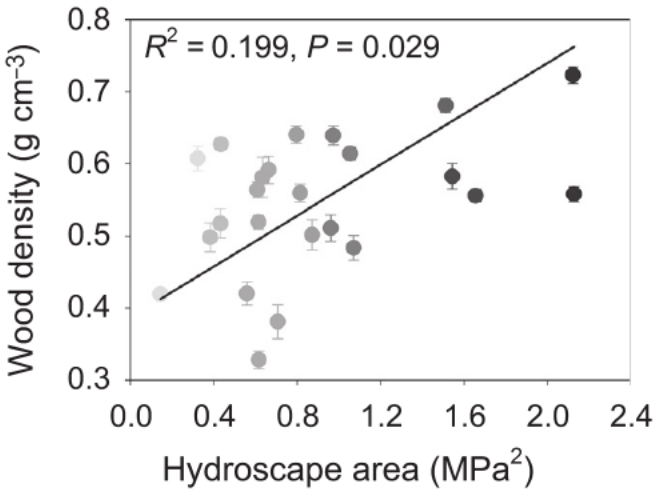

Fig. 2 Relationships between hydroscape area and wood density. See Fig. 1 for symbol codes. Values are shown as means ± SE.

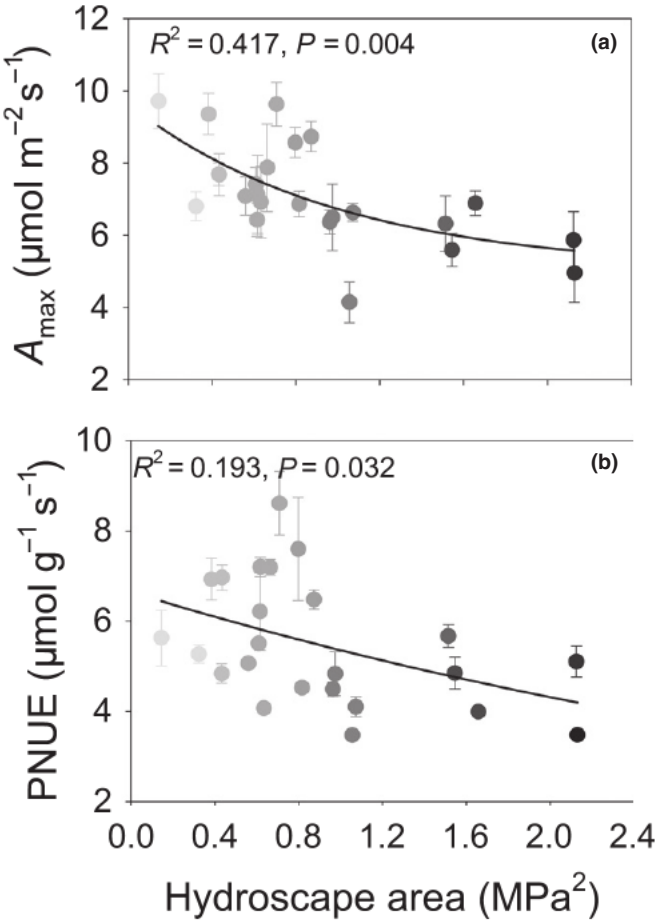

Fig. 3 Relationship between hydroscape area and maximum photosynthesis rate (A_{max}, a) and photosynthetic nitrogen-use efficiency (PNUE, b). See Fig. 1 for symbol codes. Values are shown as means ± SE.

photosynthetic capacity in the evergreen species could be compensated by maintaining functioning leaves throughout the entire year (Fu *et al.*, 2012).

We found that the degree of isohydry among the coexisting shrub species studied was strongly predictive of their resource economics strategies. Specifically, the more isohydric species (smaller hydroscape area) had lower wood density (Fig. 2), and thus conformed to a 'fast' growth strategy (Reich, 2014), since the relationship between wood density and growth rate still exists within a relatively narrow range of wood density (King *et al.*, 2006). Interestingly, the narrow range of hydroscape area in our study (about 22% of the estimated global hydroscape area range) captured a relatively wider range of wood density variation (56%) along the global plant economic spectrum (Reich, 2014), demonstrating that the ability to identify small variations in species' degree of isohydry plays an important role in identifying and characterising species' resource and growth strategies within the plant community we studied. Here we provide evidence to support the notion that definitions of iso/anisohydry should be referenced to species' relative positions along a continuum rather than

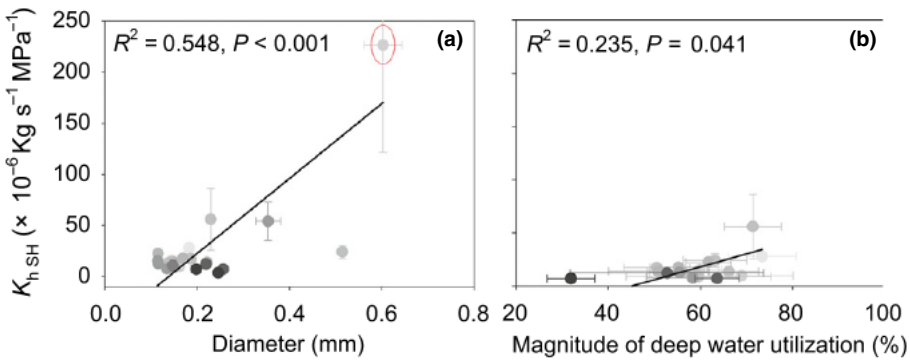

Fig. 4 Relationships between shoot hydraulic conductance ($K_{h\,SH}$) and diameter of shallow absorptive roots (a) and magnitude of deep water utilisation (b). See Fig. 1 for symbol codes. In (a): without the circled species $R^2 = 0.152$, $P = 0.066$. Values are shown as means ± SE.

a dichotomous classification (Meinzer *et al.*, 2016; Ratzmann *et al.*, 2019). Our results further suggest that within a given environment even a narrow range of species' degree of iso/anisohydry could have important ecological implications, especially in terms of species' overall resource acquisition strategies.

Surprisingly, the hydroscape area was not related to species' relative abundance and importance value, indicating that the less isohydric shrubs with slower economics strategies did not outperform the more isohydric shrubs with faster economics strategies. Thus the species' degree of isohydry failed to explain community assembly in this understory environment. These results are consistent with evidence that more isohydric species may be more competitive than less isohydric species under mesic conditions (Martens *et al.*, 2001; Mueller *et al.*, 2005; West *et al.*, 2007). Some factors may have contributed to the failure of the less isohydric species to outperform the more isohydric species under the conditions of our study. First, the less isohydric species had lower rates of carbon assimilation and PNUE (Fig. 3), and lower magnitude of deep water utilisation (Fig. 6b) during the dry season. Second, a recent study has shown that there may be no benefit of being less isohydric in hydraulic damage prevention either during or after a drought event and that the less isohydric species even took longer to recover their hydraulic function postdrought (Fig. 6a; Kannenberg *et al.*, 2019). Third, the light limitation in the studied plantations may be not severe enough to affect plant growth and distribution, since the mean light transmission across sampling sites was about 39% in the dry season (Jiang *et al.*, 2018), which is high for an understory environment (Uriarte *et al.*, 2005).

Coordination of species' hydraulic efficiency with root water acquisition

Species with higher hydraulic efficiency often have lower hydraulic safety (Pratt *et al.*, 2007; Markesteijn *et al.*, 2011; Pratt & Jacobsen, 2017; Zhu *et al.*, 2017; Li *et al.*, 2018), although some evidence suggests this may not always be the case (Choat *et al.*, 2007; Pratt *et al.*, 2010; Gleason *et al.*, 2016). In addition to higher hydraulic capacitance of above-ground xylem (Pratt & Jacobsen, 2017), we found that the potentially risky higher hydraulic efficiency could be compensated by longer persistence of shallow absorptive roots and stronger ability to utilise deep soil water.

We showed that species with higher shoot hydraulic efficiency had thicker diameter of shallow absorptive roots (Fig. 4a). Thicker shallow absorptive roots have thicker cortexes (Kong *et al.*, 2014, 2019) and can store more water for transient buffering of fluctuations in xylem tension during soil drying (Jupa *et al.*, 2016), thus leading to a longer survival during droughts (Kong *et al.*, 2019). Moreover, termites and ants are more active in dry conditions (Lal, 1988), and stronger chemical defences in thicker shallow absorptive roots could serve as protection against herbivory (Kong *et al.*, 2014) during droughts. By contrast, thin absorptive roots generally have higher SRL (Fig. S7, Ma *et al.*, 2018), could explore markedly greater volumes of soil per unit of carbon invested, and thus have greater ability to acquire shallow soil resources (Pregitzer *et al.*, 2002; Guo *et al.*, 2008; Liu *et al.*, 2015b). However, we found that species' hydraulic efficiency was not related to SRL of shallow absorptive roots. The preceding mechanisms and findings collectively suggest that species' hydraulic transport efficiency was coordinated with the persistence of shallow absorptive roots rather than their capacity to acquire water. We further found that the species with higher hydraulic efficiency also had higher capacity for deep water acquisition (Fig. 4b).

Conservative shallow absorptive roots (thicker diameter) explore soil at the cost of low carbon-use efficiency (Ma *et al.*, 2018) and more acquisitive deep roots (higher capacity for deep water acquisition) are also prone to be associated with relatively greater carbon investment (Feddes *et al.*, 2001; Schymanski *et al.*, 2008), while efficient hydraulic pathways are associated with low carbon investment in thin vessel walls and low xylem density (Pratt & Jacobsen, 2017). Therefore, the coordination between hydraulic efficiency and water acquisition by roots also describes a carbon allocation pattern in constructing the entire hydraulic system. That is, along the root-to-leaf continuum, low carbon investment in constructing xylem conduits to achieve high transport efficiency has to be offset by high carbon investment in roots.

Dependence of species' degree of isohydry on below-ground hydraulic traits

Recent studies on above-ground organs have shown that hydraulic transport efficiency at the leaf and stem levels tends to

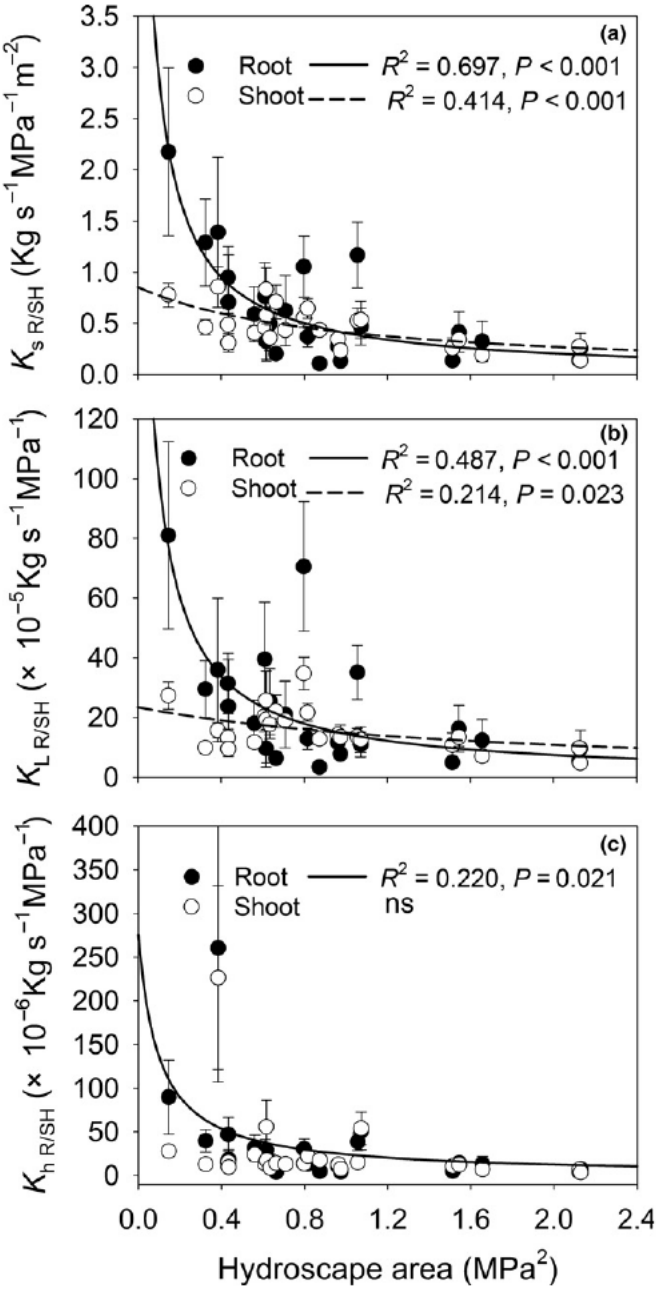

Fig. 5 Relationships between hydroscape area and stem-specific hydraulic conductance of roots and shoots ($K_{s\ R/SH}$) (a), leaf-specific hydraulic conductance of roots and shoots ($K_{L\ R/SH}$) (b), and hydraulic conductance of roots and shoots ($K_{h\ R/SH}$) (c). Values are shown as means ± SE.

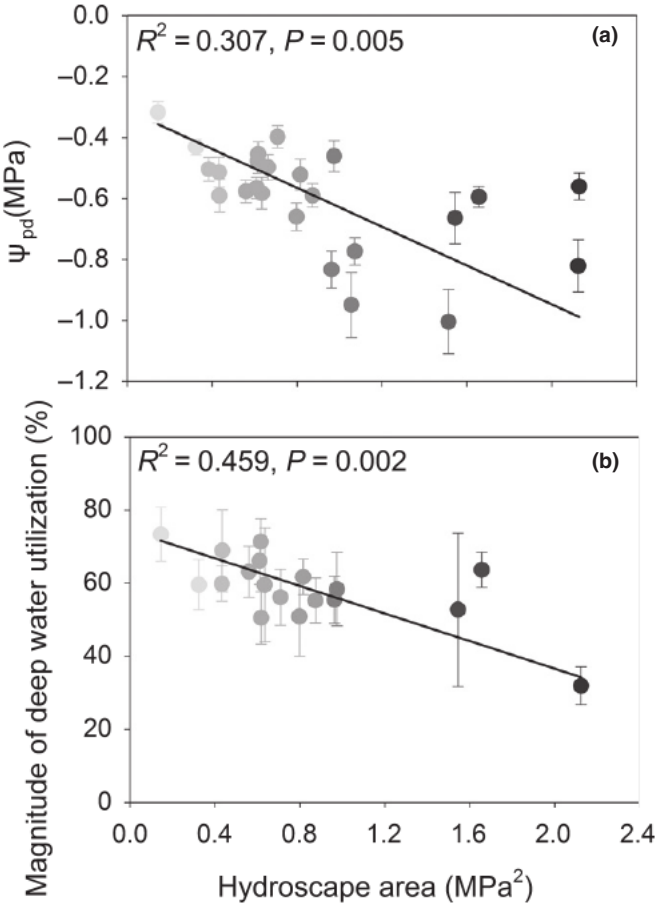

Fig. 6 Relationships between hydroscape area and predawn leaf water potential (Ψ_{pd}) (a), and magnitude of deep water utilisation (b). See Fig. 1 for symbol codes. Values are shown as means ± SE.

increase with increasing isohydry (Fu & Meinzer, 2019; Fu *et al.*, 2019). Consistent with this, we found that the more isohydric species had higher whole-plant (root and shoot) hydraulic efficiency (Fig. 5). The higher water supply capacity was required to support a higher photosynthetic capacity and PNUE in leaves of the more isohydric species (Figs 3, S5, S6). Interestingly, we found that $K_{s\ R}$ (or $K_{L\ R}$) increased faster than $K_{s\ SH}$ (or $K_{L\ SH}$) with decreasing hydroscape area over the lower range of hydroscape area (Fig. 5). That is, in order to be extremely isohydric, the adaptive trends of species in our mesic study area were characterised mainly by adjusting the hydraulic efficiency of root system rather than that of shoot. Similarly, a recent modelling exercise showed that variation in root vulnerability to embolism was more important in maintaining hydraulic function along the soil-to-leaf continuum than variation in branch vulnerability (McCulloh *et al.*, 2019).

The root system represents a critical component of the plant hydraulic pathway and root and shoot function are tightly linked (Scott *et al.*, 1987; Losso *et al.*, 2016), with the accumulation of root embolism ultimately leading to catastrophic failure of xylem water transport and plant death (Brodribb & Cochard, 2009; Nardini *et al.*, 2011). Therefore, the hydraulic safety of the root system is of vital importance for maintenance of root function in drying soil (Kavanagh *et al.*, 1999; Martínez-Vilalta *et al.*, 2002). With increasing transport efficiency, root xylem becomes even more susceptible to implosion than that of stems because root vessels are not supported by a robust fiber matrix as in stems (Pratt *et al.*, 2007). Moreover, studies have shown that roots were generally more vulnerable to embolism than stems, and that the hydraulic failure of roots plays a leading role in shoot dieback (Maherali *et al.*, 2006; Rodríguez-Calcerrada *et al.*, 2017). Then, why would the extreme isohydric species tend to increase their hydraulic efficiency mainly at the expense of their root hydraulic safety rather than that of

shoots? One possible explanation for this observation is that the function of root system may be more readily restored after drought than shoots, either by refilling of embolised conduits with the advent of soil and root rewetting, or growth of new roots (Kolb & Sperry, 1999; Jaquish & Ewers, 2001). Furthermore, root xylem embolism acts in concert with stomata to limit water loss, as indicated by the negative relationship between stomatal conductance and the percent loss of root conductivity at daily and seasonal time scales, which may serve to maintain the minimum leaf water potential above critical values that would provoke embolism in stems (Domec *et al.*, 2004; Domec *et al.*, 2006).

Typically, isohydric species close stomata earlier during drought and show a more conservative stomatal control of transpiration, while anisohydric species close stomata later (McDowell *et al.*, 2008, 2013; Martínez-Vilalta & Garcia-Forner, 2017). Our results, however, suggest that 'open source' (increasing the deep water source) rather than 'reduce expenditure' (closing stomata to decrease conductance and thus A_{max}) is a plausible mechanism for the extreme isohydric behaviour in our study site. For 22 of 24 shrub species, the shoot hydraulic conductance in the dry season was comparable to that in wet season. For the remaining two shrub species, the shoot hydraulic conductance in the dry season was even higher than in the wet season (Table S1), which is likely due to higher mean photosynthetically active radiation (PAR) in the dry season (383.18 ± 9.91 μmol m^{-2} s^{-1}) than in the wet season (251.79 ± 6.00 μmol m^{-2} s^{-1}), and to the fact that the leaves of these two deciduous shrubs are not mature in April when shoot hydraulic conductance was measured. These results indicate that the extreme isohydric species did not reduce their photosynthetic rate and hydraulic conductance in the dry season (Fig. S5). Instead, in order to sustain their higher rates of carbon assimilation and instantaneous nitrogen-use efficiency (Fig. 3) and thus higher growth rates (lower wood density, Fig. 2), the extreme isohydric species tended to maximise water supplied to leaves by increased capacity for deep (instead of shallow) water acquisition and more efficient water transport from root to shoot in the dry season (Figs 4b, 6b). This may be a result of the quantification of isohydry being based on the variation of midday leaf water potential in the dry season, and that deep water storage was greater than shallow water storage during the dry season (Fig. S3; Yang *et al.*, 2015; Jiang *et al.*, 2020).

Conclusion

Our study provides insight into the roles of the degree of isohydry in species' overall ecological strategies. Under conditions of moderate seasonal drought and shading, all of the co-occurring shrub species studied operated at the isohydric extreme of the spectrum. However, the extreme isohydric shrub species had lower wood density (a proxy for higher growth rates) because their higher deep water acquisition capacity and greater whole-plant hydraulic efficiency allowed higher rates of carbon assimilation and PNUE. The degree of species' isohydry failed to explain their abundance and importance value in our subtropical site. Further studies are needed to determine whether the degree of isohydry is predictive of species' abundance and importance value in more drought-prone habitats. Our findings also have important implications for understanding how root functional traits contribute to the degree of species' isohydry. We have shown that, although species' hydraulic transport efficiency was coordinated with their water foraging capacity in the shallow soil layer, the more acquisitive deep roots were more crucial than shallow roots in shaping the hydraulic strategy of extreme isohydric species, and in order to be extremely isohydric the adaptive trends of species in the mesic study area were characterised by mainly adjusting the hydraulic efficiency of root system rather than that of shoot. Future studies should verify these conclusions in naturally co-occurring species with a greater range of isohydry. Expanding exploration of how competition influences species' hydraulic traits along the iso/anisohydric continuum is also a critical area for future research.

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Author contributions

XF, HW and PJ planned and designed the research. PJ conducted field work and performed the experiments. PJ, XF and FCM analysed the data and wrote the paper. PJ, XF, FCM, HW, LK and XD made the manuscript revisions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Dataset of the 24 shrub species.

Fig. S1 Phylogenetic tree of the 24 shrub species studied.

Fig. S2 Measured trajectories of Ψ_{md} vs Ψ_{pd} for quantifying hydroscape areas of 24 shrub species.

Fig. S3 Soil water content along the soil profile during the dry season.

Fig. S4 Wood density and average diameter at 40 mm above ground of the 24 shrub species.

Fig. S5 Relationships between maximum photosynthesis rate (A_{max}) and stem-specific hydraulic conductance of root, shoot ($K_{s\,R}$, $K_{s\,SH}$), and leaf-specific hydraulic conductance of root, shoot ($K_{L\,R}$, $K_{L\,SH}$).

Fig. S6 Relationship between photosynthetic nitrogen-use efficiency (PNUE) and stem-specific hydraulic conductance of shoot ($K_{s\,SH}$), and leaf-specific hydraulic conductance of shoot ($K_{L\,SH}$).

Fig. S7 Relationship between first-order root diameter and SRL (specific root length).

Table S1 Comparisons of stem-specific hydraulic conductance of shoot (SE, kg s^{-1} MPa^{-1} m^{-2}) between the wet season and dry season within species.

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