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Linking reliance on deep soil water to resource economy strategies and abundance among coexisting understorey shrub species in subtropical pine plantations

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Summary

- Strategies for deep soil water acquisition (WA_{deep}) are critical to a species' adaptation to drought. However, it is unknown how WA_{deep} determines the abundance and resource economy strategies of understorey shrub species.
- With data from 13 understorey shrub species in subtropical coniferous plantations, we investigated associations between the magnitude of WA_{deep}, the seasonal plasticity of WA_{deep}, midday leaf water potential (Ψ_{md}), species abundance and resource economic traits across organs.
- Higher capacity for WA_{deep} was associated with higher intrinsic water use efficiency, but was not necessary for maintaining higher Ψ_{md} in the dry season nor was it an ubiquitous trait possessed by the most common shrub species. Species with higher seasonal plasticity of WA_{deep} had lower wood density, indicating that fast species had higher plasticity in deep soil resource acquisition. However, the magnitude and plasticity of WA_{deep} were not related to shallow fine root economy traits, suggesting independent dimensions of soil resource acquisition between deep and shallow soil.
- Our results provide new insights into the mechanisms through which the magnitude and plasticity of WA_{deep} interact with shallow soil and aboveground resource acquisition traits to integrate the whole-plant economic spectrum and, thus, community assembly processes.

Introduction

The degree to which whole-plant performance is governed by suites of coordinated functional traits among organs is a core question in plant functional ecology (Baraloto *et al.*, 2010; Freschet *et al.*, 2010), with different patterns of functional integration expected to result in different patterns of whole-plant performance (Pigliucci, 2003; Olson *et al.*, 2009; Méndez-Alonzo *et al.*, 2012). Functional traits consistently co-vary within and across organs, in what has been described as an 'economics spectrum' that broadly summarizes trade-offs between 'slow' and 'fast' plant growth strategies (Westoby *et al.*, 2002; Wright *et al.* 2004; Fortunel *et al.*, 2012; Reich, 2014), providing insights into trends in species distributions and ecosystem processes along environmental gradients (Kraft and Ackerly, 2010; Fortunel *et al.*, 2012).

The economic spectra of aboveground plant organs have been well-documented (Westoby & Wright, 2006; Fort *et al.*, 2016). Generally, shrub species with high specific leaf area (SLA) and leaf nitrogen content (leaf N) have efficient light harvesting, leading to high growth rates and consequent low wood density (Ruíz-Robleto & Villar, 2005; Freschet *et al.*, 2010; Mommer & Weemstra, 2012; Reich, 2014). Species with fast-growth strategies tend to be more dominant in moist and fertile environments (Grime *et al.*, 1997; Reich *et al.*, 1999), whereas slow-growth strategies (Chapin *et al.*, 1993; Wright *et al.*, 2004; Reich, 2014) allow species to minimize nutrient loss, thereby increasing their competitiveness in dry and low fertility environments (Hobbie, 1992; Aerts, 1995; Pérez-Ramos *et al.*, 2012). There is rising interest in considering root traits in the context of plant economic spectra (Bardgett *et al.*, 2014; Reich, 2014), because roots are responsible for nutrient and water uptake and likely play a key role in mitigating nutrition and water stress effects on plant growth and species interactions (Mommer *et al.*, 2011; Fort *et al.*, 2015, 2016). Generally, fast-growing species tend to have smaller root diameter, higher specific root length (SRL), lower root tissue density (RTD), shorter root life span, consistently low mycorrhizal colonization (Comas & Eissenstat, 2004; Withington *et al.*, 2006; McCormack *et al.*, 2012; Reich, 2014; Kong *et al.*, 2015; Li *et al.*, 2017), and have the advantage of efficient nutrient

and water uptake (Eissenstat, 1992; Roumet *et al.*, 2006; Prieto *et al.*, 2015). Root economic traits also may explain a species' success in ecosystems with different resource availabilities (Prieto *et al.*, 2015; Fort *et al.*, 2016). For example, plant communities in nutrient-poor regions display an overall 'slow' strategy with low SRL and root length density, high root tissue density, whereas communities in nutrient-rich areas display a 'fast' strategy with opposite trait values (McCormack *et al.*, 2012; Liu *et al.*, 2015; Prieto *et al.*, 2015; Fort *et al.*, 2016; Li *et al.*, 2017).

The preceding studies have focused almost entirely on the contributions of fine root traits in shallow soil to species' operating ranges along plant economic spectra and to community assembly. Globally, however, woody plants (trees and shrubs) are reported to distribute 60% of their roots below 20 cm depth (Canadell *et al.*, 1996; Jackson *et al.*, 1996) and could have maximum rooting depths of 20–70 m with a distribution peak at 1–2 m (Schenk & Jackson, 2002; Fan *et al.*, 2017). Fine roots in shallow soil layers generally have smaller diameters and lower RTD to adapt to the less predictable water availability (Prieto *et al.*, 2015; Fort *et al.*, 2016, 2017); however, deep fine roots (branching from tap roots and deep lateral roots) have a thicker stele with wider xylem conduits to minimize flow resistance and maximize deep water uptake and transport efficiency (McElrone *et al.*, 2004; Wang *et al.*, 2016). Dimorphic root systems enable woody plants to switch their major water source from shallow layers in the wet season to deep layers in the dry season (Dawson & Pate, 1996; Andrade *et al.*, 2005; Quesada *et al.*, 2008). A widely used framework for classifying whole-plant hydraulic strategies is the degree of plant iso/anisohydry. Broadly, plants have been ranked along a continuum of isohydry to anisohydry, according to their stringency of control of midday leaf water potential (Ψ_{md}) as soil water potential decreases (Klein, 2014; Martínez-Vilalta *et al.*, 2014; Skelton *et al.*, 2015; Meinzer *et al.*, 2016). Deep roots may help plants to avoid drought stress by buffering the declines of Ψ_{md} during dry periods (Bucci *et al.*, 2009), and are thus likely to be present in more isohydric species (Martínez-Vilalta & Garcia-Forner, 2017). Because deep roots can contribute more water to transpiration than shallow roots during drought (Bleby *et al.*, 2010, Yang *et al.*, 2017), a flexible soil water acquisition strategy along the soil profile appears to be vital for species growing in water-limited environments, especially in seasonally dry regions (Dawson & Pate, 1996; Chen *et al.*, 2015).

The development of hydrogen and oxygen stable isotope techniques has revolutionized our understanding of plant acquisition and use of deep soil water (Ehleringer & Dawson, 1992; Dodd *et al.*, 1998; Dawson *et al.*, 2002). Because isotopic fractionation does not occur during water uptake by roots, the isotopic composition of stem xylem water can provide an estimate of relative water uptake from different soil depths when vertical gradients of $\delta^{18}O$ and δD in soil water are sufficiently large and consistent across the rooting depth (Phillips *et al.*, 2005). The depth of soil water extraction by roots may show considerable seasonal variation within species (Schwinning, 2008; Bendevis *et al.*, 2010; Nie *et al.*, 2011). For instance, *Juniperus ashei* growing adjacent to a spring in Texas switched its major water source from deep soil during the dry summer to shallow soil during the moist winter (McCole & Stern, 2007), whereas its water sources on an upland site with no springs or other evidence of deep water were generally shallow and unstable even during the dry season (Schwinning, 2008; Heilman *et al.*, 2009). Water sources also vary across plant growth forms and species (Jackson *et al.*, 1999; Schwinning *et al.*, 2004; Liu *et al.*, 2010). Generally, trees and shrubs tend to tap water from deeper soil than grasses in mixed woody-herbaceous systems (Le Roux *et al.*, 1995; Asbjornsen *et al.*, 2008; Goldstein *et al.*, 2008). Among co-occurring woody species, however, some utilize only shallow or deep soil water, whereas others tap both shallow and deep soil water (West *et al.*, 2007; Eggemeyer *et al.*, 2009; Liu *et al.*, 2010). Interspecific differences in the ability to utilize deep soil water were found to be strongly driven by deep fine root morphological traits (Fort *et al.*, 2017). Such hydrological niche partitioning among coexisting species plays a crucial role in minimizing competition and improving stability of community structure in water-limited ecosystems (Moreno-Gutiérrez *et al.*, 2012; Yang *et al.*, 2015). However, the extent to which the ability to switch between shallow and deep water acquisition contributes to species' resource economic spectra and distributions has yet to be addressed. Addressing these questions would broaden understanding of individual ecological strategies and vegetation community assembly processes.

Understorey vegetation, as a forest ecosystem driver, plays a key role in influencing soil microbial community and nutrient dynamics, tree growth and regeneration, and forest species diversity and succession (Nilsson & Wardle, 2005; Diaz *et al.*, 2006; Wu *et al.*, 2011; Mitchell *et al.*, 2012; Fu *et al.*, 2015). Although the understorey vegetation may have larger influences on ecosystem functioning than its relative biomass suggests, the resource acquisition strategies and spatial growth of understorey vegetation are much less studied than those of trees in forest communities (Nilsson & Wardle, 2005; Wu *et al.*, 2011; Mariotte, 2014). In this study, we first quantified shallow (0–20 cm), intermediate (20–60 cm) and deep (60–200 cm) water source acquisition over the dry and wet seasons, and their seasonal plasticity for 13 woody shrub species in subtropical coniferous plantations with a marked dry season (Yang *et al.*, 2015). We then examined the role of deep water source acquisition in the dry season as a component of species' overall hydraulic strategies as indicated by regulation of leaf water potential and as a determinant of species abundance. We also investigated the relative reliance on deep soil water sources during the dry season and its seasonal plasticity in relation to plant economic traits across organs (intrinsic and instantaneous photosynthetic water-use efficiency, first-order root diameter, SRL, and RTD in shallow soil, wood density, SLA and leaf N). First, we expected deep water use in the dry season to be an important component of shrub hydraulic strategies. In particular, species with greater reliance on deep water sources were expected to have higher leaf water potential during the dry season. Second, we expected the proportion of deep water source utilization by the most common shrub species to be neither very high nor very low compared with the rare shrub species, because common species usually occupy core positions within community trait space, whereas rare species are functionally peripheral (Umaña *et al.*, 2015). Third, we expected the shrub species with

higher seasonal plasticity of deep water acquisition to have rapid shallow resource capture (finer roots, lower TD, higher SRL), greater efficiencies of light harvesting (higher SLA and leaf N) and water use, and higher relative growth rates (lower wood density), because an integrated analysis suggests that being fast or slow is a species-level strategy (Reich 2014).

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. This area is strongly influenced by the subtropical eastern Asian monsoon climate, with frequent seasonal droughts due to the unevenly distributed rainfall. According to the multi-year mean monthly Budyko aridity index from 2003 to 2010, drought periods were defined from July to October, and the nondrought periods spanned from November to June (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. In 1983, pure coniferous plantations (including *Pinus massoniana* and *P. elliottii*) were planted on barren grassland at the Qianyanzhou Ecological Station. By 2003, the forest cover at the station had increased from 0.43% to *c.* 70% and the number of shrub species reached 100 (Hu *et al.*, 2006).

Basic information on sampling sites

Thirty three plots (30 × 30 m, 18 for *P. massoniana* and 15 for *P. elliottii*) were established and separated by > 10 m. The main shrub species in plots were *Eurya muricata, Adinandra millettii*, *Vaccinium bracteatum*, *Rhaphiolepis indica*, *Camellia oleifera* and *Quercus fabri* (Table 1).

The stand structures of each plot (stem density, diameter at breast height, light transmission), and allocation of fine-root biomass at different depths (0–20, 20–40, 40–60, 60–80, 80–100, 100–150, 150–200 cm) were investigated in August 2015. Details can be found in Jiang *et al.* (2018). Structural traits for the *P. massoniana* and *P. elliottii* stands are shown in Supporting Information Table S1. The structural traits for the 13 shrub species in the two stand types are shown in Table S2. A pre-test experiment conducted in the wet season (January to May) and dry season (July to October) showed that across all the sampling plots, there was a significant difference in soil water content (SWC) down to 100 cm depth between the wet season (24.08 ± 0.74%) and dry season (17.38 ± 0.60%) ($P < 0.001$, $t = -7.071$). The coefficient of variation (CV) of SWC across plots during the dry season was 17.82%.

Water sampling and isotopic analysis

Because the presence of roots may not be a reliable indicator of actual water uptake dynamics in either time or space (Ehleringer & Dawson, 1992; Dawson *et al.*, 2002; Volkmann *et al.*, 2016), we determined reliance on deep vs shallow water sources using stable isotope analyses of xylem and soil water. Although a previous study at the study site showed that $\delta^{18}O$ and δD had similar trends along the soil vertical profile, when xylem water isotopes were compared with vertical profiles of $\delta^{18}O$ and δD in the soil, they yielded inconsistent inferences concerning depths of water uptake (Yang *et al.*, 2015). Oxygen stable isotopes were shown to be more sensitive than hydrogen isotopes in detecting uptake of deep soil water, because the accuracy in δD analysis was relatively lower as compared to $\delta^{18}O$ when the Isotopic Ratio Infrared Spectroscopy (IRIS) method is applied (Wen *et al.*, 2012). Therefore, we used oxygen isotopes to evaluate the depths of water uptake.

Plant and soil sampling were carried out in August 2016 (dry season) and April 2017 (wet season), respectively. For the measurements of plant water isotopic composition, plant samples

Table 1 Species abbreviations, families, life forms, wood density (SE, g cm^{-3}) and sampling number for plant water isotopic composition measurement of each species.

Species	Abbreviation	Family	Life form	Code	Wood density	$N_{Wet\ seasosn}$	$N_{Dry\ season}$
Rhus chinensis	RC	Anacardiaceae	DB	×	0.297 (0.008)	12	19
Choerospondias axillaris	CA	Anacardiaceae	DB	▲	0.467 (0.010)	12	5
Michelia maudiae	MM	Magnoliaceae	EB	■	0.469 (0.023)	17	16
Adinandra millettii	AM	Theaceae	EB	▼	0.518 (0.009)	32	30
Liquidambar formosana	LF	Hamamelidaceae	DB	★	0.520 (0.010)	15	13
Schima superba	SS	Theaceae	EB	♦	0.558 (0.014)	26	20
Camellia oleifera	CO	Theaceae	EB	⊕	0.596 (0.001)	26	19
Quercus fabri	QF	Fagaceae	DB	◬	0.598 (0.009)	13	7
Vaccinium bracteatum	VB	Ericaceae	EB	⬢	0.600 (0.004)	25	19
Symplocos confusa	SC	Symplocaceae	EB	●	0.601 (0.010)	8	3
Eurya muricata	EM	Theaceae	EB	⊞	0.617 (0.010)	33	31
Viburnum dilatatum	VD	Caprifoliaceae	DB	△	0.681 (0.021)	9	16
Rhaphiolepis indica	RI	Rosaceae	EB	□	0.731 (0.005)	19	5

$N_{Wet\ seasosn}$, $N_{Dry\ season}$, sampling number in wet and dry season, respectively. Life form: EB, evergreen broadleaf; DB, deciduous broadleaf.

from the nonphotosynthetic tissues were collected during mid-morning, *c.* 10:00 h, when transpiration was high and plants had reached stable isotope equilibrium status (Rong *et al.*, 2011; Cui *et al.*, 2017). We selected 13 woody shrub species (247 and 203 samples in the wet and dry season, respectively) from the 33 plots based on the following criteria. First, the basal diameter of the individuals sampled ranged from 10 to 25 mm to minimize potential effects of plant age on deep soil water uptake. Second, each species was represented by at least three replicate samples (Table 1) in both the wet and dry season, and each sample contained two or three individuals. Leaves and green tissue surrounding the xylem were removed from the twigs sampled to avoid contamination by isotopically enriched water (Ehleringer & Dawson, 1992). The stem samples were then immediately placed in glass vials sealed with parafilm, and placed in a cooler. Soil cores down to 200 cm depth were sampled in the centre of each plot. Samples from these cores were collected at depths of 0–20, 20–60, 60-100, 100–150 and > 150 cm (depending on the maximum sampling depth).

In the laboratory, soil and plant samples for isotopic analysis were kept frozen at −20°C in a freezer before water extraction. Water was extracted from samples using an automatic cryogenic vacuum distillation system (Li-2100, LICA, Beijing, China). Extraction times were 2.5 h for soil samples and 3 h for plant samples. Water samples were analyzed for isotopic ratios of $\delta^{18}O$ using a liquid water isotope analyzer (912-0050, LGR, San Jose, CA, USA). The IsoSource model (the multi-source mass balance approach, http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm) was used for the calculation of the relative contribution of soil water at different depths to plant xylem water (Phillips *et al.*, 2005). For the IsoSource analysis, the fractional increment was set at 1%, and the mass balance tolerance at 0.1‰ (Phillips & Gregg, 2003).

Measurement of plant physiological parameters and economic traits

Midday leaf water potential (12:00–13:00 h, Ψ_{md}) was measured on sunny days in four sampling rounds during the dry season of 2017 (from July to October). To minimize the effects of day-to-day variability in environmental conditions and capture values of Ψ_{md} close to the seasonal minimum, each sampling round of two or three consecutive days was initiated at least 1 wk after rainfall events. On each sampling day, 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.

Net photosynthetic rates (A), leaf transpiration (E) and stomatal conductance to water vapour (g_s) were measured *in situ* using a portable photosynthesis system (Li-6400XT, Li-Cor, Lincoln, NE, USA). The system was set to maintain a constant CO_2 concentration of 400 μmol mol^{-1}, leaf temperature (20°C and 30°C in the wet and dry seasons, respectively), PAR (800 μmol m^{-2} s^{-1}, which was roughly twice mean values in the understorey during gas exchange measurements) and leaf-to-air vapour pressure deficit (1 kPa). These leaf gas exchange traits were measured in at least 10 sun leaves from at least five individuals per species during the mid-morning (09:00–11:00 h) on sunny days in August 2016 and April 2017. After the gas exchange measurements, the leaves enclosed in the chamber were collected and scanned. Leaf areas were calculated using ImageJ software (v.1.51j8, National Institutes of Health, Maryland, USA). Leaf gas exchange parameters were then re-calculated based on the true leaf area. Intrinsic and instantaneous water-use efficiency (WUE) were calculated as A/g_s and A/E, respectively (Maseyk *et al.*, 2010).

For SLA determinations, at least 20 fully expanded sun leaves were collected from at least five individuals per species in August 2016 and April 2017, respectively. After measuring their areas using ImageJ, the leaves were oven-dried at 70°C, weighed and then ground in a ball mill (WS-MM301, Germany). The SLA was calculated as the ratio of leaf area and leaf dry mass. Leaf N was determined on a continuous-flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan, Bremen, Germany). Area-based leaf nitrogen content (N_{area}) was calculated as the ratio of leaf N and SLA.

Wood density was measured in August 2016. Stem segments from at least six individuals of each species were excised at 20–30 cm above ground level. After removing the bark and pith with a razor blade, wood density was determined from volumetric displacement and oven-dried mass.

First-order root traits in shallow soil were measured in May 2018. Root branches with intact terminal branch orders in topsoil (0–20 cm) were traced back to at least five individuals of each of the study species following the procedure described in Pregitzer *et al.* (2002). The root branches were gently washed with tap water to remove adhering soil, then stored at −20°C until the measurement of root traits. At least 30 first-order roots of each individual plant were collected as one subsample. The first-order roots of each subsample were arranged in water with minimal overlap and scanned on an Epson Expression 10 000 XL desktop scanner. Root samples were then oven-dried at 65°C for 48 h and weighed. From the scanned images, the average first-order root diameter and length were measured using WinRHIZO software (Regent Instruments Inc., Quebec City, QC, Canada). RTD was calculated as the ratio of root dry mass to its volume assuming that a root was a cylinder. SRL was calculated as the root length divided by its dry mass.

Data analysis

Across all plots, the 0–20 cm and 20–60 cm layers of the upper 2 m of soil contained 63–86% and 10–26% of the total fine root biomass, respectively, amongst different growth forms (Fig. S1). Moreover, the $\delta^{18}O$ values for soil water in the upper 60 cm were different from those below 60 cm depth (Fig. 1b). Therefore, we divided the soil profile into three layers: 0–20 (shallow layer),

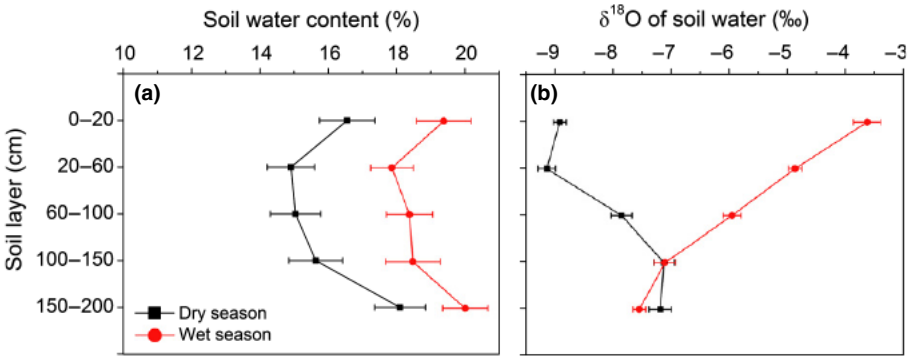

Fig. 1 Soil water content (a) and $\delta^{18}O$ values for soil water (b) along the soil profile during the dry and wet seasons. Values are shown as means ± SE.

20–60 (intermediate layer) and 60–200 cm (deep layer). The deep soil water source was represented by the sum of soil water sources in the ranges 60–100, 100–150 and >150 cm depth. Because *P. massoniana* and *P. elliottii* had similar root distribution and water acquisition along the soil profile during both the dry and wet seasons (Yang *et al.*, 2015; Yang *et al.*, 2017) and soil water source partitioning for each of the 13 understorey shrub species was similar, regardless of which pine species was present (Table S3), we pooled the data for the shrub species from *P. massoniana* and *P. elliottii* plantations.

The plasticity of reliance on deep water sources between the wet and dry seasons (DW_p) was calculated as:

$$DW_p = \frac{2 \times (DW_d - DW_w)}{DW_d + DW_w} \quad \text{Eqn 1}$$

(DW_d, mean of the deep water source proportion in the dry season; DW_w, mean of the deep water source proportion in the wet season). Similarly, plasticity of *A*/*E* and SLA also were calculated in this way. A negative plasticity value indicates that the mean value in the dry season is less than that in the wet season. To characterize interspecific and intraspecific variation reliance on deep water sources, we calculated the CV of the deep water source proportion across and within species during the dry and wet season. A two-way ANOVA was used to determine effects of species, season and their interactions on deep water source proportions. Deep water source proportions between seasons across species were compared by *t*-test. All statistical processing was conducted in SPSS (2010, v.19.0; SPSS Inc., Chicago, IL, USA). 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). To evaluate the relative position of each shrub species with respect to the deep water source proportion at the community level, we calculated the community weighted mean (CWM) of the deep water source proportion:

$$CWM_t = \sum_{i=1}^{S} a_i \times t_i \quad \text{Eqn 2}$$

(a_i, relative importance value of species *i*; t_i, median of deep water source proportion of species *i*). The distance of a species from the CWM (ΔCWM) for deep water source was calculated as the absolute difference between the species-median deep water source proportion for species *i* and the CWM of deep water source proportion. A small distance value indicates that a species is close to the mean trait value of the community, whereas a large distance value indicates that a species occupies an extreme position in the community-wide trait distribution (Umaña *et al.*, 2015). We also calculated Pearson's correlation coefficients between the absolute values of the distance and the importance value. Correlations between deep water reliance parameters and plant hydraulic and economic traits (leaf water potential, leaf gas exchange traits, first-order root diameter, SRL, RTD, wood density, SLA and leaf N) across species were tested in SIGMAPLOT software (v.12.0, San Jose, CA, USA). Highly significant and moderately significant were defined as $P < 0.05$ and 0.10, respectively.

Results

Soil water content and soil water $\delta^{18}O$ values

During the field sampling for $\delta^{18}O$ measurements, soil water content throughout the 0–200 cm depth was significantly lower in the dry season than that in the wet season (Fig. 1a). The $\delta^{18}O$ values of soil water down to 100 cm were significantly lower in the dry season than in the wet season (Fig. 1b). Moreover, the $\delta^{18}O$ values of soil water significantly increased with depth in the dry season, but significantly decreased with increasing soil depth in the wet season (Fig. 1b).

Soil water use patterns and midday leaf water potential

Soil water source proportions of the three soil layers varied significantly among species and seasonally (Fig. 2). All species relied mainly on shallow soil water during the wet season (Fig. 2a). During the dry season, 11 of 13 species relied mainly on deep soil water, with the exception of *Symplocos confusa* and *R. indica* (Fig. 2c). For *S. confusa*, 48.0% of soil water uptake was from the intermediate layer (Fig. 2b) and 21.4% from the deep layer (Fig. 2c). For *R. indica*, the intermediate and deep layers each contributed *c.* 30.0% to the total soil water uptake (Fig. 2b,c). The higher relative contribution of the intermediate depth water resource in *S. confusa* and *R. indica* resulted in their small seasonal variation in reliance on the deep water source (Figs 2c, S2). The 13 shrub species studied showed a wide range of relative reliance on deep soil water sources in the dry season, ranging from 21.4%

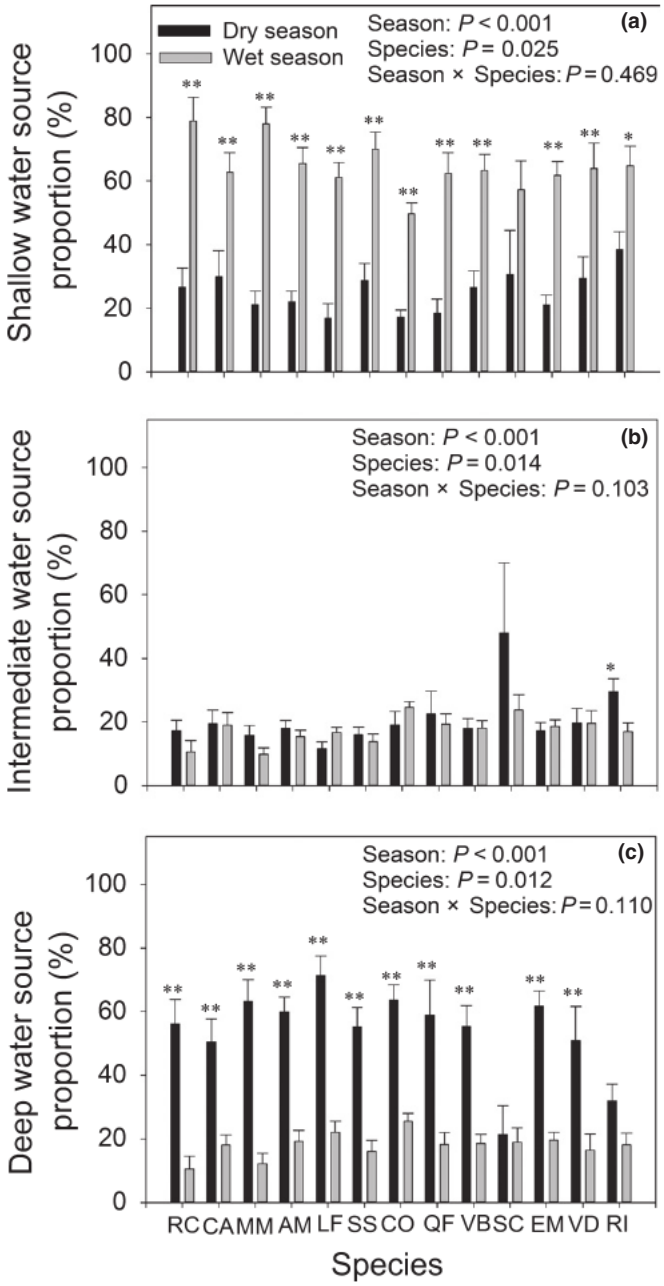

Fig. 2 Shallow (a), intermediate (b), deep (c) soil water source proportion (± SE) in the dry and wet seasons for 13 shrub species. Asterisks indicate significant differences in deep water source proportion between seasons within species: *, $P < 0.05$; **, $P < 0.01$. Species were ordered by wood density from low to high. See Table 1 for species abbreviations.

in *S. confusa* to 71.3% in *Liquidambar formosana*. The plasticity of deep water source utilization between seasons varied ≈ 11-fold, from 0.126 in *S. confusa* to 1.366 in *Rhus chinensis* (Fig. S2). Considering that 12 of 13 species showed no seasonal variation in reliance on the intermediate depth soil water source and 11 of 13 species showed significant seasonal variation in reliance on the deep water source (Fig. 2b,c), we focused on the contribution of the deep water source to the species' water use strategies, dominance and economics spectra. In the dry season, the seasonal minimum Ψ_{md} varied ≈ 2.2-fold among species, ranging from −1.80 MPa in *R. indica* to −0.82 MPa in *S. confusa* (Fig. 3). However, the proportion of deep water source utilization in the dry season was not related to dry season Ψ_{md} ($r = 0.193$, $P = 0.526$, Fig. 3).

Deep water source variation in the dry season and species abundance

We found a moderately negative correlation between intraspecific variation in reliance on deep water sources in the dry season and species' relative occurrence frequency across the sampling sites ($r = -0.546$, $P = 0.054$), indicating that common species tended to show lower variation in reliance on deep water in the dry season. The relative positions of the 13 study species within the entire range of deep water utilization parameters were quantified across sampling sites. For the deep water source proportion in the dry season, *V. bracteatum*, *A. millettii* and *Q. fabri* occupied core positions within the community, whereas *S. confusa*, *R. indica* and *L. formosana* occupied the periphery positions (Fig. 4a). Across species, there was a moderately negative correlation between ΔCWM of deep water source in the dry season against the species' importance value (Fig. 4b), indicating that common species tended to have neither very high nor very low reliance on deep water in the dry season.

Deep water utilization and plant economic traits

Across species, the proportion of deep water utilization in the dry season was not significantly associated with the light-harvesting traits SLA ($r = 0.026$, $P = 0.934$) and leaf N ($r = 0.179$, $P = 0.558$), or with wood density ($r = 0.368$, $P = 0.216$), or the shallow resource uptake traits first-order root diameter ($r = 0.233$, $P = 0.444$), SRL ($r = -0.115$, $P = 0.709$) and RTD ($r = 0.011$, $P = 0.973$). Interestingly, intrinsic WUE was positively associated with N_{area} (Fig. 5a) and deep water reliance in the dry season (Fig. 5b); however, higher deep water source proportion was not associated with higher N_{area} ($r = 0.301$, $P = 0.318$). Reliance on

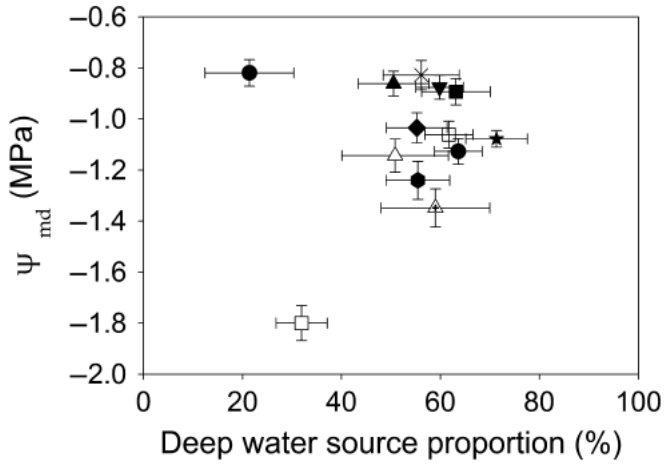

Fig. 3 Relationships between deep water source proportion and midday leaf water potential (Ψ_{md}) in the dry season. See Table 1 for species abbreviations and symbol codes. Values are shown as means ± SE.

deep water sources was not significantly related to the instantaneous WUE in the dry season ($r = 0.141$, $P = 0.647$). However, the plasticity of deep water source utilization between seasons was negatively associated with seasonal plasticity of instantaneous WUE (Fig. 6), but was not associated with plasticity of intrinsic WUE ($r = 0.035$, $P = 0.909$).

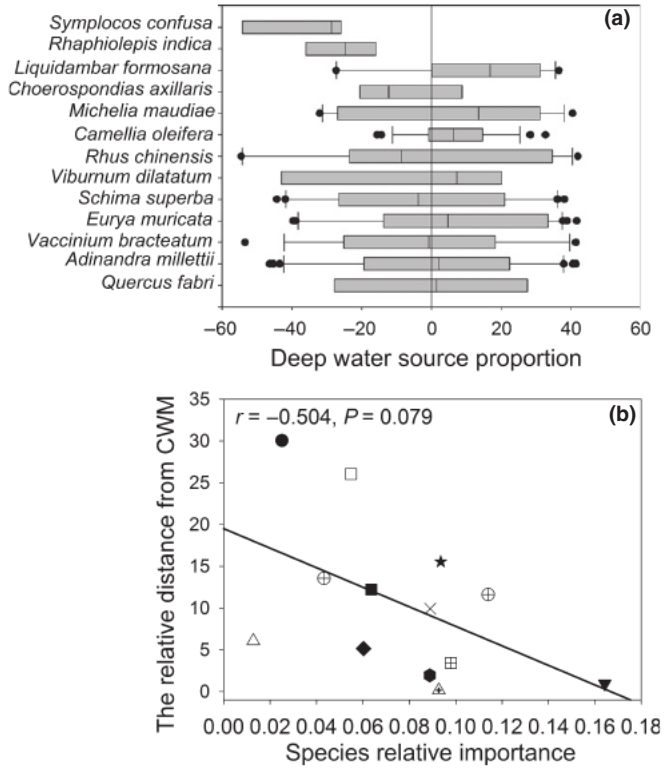

Fig. 4 (a) The relative positions of species with respect to the deep water source proportion in the dry season. The *x*-axis represents the difference between median deep water source proportion for the species and community weighted mean (CWM) deep water source proportion across sampling sites. The *y*-axis arrays species from bottom to top based on how close they are to the CWM value. Each boxplot represents the distribution of deep water source proportion by species: the bars represent the maximum and minimum, the ranges represent the upper and lower quartile, the vertical lines represent the median, and the dots represent the outliers. (b) Relationship between ΔCWM of deep water source in the dry season (the absolute difference between the species-mean value and the CWM value) against the relative importance across species. See Table 1 for species symbol codes.

The plasticity of deep water source utilization between seasons was negatively correlated with wood density across the 13 shrub species (Fig. 7), indicating that species with higher variance in reliance on deep water between seasons tended to exhibit lower wood density. The plasticity of deep water source utilization between seasons was negatively correlated with seasonal plasticity of SLA (Fig. 8). Across the 13 shrub species, however, plasticity of deep water source utilization between seasons was not significantly correlated with first-order root diameter ($r = 0.281$, $P = 0.353$), SRL ($r = 0.025$, $P = 0.935$) and RTD ($r = -0.201$, $P = 0.509$).

Discussion

Deep water source reliance and plant hydraulic strategy

We found that the species differed significantly in their reliance on deep water sources during the dry season and in the plasticity of reliance on deep water sources between seasons (Fig. 2c). Inconsistent with our hypothesis, higher reliance on deep water sources did not lead to higher values of dry season Ψ_{md} (Fig. 3). The unexpected lack of relationship between reliance on deep water and Ψ_{md} could reflect alternative strategies for adaptation to seasonal drought, such as maintaining or increasing whole-plant leaf-specific hydraulic conductance through partial leaf shedding (Bucci *et al.*, 2005; Méndez-Alonzo *et al.*, 2012; Pineda-García *et al.*, 2013), or differences in stringency of stomatal regulation of Ψ_{md}.

Our findings also highlight the role of belowground resource-use strategies in governing whole-plant hydraulic strategies. The reliability of the plant iso/anisohydry framework in predicting species' vulnerability to drought-induced mortality has been challenged recently (Martínez-Vilalta & Garcia-Forner, 2017; Hochberg *et al.*, 2018). However, iso/anisohydry is still a strong predictor of plant drought responses (Novick *et al.*, 2019) when water stress is moderate and before growth cessation occurs (Volaire, 2018). The degree of plant iso/anisohydry has been shown to be associated with a series of coordinated stem and leaf functional traits (Klein, 2014; Martínez-Vilalta *et al.*, 2014; Fu & Meinzer, 2019). However, the role of belowground functional traits in determining species' hydraulic strategies is seldom evaluated in an experimental context (Fort *et al.*, 2017), despite the contribution of deep water access to drought avoidance thereby

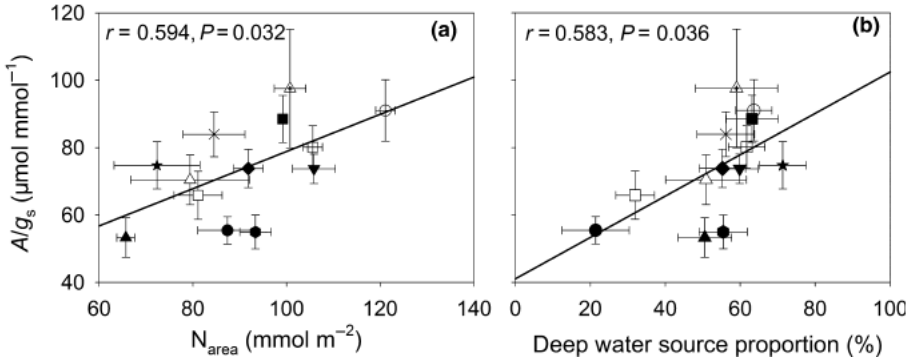

Fig. 5 Relationship between intrinsic water-use efficiency (A/g_s) and (a) area-based leaf nitrogen content (N_{area}), and (b) deep water source proportion in the dry season. See Table 1 for species symbol codes. Values are shown as means ± SE.

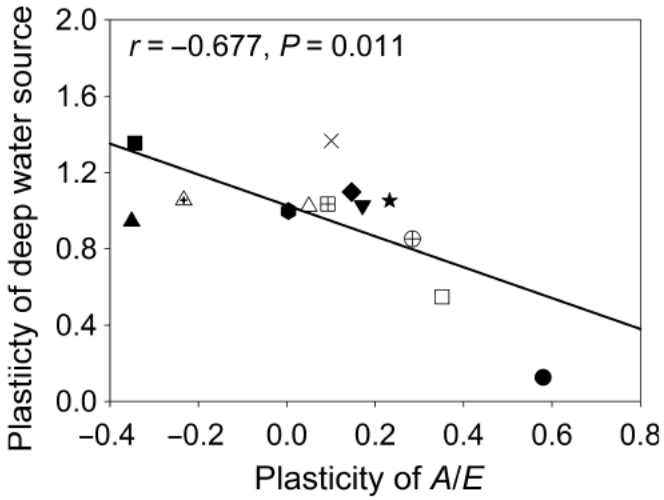

Fig. 6 Relationship between plasticity of deep water source proportion and plasticity of instantaneous water-use efficiency (*A*/*E*) between seasons. See Table 1 for symbol codes.

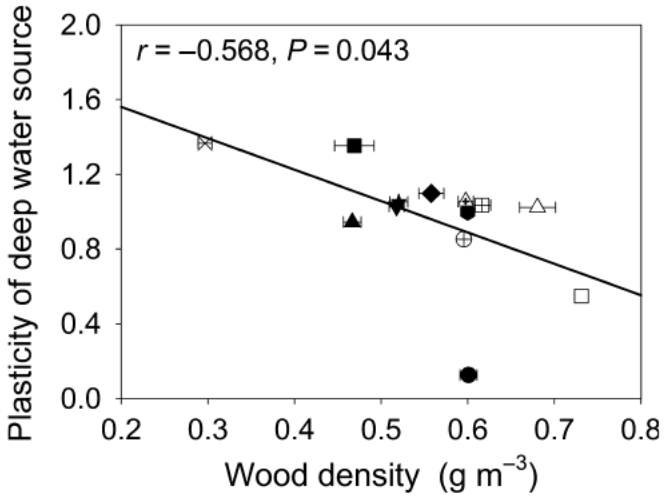

Fig. 7 Relationship between wood density and plasticity of deep water source proportion between seasons. See Table 1 for symbol codes. Values are shown are means ± SE.

conferring a potential competitive advantage in terms of water use strategy (Stark *et al.*, 2015; Brum *et al.*, 2019). Wood density and the sensitivity of intrinsic water-use efficiency (WUE) to environmental variation are proxies for the degree of plant iso/anisohydry, with lower wood density and higher sensitivity of intrinsic WUE implying more isohydric behaviour (Fu & Meinzer, 2019; Yi *et al.*, 2019). In our study, plasticity of reliance on deep water sources was negatively correlated with wood density and plasticity of instantaneous WUE (Figs 6b, 7), indicating that lower plasticity of deep water utilization is associated with more anisohydric behaviour. However, a previous study reported that more anisohydric species had greater plasticity of leaf hydraulic parameters (Johnson *et al.*, 2018). Although the mounting evidence suggests that plasticity of drought tolerance traits in different organs is integrated, the paradoxical results

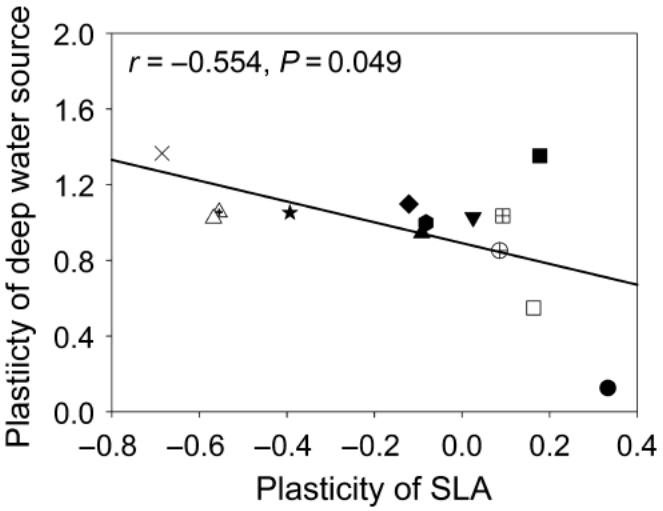

Fig. 8 Plasticity of deep water source proportion in relation to plasticity of specific leaf area (SLA) between seasons. See Table 1 for symbol codes.

indicated that overall plant hydraulic strategies may be organ-dependent.

Correlation between deep water source reliance and species abundance

Consistent with our hypothesis, we found that common species tended to have lower intraspecific variation in their deep water source reliance in the dry season compared to rare species across the sampling sites in the study area. Our results indicate that common species optimized their deep water reliance to adjust to local conditions, despite the modest variation of soil water content across the sampling plots. Our results support the assumption that species having low trait variation around optimal trait values are able to easily dominate the local environment (Umaña *et al.*, 2015). However, at a regional scale with larger environmental heterogeneity, species relative abundance was reported to be positively related to intraspecific variation in root branching intensity and mycorrhizal colonization but not related to first-order root diameter (Li *et al.*, 2017). Considering that first-order root diameter is a phylogenetically conserved root trait (Kong *et al.*, 2014), whereas deep water reliance showed highly plastic responses to the environment (Fig. 2; Snyder & Williams, 2007), we might expect an important role of deep water utilization in adapting to water resource gradients at regional scales. Although a recent study suggests that species traits are not necessarily near 'optimum' in habitats where they occur frequently and abundantly (Mitchell *et al.*, 2018), our results further showed that common species tended to have neither very high nor very low deep water reliance in the dry season, complementing a growing body of evidence that rare species tended to occupy the periphery of the community traits space (Shipley *et al.*, 2011; Umaña *et al.*, 2015; Li *et al.*, 2017) when species occurred in locations facing strong stabilizing selection for particular traits (Muscarella & Uriarte, 2016).

Deep water use patterns along a 'fast-slow' plant economics spectrum

We found that species' deep water use patterns contributed to their carbon capture and water economy. Species with higher intrinsic WUE had better access to deep water in the dry season (Fig. 5). Moreover, our results showed that there was a positive relationship between N_{area} and intrinsic WUE, which is consistent with previous studies showing that carbon isotope discrimination decreased with increasing N_{area} (Clearwater & Meinzer, 2001; Adams *et al.*, 2016), but inconsistent with the finding that intrinsic WUE decreased with increasing N_{area} across species representing a spectrum of iso/anisohydry (Meinzer *et al.*, 2017). The contrasting pattern observed here could be explained by an uncoupling between deep water reliance in the dry season and N_{area}. Specifically, species with higher intrinsic WUE may resort to higher N_{area}, or higher deep water reliance in the dry season, but do not need to have both higher N_{area} and higher deep water reliance in the dry season. The intra- and interspecific variations in deep water source utilization also provide insight into how species with different belowground resource-use strategies may cope with the trade-off between carbon uptake and water loss. Our results suggest that the capacity for utilization of deep soil water and its plasticity yield different scenarios depending on the measure of species-specific WUE employed (Figs 5b, 6). Increasing capacity for deep water utilization was positively associated with intrinsic WUE (Fig. 5b). By contrast, plasticity of deep water utilization was negatively associated with plasticity of instantaneous WUE (Fig. 6).

Our results may represent the first evidence that species with fast strategies (low wood density) also have a plastic deep root mode, indicated by the negative correlation between stem density and plasticity of deep water reliance between seasons across species (Fig. 7). Our results suggest that a deep root system plays an important role in the plant economic spectrum and that the plant economic spectrum is related not only to the values of plant functional traits, but also to the plasticity of plant functional traits across environmental variation (Figs 6–8).

For the shallow portion of the root system, a global dataset showed that species with thinner first-order roots had a fast strategy of the shallow fine root system with respect to resource acquisition (Ma *et al.*, 2018). Inconsistent with our hypothesis, we found no significant correlation between shallow fine root economy traits (first-order root diameter, SRL, RTD) and deep water utilization parameters across species, suggesting independent dimensions of soil resource acquisition between deep and shallow soil. This is consistent with previous studies showing that the form and function of deep fine roots may exhibit some differences from shallow fine roots (Prieto *et al.*, 2015; Wang *et al.*, 2016; Fort *et al.*, 2016). These variations of root traits along the soil profile are likely the result of root specialization to acquire different resources (Fort *et al.*, 2016), because nutrient availability often declines, whereas bulk density tends to increase with soil depth (Schenk, 2005; Ugawa *et al.*, 2010).

However, the decoupling observed between shallow and deep root system traits along the soil profile does not necessarily imply that the vertical trends in an integrated series of traits are functionally discontinuous. Instead, there is a trend of unified evolutionary changes in resource transport efficiency of interdependent organs within species (Martínez-Vilalta & Piñol, 2002; McElrone *et al.*, 2004; Fortunel *et al.*, 2012). Similarly, Li *et al.* (2015) found two independent trait dimensions at the leaf level in that leaf economics traits related to light capture and photosynthesis were decoupled from hydraulic traits related to leaf water transport capacities and temperature regulation. These results collectively suggest that independent trait dimensions within plant organs may be an intrinsic mechanism for plants to adapt to multiple environment gradients and may facilitate species coexistence.

Conclusion

Our data highlight an important role played by deep water utilization patterns in plant economic spectra for the understorey shrubs at our study site. Higher capacity for deep resource acquisition was associated with higher intrinsic WUE but was not necessary to maintain less negative midday leaf water potentials. Thus, the common species in the study site may not have experienced selective pressure for high reliance on deep water sources in the dry season. However, we found that fast strategy species (indicated by lower wood density) showed greater plasticity of soil water resource utilization between seasons. If the notion that fast species grow best and dominate under higher resource availability (Reich, 2014) is broadly applicable, our results suggest that plasticity of plant functional traits and deep resource acquisition strategy have important implications for understanding plant performance and thus community assembly processes. Because this study was conducted in subtropical plantations, the broader applicability of our findings should be investigated in natural forests. Mycorrhizal symbioses and root morphology traits together shape the uptake capacities of roots (Chen *et al.*, 2016), and mycorrhizal type may offset selection for features of the root economics spectrum (Weemstra *et al.*, 2016). Further investigations of the plasticity of mycorrhizal, morphological and architectural traits of deep roots are needed to shed further light on the role of deep root function in shaping species' resource economy spectra and distribution.

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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 analyzed the data and wrote the paper; and 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.

Fig. S1 Vertical distribution of fine root biomass of *P. massoniana*, *P. elliottii*, shrubs, and herbs.

Fig. S2 Plasticity of deep water source proportion between seasons of 13 shrub species.

Table S1 Structural traits for the *P. massoniana* ($n = 18$) and *P. elliottii* ($n = 11$) stands.

Table S2 Structural traits for 13 shrub species in the *P. massoniana* and *P. elliottii* stands.

Table S3 Summary of ANOVA analysis of plantation types on water source proportion within species.

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