Received: 31 July 2022 | Accepted: 26 September 2022

DOI: 10.1111/1365-2745.14007

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Spatio-temporal variation in deep soil water use patterns of overstorey and understorey layers in subtropical plantations predicts community assembly

Peipei Jiang[1,2] | Frederick C. Meinzer[3] | Huimin Wang[2,4] | Xiaoqin Dai[2,4] | Shengwang Meng[2,4] | Liang Kou[2,4] | Yifan Chen[5] | Xiaoli Fu[2,4]

[1]Key Lab of Plant Stress Research, College of Life Sciences, Shandong Normal University, Ji'nan, Shandong, China

[2]Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

[3]USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

[4]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

[5]Industry Development Planning Institute, NFGA, Beijing, China

Correspondence
Xiaoli Fu
Email: fuxl@igsnrr.ac.cn

Funding information
National Natural Science Foundation of China, Grant/Award Number: 31730014, 32122060 and 32201520

Handling Editor: Kun-Fang Cao

Abstract

1. Deep soil water utilization allows plants to cope with drought stress. However, little is known about the roles of the understorey layers in driving spatio-temporal variations of deep soil water in forests and how the patterns of deep soil water use among life-forms contribute to community assembly processes.
2. We assessed the spatio-temporal patterns and determinants of deep water utilization of tree, shrub and herb layers in subtropical coniferous plantations and investigated associations between deep water use parameters and dominance and richness of understorey vegetation.
3. We found that the understorey layer had a higher reliance on deep soil water in the dry season, a larger seasonal plasticity of deep soil water uptake, but lower spatial variability in deep soil water utilization than the tree layer. We showed that greater reliance of the tree layer on deep soil water was associated with decreased shrub layer diversity, whereas greater reliance of the shrub layer on deep water was associated with increased herb layer diversity.
4. *Synthesis*. Our results highlight the roles of understorey layers in driving the temporal dynamics of deep soil water in forests and improve our understanding of how deep soil water use patterns among life-forms shape community assembly in forests.

KEYWORDS
biodiversity index, deep soil water utilization, fine root biomass, seasonal dynamics, spatio-temporal pattern, stable isotopes, water use efficiency

1 | INTRODUCTION

In recent decades, global climate change-related droughts have become more frequent, intense, widespread and longer-lasting (Kim et al., 2021; Sheffield et al., 2012; Trenberth et al., 2014), leading to world-wide increases in forest mortality and therefore changes in the community structure and function of forest ecosystems (Adams et al., 2017; Pederson et al., 2014; Ripullone et al., 2020). Hydraulic failure is one of the most important causes of drought-induced plant mortality (McDowell et al., 2011). Access to deep soil water

reservoirs could allow vegetation to recover and survive in hydrologic refugia, mitigating hydraulic vulnerability and mortality risk (Brum et al., 2019; Chitra-Tarak et al., 2021; McLaughlin et al., 2017). Identifying patterns of deep soil water utilization in forest ecosystems has important implications for understanding adaptations to changes in the terrestrial hydrologic cycle and resistance of forests to future expected anomalous droughts and heat waves (Chitra-Tarak et al., 2018; Lee et al., 2005; Ripullone et al., 2020).

At the ecosystem level, deep soil water utilization shows considerable temporal and spatial variation and can be detected by the soil water dynamics along the vertical profile. In the dry season, the shallow soil water content generally remains relatively low and the deep soil water content shows a downward trend, indicating that vegetation increases the consumption of deep soil water to ensure growth (Jia & Shao, 2014; Li et al., 2021; Markewitz et al., 2010). In the wet season, the consumption of deep soil water by vegetation decreases due to adequate shallow soil water, allowing the deep soil water to be replenished by precipitation (Cao et al., 2018). Also, topography, soil properties and the interactions among them can impact the spatial variation of deep soil water content (Fu et al., 2018; Montenegro & Ragab, 2012; Wang et al., 2015). With the development of stable isotope techniques, temporal and spatial variation in deep soil water utilization patterns among and within species has been characterized (Dawson & Pate, 1996; Eggemeyer et al., 2009; Stratton et al., 2000). Generally, woody plants with deeper and dimorphic root systems can switch their major water source from shallow soil layers in the wet season to deep soil water in the dry season (Barron-Gafford et al., 2017; Kulmatiski et al., 2010; Le Roux et al., 1995; Wang, An, et al., 2020; Ward et al., 2013). However, deep water use strategies of woody plants can be variable due to the high spatial heterogeneity of soil water resources (Carrière et al., 2020). Plants growing on continuous dolostone outcrops and nearby thin soils relied largely on deep soil water both in the wet and dry seasons due to the low water holding capacity of shallow soils (Nie et al., 2011). Additionally, plants growing adjacent to a spring switched their major water sources from shallow to deep soil during the dry season (McCole & Stern, 2007), whereas their water sources on an upland site with no evidence of deep water were generally shallow and unstable even during the dry summer (Bendevis et al., 2010; Schwinning, 2008).

Compared with woody species, herbs are likely to be less reliant on deep water resources and more sensitive to reduced water availability in the upper portion of the soil profile. In a number of studies conducted in forests, herbs were found to rely primarily on shallow soil water (Asbjornsen et al., 2008; Eggemeyer et al., 2009; Le Roux et al., 1995). A recent meta-analysis of arid and semi-arid ecosystems showed that increased precipitation consistently enhanced fine root biomass of woody plants, but had variable effects on herbs, whereas decreased precipitation reduced root biomass of herbs but not woody plants (Wang, Huang, & Hu, 2020). In other studies, the gross primary productivity (GPP) of shallow-rooted herbs was more sensitive to interannual variation in precipitation and vapour pressure deficit (VPD) than that of deep-rooted trees and shrubs (Chen et al., 2021; Liu et al., 2020; Zhang et al., 2019). These findings, coupled with the preceding examples of divergent strategies of deep soil water utilization within and among woody species, imply that the community-level effects of tree, shrub and herb layers within a forest ecosystem on the spatio-temporal dynamics of ecosystem deep soil water should differ. However, spatio-temporal variations of deep soil water utilization of understorey vegetation at the community-level within forest ecosystems seem to be a frequently overlooked question in ecosystem hydrology studies, despite mounting evidence showing that the subordinate understorey vegetation can punch above its weight in driving below-ground biodiversity and nutrient cycling (Bengtsson et al., 2000; Carneiro et al., 2007; Nilsson & Wardle, 2005). We hypothesized that in pure pine plantations, the spatio-temporal variation in deep water use by the understorey layer may be larger than that of the dominant tree layer because the number and range of subordinate species is highly variable across patches (Fujii et al., 2009; Wallrup et al., 2006) and the divergent species-specific differences in deep water utilization would confer more variability of deep water utilization at the species-group level (understorey layer).

Uptake of deep soil water by plants does not necessarily mean that they are deeply rooted. Instead, coexisting deep-rooted species can draw water up from deep soil layers and redistribute it into shallow layers (so-called hydraulic lift) where shallow-rooted species can take up the hydraulically redistributed water (Brooks et al., 2006; Goldstein et al., 2008; Hao et al., 2013). Hydraulic lift can favour the growth of herbs in the dry season allowing them to scavenge the deep water lifted by overstorey trees (Yu & D'Odorico, 2015), and this facilitation would be much greater and last longer during drier years (Barron-Gafford et al., 2021). Hydraulic lift by deep-rooted trees may also contribute to the survival of seedlings of surrounding shallow-rooted shrubs, although the influence of facilitation might not offset competition from neighbours and might change during the year (Muler et al., 2018; Prieto et al., 2011). Previous findings suggest that nocturnal hydraulic lift can recharge up to 35%–80% of the water taken up from shallow layers during the dry season (Brooks et al., 2002; Meinzer et al., 2004). The substantial contribution of water hydraulically redistributed by the dominant tree community to shallow soil layers leads to our second hypothesis that the spatio-temporal variation of deep soil water utilization by the dominant deep-rooted tree community should tightly regulate water utilization of the subordinate relatively shallow-rooted understorey community, eventually driving the understorey vegetation community structure. To our knowledge this hypothesis has never been tested within forest ecosystems.

To test the first hypothesis, we used a stable isotope technique to quantify the magnitude of deep soil water utilization by trees and dominant species in the shrub and herb layers in the wet (WW) and dry seasons (DW) across 29 plots in subtropical pine plantations with a marked dry season (Yang et al., 2015). By combining these data with community structure survey data, we evaluated the magnitude of water utilization of the shrub and herb layers at the community level. We then calculated and compared deep water utilization parameters during the dry season (DW) and plasticity of deep water utilization

between the wet and dry seasons (DWP) as well as their spatial variability for the tree, shrub and herb layers. We also measured the soil characteristics, plant photosynthesis-related attributes and the vertical distribution of fine root biomass among life-forms across the 29 plots, and tested potential influences of these abiotic and biotic factors on DW/DWP of different life-forms. To test the second hypothesis, we examined the associations between the DW and DWP among and within life-forms and investigated the roles of DW and DWP of the dominant tree layer in determining the dominance, richness and evenness of the subordinate shrub and herb layers.

2 | MATERIALS AND METHODS

2.1 | Site description

The study site was the Qianyanzhou Ecological Station of the Chinese Academy of Sciences (26°44′39′′N, 115°03′33′′E), located in a typical hilly red-soil region of subtropical China. This area is strongly influenced by the subtropical monsoon climate, with seasonal droughts due to the unevenly distributed rainfall. The mean annual temperature and annual precipitation are 18.0°C and 1509.0 mm respectively. According to the multi-year mean monthly Budyko aridity index from 2003 to 2010, drought periods were identified from July to October, and the nondrought periods spanned from November to June (Yang et al., 2015). The soil is an iron-rich red soil classified as Typic Dystrudept and Udept Inceptisols according to the USDA soil taxonomic system. The vegetation at the study site was dominated by *Pinus massoniana* and *P. elliottii* plantations initially planted in 1983. According to the community survey data, the shrub layer was dominated by *Loropetalum chinense*, *Adinandra millettii*, *Toxicodendron vernicifluum*, *Camellia oleifera*, *Eurya muricata* and *Rhus chinensis*. The herb layer was dominated by *Lophatherum gracile*, *Woodwardia japonica*, *Dryopteris atrata* and *Dicranopteris dichotoma*.

This study was conducted in 29 permanent pine plantation plots (18 for *Pinus. massoniana* and 11 for *P. elliottii*). The plots (30 m × 30 m) were separated by more than 10 m. Soil profiles of the plantations are highly heterogeneous, characterized by high variation in rock fragment content and soil water content. Across the 29 plots, the rock fragment content of the 0–80 cm layer ranged from 0 to 37.5%. The coefficient of variation (CV) of the rock fragment content down to 80 cm depth and soil water content down to 100 cm depth during the dry season across plots was 107% and 17.8% respectively. The trait measurements described below were performed in August 2016 (the dry season) and April 2017 (the wet season; Table 1).

2.2 | Stand structure, fine root biomass distribution and soil properties

In each plot, all trees were numbered and their diameter at breast height and height measured. The stem density was calculated as the number of trees divided by the area of the plot. Three shrub subplots (5 × 5 m) were established along the diagonals of each plot. In each subplot, the height, basal diameter, east–west and north–south width of the crown and number of individuals of each shrub species were recorded. One herb quadrat (1 × 1 m) was established within each shrub subplot. In each quadrat, the height, coverage and number of individuals of each herb species were recorded.

In each plot, soil cores (10 cm diameter) were collected every 20 cm from the surface to 200 cm at the upslope, midslope and downslope portions of the plot. Living roots were carefully extracted by hand and gently washed in tap water. The roots were then categorized as belonging to trees, shrubs or herbs, based on their contrasting traits in terms of morphological structure, colour and mechanics (e.g. rough or smooth, rigid or soft). Roots of the overstorey pine species were easily distinguished by their dark red epidermis and were generally dichotomously branched with ectomycorrhizal structures (Kou et al., 2018). Roots of herbs were whiter or black, rough and rigid (Rolo & Moreno, 2012), while roots of shrubs had more obvious xylem structure and were fleshier and more brightly coloured (Jiang et al., 2018). We processed the root samples of trees and shrubs using an order-based approach by dividing their fine roots into absorptive (one to three order) and transport (four to five order) categories. Details are given in Jiang et al. (2018). The rock fragment content (by volume) of each soil core was calculated using a stone density of 2.65 g cm^{-3} (Diochon et al., 2009). Differences between the volumes of the soil cores and the stones were used to calculate the soil bulk density (Diochon et al., 2009).

2.3 | Deep soil water utilization

We determined plant deep water utilization using stable isotope analyses of xylem and soil water. During mid-morning (*c.* 10:00 h), samples from nonphotosynthetic tissues were collected. In each plot, tree stems were sampled from the south side of two to three sample trees, and phloem tissue was removed to avoid potential contamination of stem water by isotopically enriched water (Querejeta et al., 2007). In each plot, 10 shrub species were selected and the mean basal coverage of these species relative to the total basal coverage of all shrubs was 63.6 ± 3.3% across 29 plots, and the fraction of deep water utilization of these shrubs was used to characterize the overall deep water utilization of the shrub layer. In each plot, three fern species were selected and the mean coverage of these species relative to the total coverage of all herbs was 75.3 ± 5.8% across 29 plots, and the deep water utilization of these ferns was used to characterize the overall deep water utilization of the herb layer. Each shrub and fern sample contained two or three individuals. For shrubs, the leaves and green stem tissue were removed from the twigs to avoid contamination by isotopically enriched water (Ehleringer & Dawson, 1992). For ferns, the thick and fleshy root crowns were collected, because the $\delta^{18}O$ of this part is the least variable and can represent a satisfactory proxy for water uptake from different soil depths (Barnard et al., 2006). The plant samples were immediately cut into small segments, placed in glass vials and sealed

TABLE 1 Abbreviations and units of the traits studied

Parameter	Abbreviation	Unit
Soil properties		
Rock fragment content	RC	%
Soil water content	SWC	%
Soil bulk density	BD	$g\,cm^{-3}$
Photosynthesis-related attributes		
Light-saturated photosynthetic rate	A_{max}	$\mu mol\,m^{-2}\,s^{-1}$
Stomatal conductance	g_s	$mol\,m^{-2}\,s^{-1}$
Intrinsic water use efficiency	A/g_s	$\mu mol\,mol^{-1}$
Instantaneous nitrogen use efficiency	PNUE	$\mu mol\,g^{-1}\,s^{-1}$
Fine root biomass among life-forms		
Absorptive fine root biomass of trees	$Tree_{Absorptive}$	$g\,m^{-2}$
Transport fine root biomass of trees	$Tree_{Transport}$	$g\,m^{-2}$
Total fine root biomass of trees	$Tree_{Total}$	$g\,m^{-2}$
Absorptive fine root biomass of shrubs	$Shrub_{Absorptive}$	$g\,m^{-2}$
Transport fine root biomass of shrubs	$Shrub_{Transport}$	$g\,m^{-2}$
Total fine root biomass of shrubs	$Shrub_{Total}$	$g\,m^{-2}$
Total fine root biomass of herbs	$Herb_{Total}$	$g\,m^{-2}$
Community structure parameters		
Basal area	BA	$m^2\,ha^{-1}$
Stem density of trees	SDT	$trees\,ha^{-1}$
Dominance of shrubs	DOS	/
Richness of shrubs	ROS	/
Evenness of shrubs	EOS	/
Dominance of herbs	DOH	/
Richness of herbs	ROH	/
Evenness of herbs	EOH	/

Note: The fine root biomass in the table refers to the biomass in the 60–200 cm soil layer.

with parafilm, and placed in a cooler with ice packs. Soil cores were collected at 0–20, 20–60, 60–100, 100–150 and 150–200 cm depth in each plot.

In the laboratory, soil and plant samples for isotopic analysis were kept frozen at −20°C in a freezer prior to water extraction. Water was extracted from samples using an automatic cryogenic vacuum distillation water extraction system (Li-2100), with extraction times of 2.5 h for soil samples and 3 h for plant samples. Water samples were analysed for isotopic ratios of δD and $\delta^{18}O$ using a liquid water isotope analyser (912-0050, LGR). The IsoSource model was used for the calculation of the relative contribution of soil water at different depths to plant water (Phillips et al., 2005; Phillips & Gregg, 2003). Since the accuracy in δD analysis was relatively lower than that of $\delta^{18}O$ when the isotopic ratio infrared spectroscopy (IRIS) method was applied (Wen et al., 2012), we used $\delta^{18}O$ to evaluate the depths of water uptake.

Across the 29 plots, the 0–60 cm soil layers contained more than 90% of the total fine root biomass of the 0–200 cm soil profile among life-forms (Figure S1). The $\delta^{18}O$ values of the upper 60 cm soil were different from those below 60 cm depth (Figure S2). Therefore, we defined the deep soil layer as the layer below 60 cm. The water source proportion for deep soil water from 60 to 200 cm was represented by the sum of soil water sources in the ranges 60–100, 100–150 and 150–200 cm depth.

2.4 | Photosynthesis-related indexes

Light-saturated photosynthetic rates (A_{max}) and stomatal conductance to water vapour (g_s) were measured using a portable photosynthesis system (Li-6400XT, Li-Cor) with an artificial light source. Intrinsic water use efficiency was calculated as A/g_s (Maseyk et al., 2010). On sunny days, these photosynthesis-related 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). Steady-state measurements were made following equilibrium (4 min or longer) under a constant photosynthetically active radiation of $800\,\mu mol\,m^{-2}\,s^{-1}$ (which was roughly twice mean values in the understorey during gas exchange measurements), leaf temperature of 30°C, CO_2 concentration of $400\,\mu mol\,mol^{-1}$ and leaf-to-air vapour pressure deficit of 1 kPa. Leaf total nitrogen concentration (leaf N) was determined

through combustion by an elemental analyser (vario MACRO cube). Specific leaf area (SLA) was calculated as the leaf area divided by its dry mass. Area-based leaf N concentration (N_{area}, $g\,m^{-2}$) was calculated as the ratio of leaf N to SLA. Instantaneous nitrogen use efficiency (PNUE, $\mu mol\,g^{-1}\,s^{-1}$) was calculated as A_{max}/N_{area} (Field & Mooney, 1986).

2.5 | Statistical analysis

Considering that the vertical distribution of the soil water $\delta^{18}O$ values and deep soil water source proportions of *P. massoniana* and *P. elliottii* plantations were similar (Figures S2 and S3), we pooled the data from the two plantation types.

At the species level, the seasonal plasticity of deep soil water utilization (DWP) was calculated as:

$$DWP = \frac{2 \times (DW - WW)}{DW + WW} \quad (1)$$

where DW is the deep soil water utilization in the dry season and WW is the deep soil water utilization in the wet season. In each plot, the community-weighted mean DW and photosynthesis-related indices (e.g. A_{max}, g_s, A/g_s and PNUE) of shrubs and herbs were then calculated. First, the weight of each shrub (or herb) species in each subplot was calculated as the number of individuals divided by the total number of individuals of shrubs (or herbs), and then the weight of each species in each plot was calculated as the average weight across three subplots. Second, the community-weighted mean DW of each plot was calculated as the sum of the product of DW (or photosynthesis-related indexes) of each species and their weight. Because the DWP could be either negative or positive, we used the standard deviation (SD) to evaluate the spatial variability of DW in the dry season and the DWP across plots (Chen et al., 2019). The dominance, richness and evenness of shrubs and herbs in each plot were calculated using 'Biodixcel.xlsx' in Microsoft Office Excel 2007 (Kong et al., 2012). A one-way analysis of variance (ANOVA) was used to analyse the differences of DW among life-forms (trees, shrubs, herbs) in SPSS (2010, ver.19.0; SPSS Inc.). We examined the relationships between the DW and DWP within and among life-forms by the Spearman's rank correlation coefficients in SPSS, because we were interested in assessing ranking consistency of DW and DWP across plots. Significance of relationships between the DW (and DWP), soil properties (soil rock fragment content, bulk density and water content) at shallow (0–60 cm depth) and deep (60–200 cm depth) layers, fine root biomass in deep soil layers, photosynthesis-related attributes (A_{max}, g_s, A/g_s, PNUE) and community structure parameters (stem density of trees and dominance, richness and evenness of shrubs and herbs) were also evaluated using Spearman's rank correlation coefficients in SPSS. Functions fitted to the data in the figures were conducted by the standardized major axis (SMA) tests in R software (v.3.4.3, R Development Core Team, 2017). Abbreviations and units of the traits studied are shown in Table 1.

3 | RESULTS

3.1 | Soil water content, fine root allocation and deep soil water utilization

In our study, the soil water content throughout the 0–200 cm depth of the soil profile was significantly lower in the dry season than that in the wet season (Figure S4). In the dry season, there were no significant differences between the shallow and deep layer soil water content (Figure S5a), but soil water storage in the deep layer was significantly higher than that in shallow layer (Figure S5b). The vertical distribution of total fine root biomass varied among life-forms (Figure 1). In the shallow soil layer, the root biomass of herbs was significantly higher than that of woody plants. In the deep soil layer, the root biomass of shrubs and herbs was similar, but both were significantly lower than that of trees. The tree layer and understorey vegetation showed different deep water use patterns (Figure 2a). For the tree layer, 43.5% and 41.4% of soil water uptake were from the deep layer in the wet and dry seasons respectively. This indicates that the tree layer had a modest reliance on deep soil water year-round, resulting in little seasonal plasticity of deep soil water utilization. For the shrub and herb layers, the deep layer contributed only 20.7% and 25.3%, respectively, to the total soil water uptake in the wet season, but contributed 63.8% and 53.6% in the dry season. Compared with the tree layer, the understorey vegetation had a lower reliance on deep water resources in the wet season but a higher reliance on deep water resources in the dry season, which was manifested as a larger seasonal plasticity of deep soil water utilization (Figure 2b).

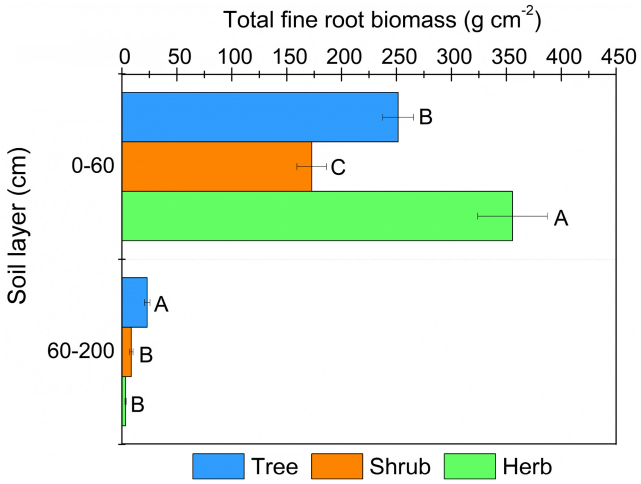

FIGURE 1 Vertical distribution of total fine root biomass for different life-forms across the 29 plots. Different letters indicate significant differences of total fine root biomass within a soil layer among life-forms.

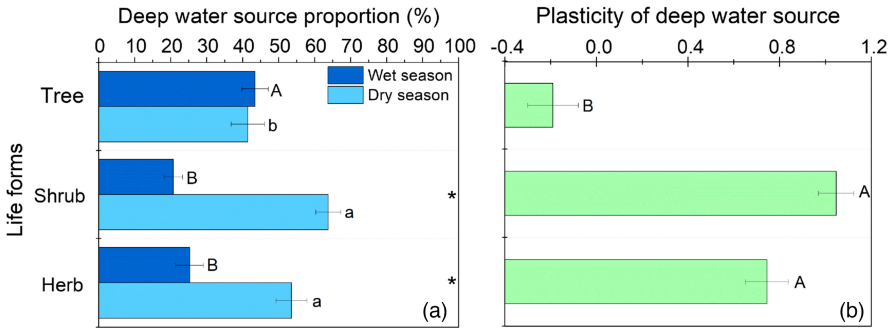

FIGURE 2 Deep soil water utilization (a) and its plasticity between the wet and dry seasons (b) for different life-forms. In (a), different upper- and lower-case letters indicate significant differences of deep soil water utilization in wet or dry season among life-forms respectively; *, represents significant differences between seasons within life-forms. In (b), different letters indicate significant differences in the seasonal plasticity of deep soil water utilization among life-forms.

3.2 | Spatial variations of deep soil water utilization parameters

Across the 29 sampling plots, DW and DWP of the three life-forms showed considerable spatial variation (Figure 3). The DW of the tree, shrub and herb layers ranged from 1.1% to 95.1% (SD = 24.7%), from 17.7% to 96.9% (SD = 18.7%) and from 2.1% to 97.0% (SD = 23.0%) respectively. The DWP of the tree, shrub and herb layers ranged from −1.949 to 0.984 (SD = 0.789), from −0.438 to 1.793 (SD = 0.595) and from −0.760 to 1.914 (SD = 0.712) respectively. Collectively, these results indicate that the tree and herb layers had larger spatial variations in DW and DWP than the shrub layer.

3.3 | Relationships between deep soil water utilization parameters and biotic and abiotic factors

For trees, the DW was positively correlated with their fine transport root biomass in the deep soil layer (Figure 4a), and the DWP was positively correlated with their transport and total fine root biomass in the deep soil layer (Figure 5a,b). For shrubs, the DW was positively associated with their A_{max} and A/g_s (Figure 4b,c), and their DWP was positively associated with the total fine root biomass of trees in deep soil layer but negatively correlated with the g_s and PNUE of shrubs (Figure 5c–e). However, the DW and DWP of shrubs were not related to the basal area and stem density of trees (Table S1). For herbs, the DW was not correlated with the examined traits (Table S2) but the DWP was positively correlated with the total fine root biomass of shrubs in deep soil layer (Figure 5f). These results indicate interactions between root biomass and DWP across life-forms with higher tree layer root allocation in the deep layer facilitating the DWP of the shrub layer and higher shrub layer root allocation in deep layer increasing the DWP of the herb layer. Soil properties had little effect on DW and DWP of the three life-forms, with the exception that DWP of herbs was positively correlated with the soil water content of the 0–60 cm layer (Figure 5g; Tables S3 and S4).

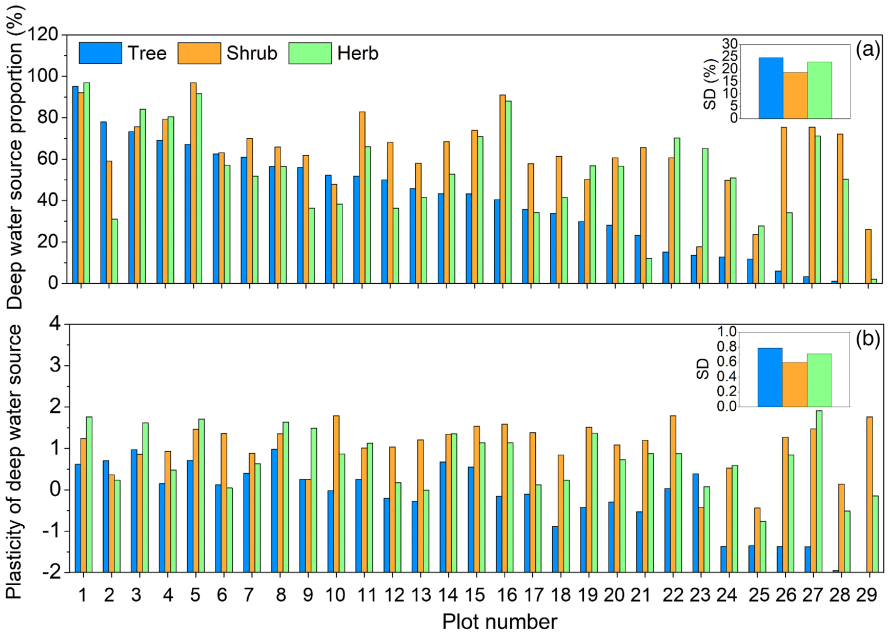

FIGURE 3 Spatial variation in (a) deep soil water utilization in the dry season (DW) and (b) seasonal plasticity of deep soil water utilization (DWP) among life-forms. Insets in (a and b) showed the standard deviation (SD) of DW and DWP.

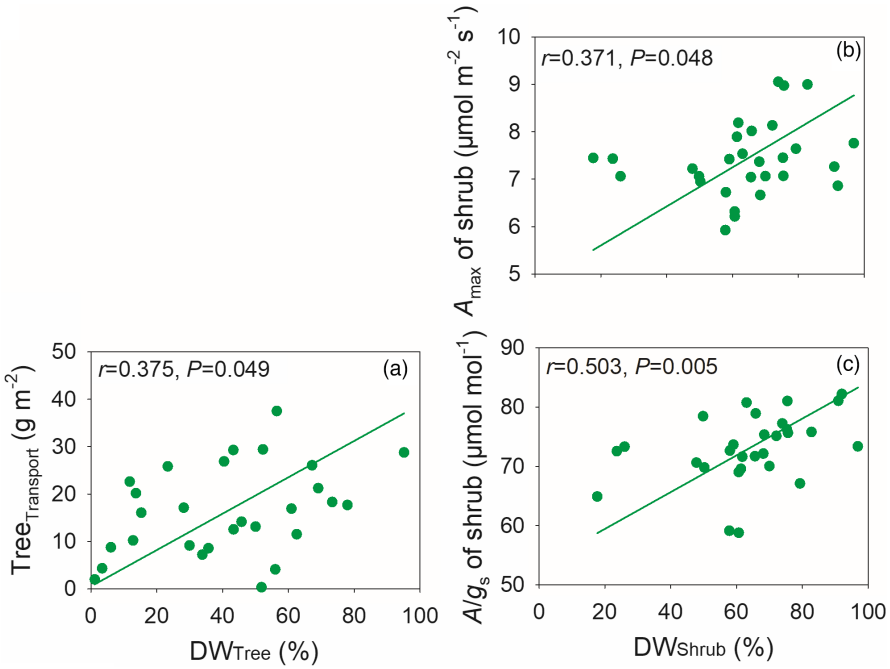

FIGURE 4 Relationships between deep soil water utilization by trees in the dry season (DW_{Tree}) and transport root biomass of trees in the deep soil layer ($Tree_{Transport}$, a); and relationships between deep soil water utilization by shrubs in the dry season (DW_{Shrub}) and their light-saturated photosynthetic rate (A_{max}, b) and intrinsic water use efficiency (A/g_s, c). The DW and photosynthesis-related indices (e.g. A_{max} and A/g_s) of shrubs are the community-weighted means.

3.4 | Correlations between deep soil water utilization parameters and community structure parameters

Across the 29 sampling plots, DW and DWP were spatially correlated within and among life-forms (Figure 6). Within life-forms, DW was spatially correlated with DWP for trees and herbs but not for shrubs. This result indicates that DW and DWP were coupled for trees and herbs, but not for shrubs. Across life-forms, the DWP of trees and the DW of shrubs were positively correlated with the DW and DWP of herbs and the DWP of shrubs was positively associated with the DWP of herbs.

More interestingly, the DW of trees was positively associated with the dominance of shrubs (Figure 7), and the DW of shrubs was positively associated with the richness of herbs (Figure 8). These results suggest interactions between DW and community structure across life-forms with higher deep water use capacity of the tree layer associated with increased dominance of the shrub layer, and higher deep water use capacity of the shrub layer associated with increased the species richness of herb layer. However, there were no relationships between community structure parameters among life-forms (Table S5).

4 | DISCUSSION

4.1 | Differences in deep water use strategies among and within life-forms

In our study, trees mainly relied on shallow soil water during both the wet and dry seasons and had little seasonal variation in deep soil water utilization as compared to shrubs and herbs. This is likely because the spasmodic rainfall events during the dry season resulted in no difference between the shallow and deep layer soil water content (Figure 5a). However, the shrub and herb layers clearly switched their major water source from shallow soil during the wet season to deep soil during the dry season. These results suggest that the understorey vegetation relied more on deep soil water in the dry season than trees, in contrast with previous findings (Asbjornsen et al., 2008; Eggemeyer et al., 2009; Xu et al., 2011). This may be a consequence of previous studies on plant water use strategies usually having been conducted at the species level (Eggemeyer et al., 2009; Liu et al., 2010; Xu et al., 2011; Yang et al., 2015), whereas our plant water utilization study was conducted at the community level. Second, this may be attributable to deciduous species deriving water from deeper soil layers than those accessed by evergreen species during the dry season, which has been verified in our study area (Jiang, Meinzer, et al., 2020) and other regions (Jackson et al., 1999; Liu et al., 2010; Querejeta et al., 2007; Stratton et al., 2000; Valentini et al., 1992). In our study, the deciduous woody shrubs accounted for 50.6 ± 2.6% of the relative basal coverage of total understorey woody shrubs across the 29 plots. Third, smaller understorey species (with average basal diameter and height about 8 mm and 1.1 m respectively) tended to preferentially use deeper sources of soil water than larger overstorey trees (with the average diameter at breast height about 18 cm) during the dry season, because the extensive horizontal area foraged by root systems of large trees may partially compensate for the reduced water content of the shallow soil layer (Meinzer et al., 1999) and the larger trees may also rely on their larger stem water storage capacity to dampen the daily fluctuation and decline in plant leaf water potential during droughts (Oliva Carrasco et al., 2015; Phillips et al., 2003; Scholz et al., 2007). Last but not least, it should be noted that the proportion of deep soil water utilization by shrubs does not necessarily reflect the extent

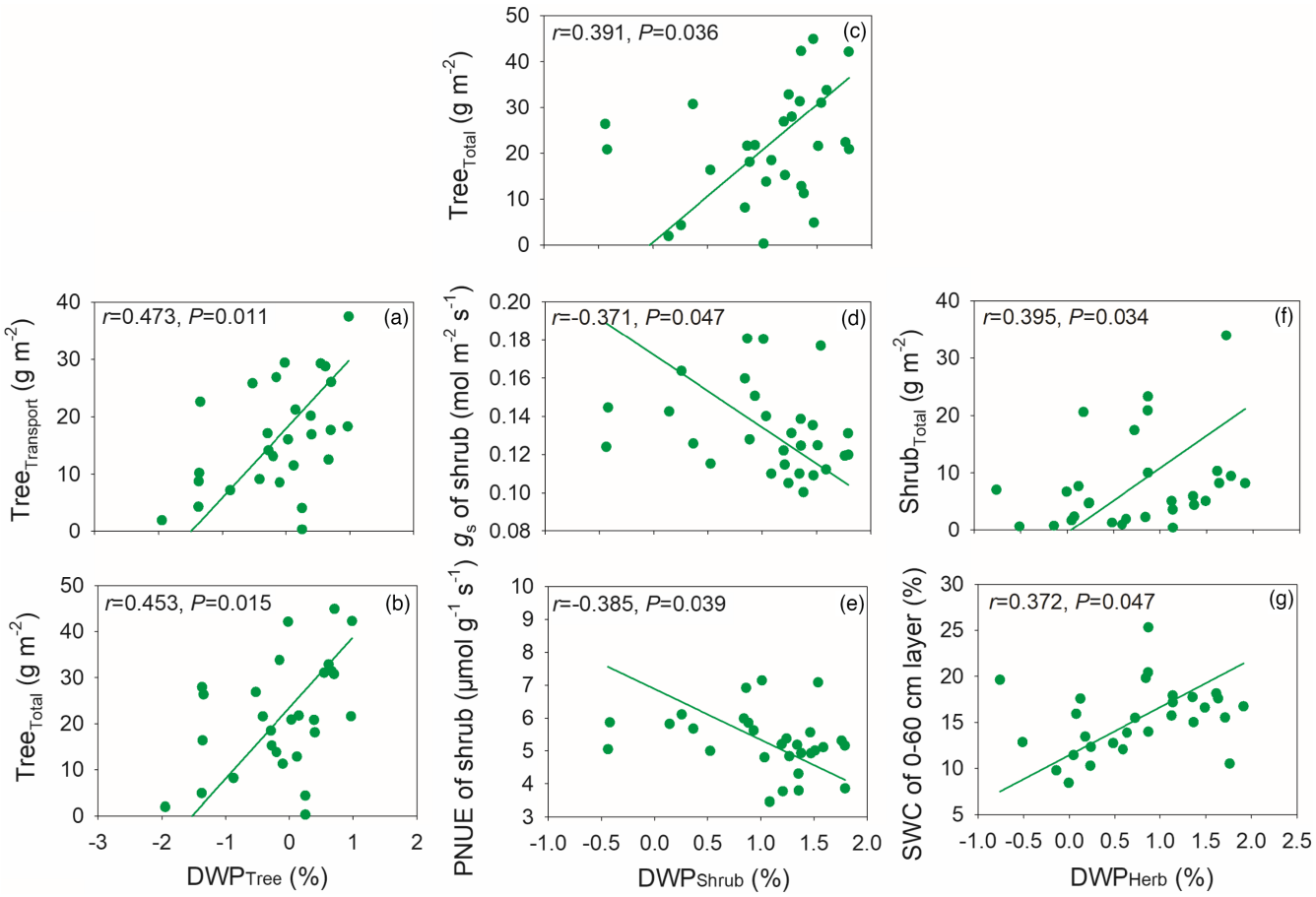

FIGURE 5 Relationships between seasonal plasticity of deep soil water utilization by trees (DWP_{Tree}) and transport root biomass of trees in the deep layer ($Tree_{Transport}$, a) and total tree fine root biomass in the deep layer ($Tree_{Total}$, b); relationships between seasonal plasticity of deep soil water utilization of shrubs (DWP_{Shrub}) and total fine root biomass of trees in the deep layer (c) and shrub stomatal conductance (g_s, d) and photosynthetic nitrogen use efficiency (PNUE, e); and relationships between seasonal plasticity of deep soil water utilization of herbs (DWP_{Herb}) and total root biomass of shrub in the deep layer (f) and soil water content (SWC, g) of the 0–60 cm layer. The DWP and photosynthesis-related indices (e.g. g_s and PNUE) of shrubs or herbs are the community-weighted means.

of direct deep water uptake by their roots. Instead, part of the deep soil water used by shrubs was likely released by the deep-rooted trees into the upper soil layers through hydraulic lift (Goldstein et al., 2008), which is supported by the finding that the deep soil water utilization plasticity of the shrub layer was related to the fine root biomass of trees and the significantly higher fine root biomass of trees in the deep soil layer than that of shrubs.

Interestingly, trees had smaller seasonal but higher spatial variation of deep soil water utilization than understorey vegetation (Figures 2 and 3). This result indicates that when studying the deep hydrologic dynamics of forest ecosystems, especially those in which transpiration of understorey vegetation comprises a considerable proportion of total transpiration, the effect of understorey vegetation should be emphasized if the focus is on temporal variation, and the effect of tree layer should be emphasized if the focus is on spatial variation.

We found that the DW of the shrub layer was positively related to its intrinsic water use efficiency (A/g_s, WUEi) but its DWP was negatively related to its PNUE, indicating the different roles of water use efficiency and photosynthetic nitrogen use efficiency in coupling the magnitude and the plasticity of deep soil water utilization. The tight positive coordination between WUEi and deep water reliance at the community level (our study) and at the species level (Hasselquist et al., 2010; Jiang, Wang, et al., 2020; Wu et al., 2021) indicates that consuming deep water more conservatively through increasing WUEi might be a common strategy for species to maintain growth during the dry season (Nie et al., 2014; Wu et al., 2021). The negative association between PNUE and deep water use plasticity indicated that shrubs from plots with a larger shift from reliance on shallow water to deep soil water in the dry season tended to have lower PNUE. This is consistent with previous studies showing that plants maximized their water use efficiency at the expense of nitrogen use efficiency under water deficit (Limousin et al., 2015; Midgley et al., 2004; Miller et al., 2001). Considering that maintaining a higher water use efficiency and a larger shift from shallow water to deep soil water reliance is isohydric behaviours (Jiang, Wang, et al., 2020; Klein et al., 2013; Martínez-Vilalta & García-Forner, 2017), the negative relationship between PNUE and deep water use plasticity observed in the present study can be explained by tighter

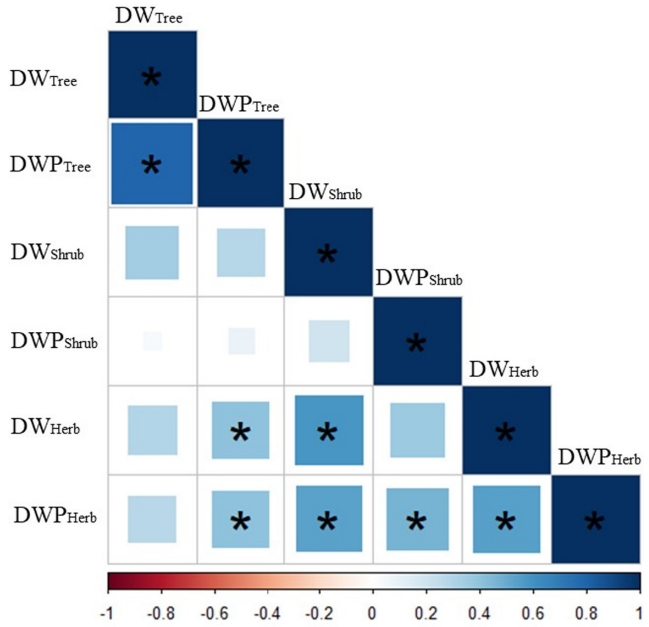

FIGURE 6 Spatial correlations between deep soil water utilization in the dry season (DW) and seasonal plasticity of deep soil water utilization (DWP) within and among life-forms. *, represents significant correlations at the 0.05 level.

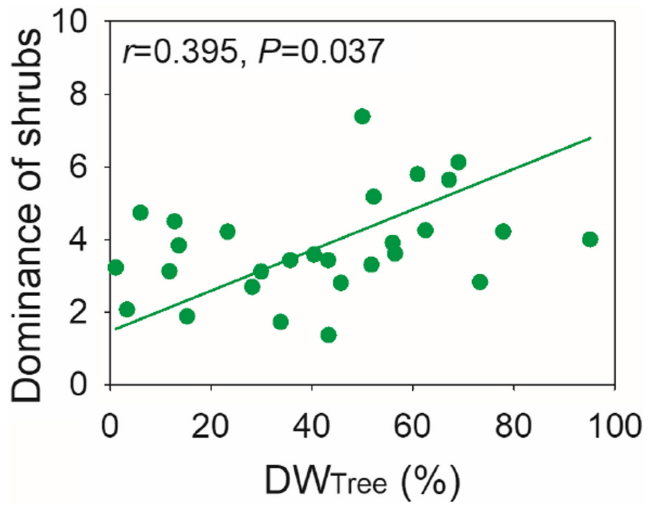

FIGURE 7 Relationship between deep soil water utilization by trees in the dry season (DW_{Tree}) and the dominance of shrubs.

stomatal regulation inducing decreases in the photosynthetic rate per Rubisco (RBUE) and thus decreasing PNUE (Figure 5d; Hikosaka & Shigeno, 2009; Warren & Adams, 2004).

Although previous studies at the species level showed that soil moisture and rock fragment content played key roles in determining plants' water use patterns (Cai et al., 2018; Korboulewsky et al., 2020; Tetegan et al., 2015; Thomas et al., 2020), we found that deep water utilization parameters of the tree and shrub layers had weak associations with the substrate characteristics. With the exception of the DWP of the herb layer being associated with the soil water content in the 0–60 cm layer, there was no significant

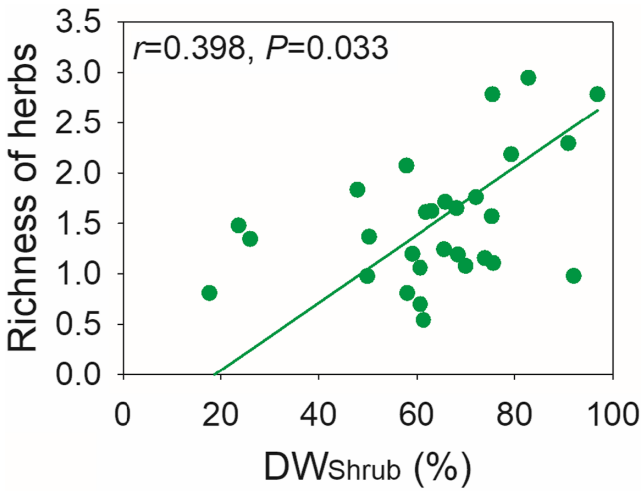

FIGURE 8 Relationship between deep soil water utilization by shrubs in the dry season (DW_{Shrub}) and the richness of herbs.

relationship between soil properties and DW (or DWP) of the tree and shrub layers (Tables S2 and S3). The greater sensitivity of the herb layer to topsoil moisture may have been attributable to it having a higher proportion of fine root biomass in the upper 60 cm than that of the shrub and tree layers (Figures 1; Figure S1). On the other hand, different shrub species vary greatly in their ability to use deep soil water (Kowaljow & Fernández, 2011; Wu et al., 2014; Zhu et al., 2020) and species differences may mask the effects of substrate characteristics.

Within life-forms, the DW and DWP of the tree and herb layers were coordinated across 29 plots (Figure 6), suggesting a spatio-temporal coordination of deep soil water utilization for the tree and herb layers. However, the temporal and spatial variations in deep soil water utilization of the shrub layer were uncoupled (Figure 6). Combined with the results that the shrub layer had a greater magnitude and plasticity of deep water reliance than the tree layer, our results suggest that the shrub layer might contribute more to the spatio-temporal dynamics of deep soil water than the tree layer in pure plantations. The artificial plantation area of China (69.33 million ha), ranking first in the world, accounts for approximately one-third of global plantations and makes up one-third of the Chinese national forests (FAO, 2015; Yang et al., 2018). Additionally, coniferous plantations in subtropical China account for approximately 65% of all plantations in China (CSFB, 2019). Hence, our results highlight the importance of the shrub layer in driving the terrestrial hydrologic cycle of global plantations.

4.2 | Cascade effects among life-forms driven by deep root allocation and deep soil water utilization

From the perspective of biomass, the dominance hierarchy among life-forms in forest ecosystems should be the tree layer, shrub layer and herb layer. In forest ecosystems, negative cascade effects of

the overstorey on the biomass and structure of understorey vegetation have been well documented and the underlying mechanisms have been investigated from the standpoint of light competition and below-ground resource competition in shallow layers (Riegel et al., 1992; Sabo et al., 2009). For example, increased overstorey basal area, canopy cover and stand density result in lower understorey vegetation biomass (Ares et al., 2010; Sabo et al., 2008, 2009), due to the increased competition for light, space, nutrients and soil water in shallow layers (Ahmad et al., 2019; Anderson et al., 2001; Sigurdsson et al., 2005).

Although hydraulic lift by deep-rooted trees has been shown to favour the growth of understorey vegetation (Barron-Gafford et al., 2021; Muler et al., 2018; Yu & D'Odorico, 2015), our findings may be the first evidence that deep soil resource utilization of the plant community at higher dominance hierarchies is an important mechanism contributing to plant community structure at lower dominance hierarchies (Figures 4 and 5). First, we found that root distribution of a higher hierarchy community could affect the function of a lower hierarchy community. Specifically, increasing deep soil layer fine root biomass of trees was associated with increased DWP of shrubs, and increasing deep soil layer fine root biomass of shrubs was associated with increased DWP of herbs. This can be explained by the result that the roots of communities at lower hierarchies were relatively shallow (Figure 1), and part of their deep water resource utilization consisted of water taken up and redistributed by the deeper root systems of species at higher hierarchies. Also, the cascade effect of deep layer fine root biomass of higher hierarchy communities on the DWP of lower hierarchy communities will further affect their above-ground physiological traits. For example, the deep roots of trees affected the DWP of the shrub layer, further influencing the g_s and PNUE of the shrub layer (Figure 5).

Second, our results showed that the plots with higher tree layer DW had higher dominance in the shrub layer, and the plots with higher shrub layer DW had higher richness in the herb layer (Figures 7 and 8). This result implies that the DW of communities at higher hierarchy drives the changes in community structure at the lower hierarchy. Interestingly, DW of tree and shrub layers can affect their next lower hierarchy community in different directions. Higher DW of the tree layer was associated with decreased shrub layer diversity, however, higher DW of the shrub layer was associated with increased herb layer diversity. For the pure plantations, higher DW of the tree layer meant that the competition for water resources in the shallow soil layer was more intense and this would promote niche differentiation among life-forms (Dawson & Pate, 1996; Leffler & Caldwell, 2005; Liu et al., 2014). Therefore, trees increased deep root allocation (Jiang et al., 2018; Rolo & Moreno, 2012; Yang et al., 2017), increasing the competition for deep water resources. Our previous study at the same study site showed that common shrub species tended to have neither very high nor very low reliance on deep water in the dry season (Jiang, Wang, et al., 2020). Therefore, it is likely that more intense competition for shallow and deep water resources among the common species benefited the rare shrub species which either relied preferentially on shallow or deep water resources. Instead, higher DW of the shrub layer led to lower abundance of dominant shrubs. The scattered rare shrubs provided more space for the opportunistic herb species, thereby increasing the diversity of the herb layer.

5 | CONCLUSIONS

Our results advance our understanding of the roles of the understorey layer in driving spatio-temporal variations of deep soil water in forests and highlight the importance of deep soil water use patterns in community assembly processes. For pure pine plantations in a subtropical area with seasonal droughts, we showed that the understorey layer had a higher reliance on deep soil water in the dry season and a larger seasonal plasticity but lower spatial variability in deep soil water utilization than the tree layer, pointing to a more important role of the understorey layer than the overstorey layer in driving the temporal dynamics of ecosystem hydrology. Moreover, we found that deep soil water utilization of plant communities at higher hierarchy was an important mechanism contributing to changes in plant community structure at lower hierarchies. Importantly, higher deep water reliance of the tree layer was associated with decreased shrub layer diversity. Therefore, we hypothesize that regions with modest droughts (e.g. our study region) that reduce the shallow soil water pools may increase the deep soil water utilization of trees thereby decreasing shrub diversity.

AUTHOR CONTRIBUTIONS

Xiaoli Fu and Peipei Jiang planned and designed the research; Peipei Jiang and Yifan Chen conducted field work and performed the experiments; Peipei Jiang, Frederick C. Meinzer, and Xiaoli Fu analysed the data and wrote the paper; Peipei Jiang, Frederick C. Meinzer, Xiaoli Fu, Huimin Wang, Xiaoqin Dai, Shengwang Meng, Liang Kou, and Yifan Chen made the manuscript revisions.

ACKNOWLEDGEMENT

This work was funded by the National Natural Science Foundations of China (31730014, 32122060 and 32201520).

CONFLICT OF INTEREST

None of the authors have a conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14007.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.3n5tb2rmf (Jiang et al., 2022).

ORCID

Peipei Jiang https://orcid.org/0000-0002-5597-9493
Frederick C. Meinzer https://orcid.org/0000-0003-2387-2031
Liang Kou https://orcid.org/0000-0002-2187-0721
Xiaoli Fu https://orcid.org/0000-0001-9116-4745

REFERENCES

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., et al. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, *1*(9), 1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Ahmad, B., Wang, Y., Hao, J., Liu, Y., Bohnett, E., & Zhang, K. (2019). Optimizing stand structure for tradeoffs between overstory and understory vegetation biomass in a larch plantation of Liupan Mountains, Northwest China. *Forest Ecology and Management*, *443*, 43–50. https://doi.org/10.1016/j.foreco.2019.04.001

Anderson, L. J., Brumbaugh, M. S., & Jackson, R. B. (2001). Water and tree–understory interactions: A natural experiment in a savanna with oak wilt. *Ecology*, *82*(1), 33–49. https://doi.org/10.1890/0012-9658(2001)082[0033:WATUIA]2.0.CO;2

Ares, A., Neill, A. R., & Puettmann, K. J. (2010). Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. *Forest Ecology and Management*, *260*(7), 1104–1113. https://doi.org/10.1016/j.foreco.2010.06.023

Asbjornsen, H., Shepherd, G., Helmers, M., & Mora, G. (2008). Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern US. *Plant and Soil*, *308*(1–2), 69–92. https://doi.org/10.1007/s11104-008-9607-3

Barnard, R. L., Bello, F. D., Gilgen, A. K., & Buchmann, N. (2006). The $\delta^{18}O$ of root crown water best reflects source water $\delta^{18}O$ in different types of herbaceous species. *Rapid Communications in Mass Spectrometry*, *20*, 3799–3802. https://doi.org/10.1002/rcm.2778

Barron-Gafford, G. A., Knowles, J. F., Sanchez-Cañete, E. P., Minor, R. L., Lee, E., Sutter, L., Tran, N., Murphy, P., Hamerlynck, E. P., Kumar, P., & Scott, R. L. (2021). Hydraulic redistribution buffers climate variability and regulates grass-tree interactions in a semiarid riparian savanna. *Ecohydrology*, *14*(3), e2271. https://doi.org/10.1002/eco.2271

Barron-Gafford, G. A., Sanchez-Canete, E. P., Minor, R. L., Hendryx, S. M., Lee, E., Sutter, L. F., … Scott, R. L. (2017). Impacts of hydraulic redistribution on grass-tree competition vs facilitation in a semi-arid savanna. *New Phytologist*, *215*(4), 1451–1461. https://doi.org/10.1111/nph.14693

Bendevis, M. A., Owens, M. K., Heilman, J. L., & McInnes, K. J. (2010). Carbon exchange and water loss from two evergreen trees in a semiarid woodland. *Ecohydrology*, *3*(1), 107–115. https://doi.org/10.1002/eco.100

Bengtsson, J., Nilsson, S. G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, *132*(1), 39–50. https://doi.org/10.1016/S0378-1127(00)00378-9

Brooks, J. R., Meinzer, F. C., Coulombe, R., & Gregg, J. (2002). Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology*, *22*(15-16), 1107–1117. https://doi.org/10.1093/treephys/22.15-16.1107

Brooks, J. R., Meinzer, F. C., Warren, J. M., Domec, J.-C., & Coulombe, R. (2006). Hydraulic redistribution in a Douglas-fir forest: Lessons from system manipulations. *Plant, Cell & Environment*, *29*(1), 138–150. https://doi.org/10.1111/j.1365-3040.2005.01409.x

Brum, M., Vadeboncoeur, M. A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L. F., Penha, D., Dias, J. D., Aragao, L. E. O. C., Barros, F., et al. (2019). Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology*, *107*(1), 318–333. https://doi.org/10.1111/1365-2745.13022

Cai, G., Vanderborght, J., Langensiepen, M., Schnepf, A., Hüging, H., & Vereecken, H. (2018). Root growth, water uptake, and sap flow of winter wheat in response to different soil water conditions. *Hydrology and Earth System Science*, *22*(4), 2449–2470. https://doi.org/10.5194/hess-22-2449-2018

Cao, R., Jia, X., Huang, L., Zhu, Y., Wu, L., & Shao, M. (2018). Deep soil water storage varies with vegetation type and rainfall amount in the Loess Plateau of China. *Scientific Reports*, *8*, 12346. https://doi.org/10.1038/s41598-018-30850-7

Carneiro, M., Fabião, A., Martins, M. C., Cerveira, C., Santos, C., Nogueira, C., Lousã, M., Hilário, L., Fabião, A., Abrantes, M., & Madeira, M. (2007). Species richness and biomass of understory vegetation in a *Eucalyptus globulus* Labill. Coppice as affected by slash management. *European Journal of Forest Research*, *126*(4), 475–480. https://doi.org/10.1007/s10342-006-0143-5

Carrière, S. D., Ruffault, J., Cakpo, C. B., Olioso, A., Doussan, C., Simioni, G., Chalikakis, K., Patris, N., Davi, H., & MartinSt-Paul, N. K. (2020). Intra-specific variability in deep water extraction between trees growing on a Mediterranean karst. *Journal of Hydrology*, *590*, 125428. https://doi.org/10.1016/j.jhydrol.2020.125428

Chen, N., Song, C., Xu, X., Wang, X., Cong, N., Jiang, P., Zu, J., Sun, L., Song, Y., Zuo, Y., Liu, J., Zhang, T., Xu, M., Jiang, P., Wang, Z., & Huang, K. (2021). Divergent impacts of atmospheric water demand on gross primary productivity in three typical ecosystems in China. *Agricultural and Forest Meteorology*, *307*, 108527. https://doi.org/10.1016/j.agrformet.2021.108527

Chen, N., Zhang, Y., Zhu, J., Zu, J., Huang, K., Li, J., Liu, Y., Cong, N., Tang, Z., Wang, L., & Zhu, X. (2019). Temperature-mediated responses of carbon fluxes to precipitation variabilities in an alpine meadow ecosystem on the Tibetan Plateau. *Ecology and Evolution*, *9*(16), 9005–9017. https://doi.org/10.1002/ece3.5439

Chitra-Tarak, R., Ruiz, L., Dattaraja, H. S., Kumar, M. S. M., Riotte, J., Suresh, H. S., McMahon, S. M., & Sukumar, R. (2018). The roots of the drought: Hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology*, *106*(4), 1495–1507. https://doi.org/10.1111/1365-2745.12925

Chitra-Tarak, R., Xu, C., Aguilar, S., Anderson-Teixeira, K. J., Chambers, J., Detto, M., Faybishenko, B., Fisher, R. A., Knox, R. G., Koven, C. D., Kueppers, L. M., Kunert, N., Kupers, S. J., McDowell, N. G., Newman, B. D., Paton, S. R., Pérez, R., Ruiz, L., & Sack, L., McMahon, S. M. (2021). Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist*, *231*(5), 1798–1813. https://doi.org/10.1111/nph.17464

CSFB. (2019). *Results of the ninth national forestry resource statistics for China*. The People's Republic of China State Forestry Bureau. (In Chinese).

Dawson, T. E., & Pate, J. S. (1996). Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: A stable isotope investigation. *Oecologia*, *107*(1), 13–20. https://doi.org/10.1007/BF00582230

Diochon, A., Kellman, L., & Beltrami, H. (2009). Looking deeper: An investigation of soil carbon losses following harvesting from a managed northeastern red spruce (*Picea rubens* Sarg.) forest chronosequence. *Forest Ecology and Management*, *257*(2), 413–420. https://doi.org/10.1016/j.foreco.2008.09.015

Eggemeyer, K. D., Awada, T., Harvey, F. E., Wedin, D. A., Zhou, X. H., & Zanner, C. W. (2009). Seasonal changes in depth of water uptake

for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C_4 grasses in a semiarid grassland. *Tree Physiology*, *29*(2), 157–169. https://doi.org/10.1093/treephys/tpn019

Ehleringer, J. R., & Dawson, T. E. (1992). Water uptake by plants: Perspectives from stable isotope composition. *Plant, Cell & Environment*, *15*(9), 1073–1082. https://doi.org/10.1111/j.1365-3040.1992.tb01657.x

FAO. (2015). *Global forest resources assessment 2015*. FAO forestry paper, 163, Rome.

Field, C., & Mooney, H. A. (1986). The photosynthesis-nitrogen relationships in wild plants. In T. J. Givnish (Ed.), *On the economy of plant form and function* (pp. 25–55). Cambridge University Press.

Fu, Z., Wang, Y., An, Z., Hu, W., Mostofa, K. M. G., Li, X., & Liu, B. (2018). Spatial and temporal variability of 0- to 5-m soil–water storage at the watershed scale. *Hydrological Processes*, *32*(16), 2557–2569. https://doi.org/10.1002/hyp.13172

Fujii, S., Kubota, Y., & Enoki, T. (2009). Resilience of stand structure and tree species diversity in subtropical forest degraded by clear logging. *Journal of Forest Research*, *14*(6), 373–387. https://doi.org/10.1007/s10310-009-0151-7

Goldstein, G., Meinzer, F. C., Bucci, S. J., Scholz, F. G., Franco, A. C., & Hoffmann, W. A. (2008). Water economy of Neotropical savanna trees: Six paradigms revisited. *Tree Physiology*, *28*(3), 395–404. https://doi.org/10.1093/treephys/28.3.395

Hao, X.-M., Chen, Y.-N., Guo, B., & Ma, J.-X. (2013). Hydraulic redistribution of soil water in *Populus euphratica* Oliv. in a central Asian desert riparian forest. *Ecohydrology*, *6*(6), 974–983. https://doi.org/10.1002/eco.1338

Hasselquist, N. J., Allen, M. F., & Santiago, L. S. (2010). Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia*, *164*(4), 881–890. https://doi.org/10.1007/s00442-010-1725-y

Hikosaka, K., & Shigeno, A. (2009). The role of Rubisco and cell walls in the interspecific variation in photosynthetic capacity. *Oecologia*, *160*(3), 443–451. https://doi.org/10.1007/s00442-009-1315-z

Jackson, P. C., Meinzer, F. C., Bustamante, M., Goldstein, G., Franco, A., Runde, P. W., & Caldas, L. (1999). Partitioning of soil among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology*, *19*(11), 717–724. https://doi.org/10.1093/treephys/19.11.717

Jia, Y., & Shao, M. (2014). Dynamics of deep soil moisture in response to vegetational restoration on the Loess Plateau of China. *Journal of Hydrology*, *519*, 523–531. https://doi.org/10.1016/j.jhydrol.2014.07.043

Jiang, P., Meinzer, F. C., Wang, H., Dai, X., Meng, S., Kou, L., Chen, Y., & Fu, X. (2022). Spatio-temporal variation in deep soil water use patterns of overstorey and understorey layers in subtropical plantations predicts community assembly. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.3n5tb2rmf

Jiang, P., Meinzer, F. C., Wang, H., Kou, L., Dai, X., & Fu, X. (2020). Belowground determinants and ecological implications of shrub species' degree of isohydry in subtropical pine plantations. *New Phytologist*, *226*(6), 1656–1666. https://doi.org/10.1111/nph.16502

Jiang, P., Wang, H., Fu, X., Dai, X., Kou, L., & Wang, J. (2018). Elaborate differences between trees and understory plants in the deployment of fine roots. *Plant and Soil*, *431*(1-2), 433–447. https://doi.org/10.1007/s11104-018-3778-3

Jiang, P., Wang, H., Meinzer, F. C., Kou, L., Dai, X., & Fu, X. (2020). Linking reliance on deep soil water to resource economy strategies and abundance among coexisting understorey shrub species in subtropical pine plantations. *New Phytologist*, *225*(1), 222–233. https://doi.org/10.1111/nph.16027

Kim, J. B., So, J. M., & Bae, D. H. (2021). Global warming impacts on severe drought characteristics in Asia monsoon region. *Water*, *12*(5), 1360. https://doi.org/10.3390/w12051360

Klein, T., Shpringer, I., Fikler, B., Elbaz, G., Cohen, S., & Yakir, D. (2013). Relationships between stomatal regulation, water-use, and water-use efficiency of two coexisting key Mediterranean tree species. *Forest Ecology and Management*, *302*, 34–42. https://doi.org/10.1016/j.foreco.2013.03.044

Kong, F., Yu, R., Xu, Z., & Zhou, M. (2012). Application of excel in calculation of biodiversity indices. *Marine Sciences*, *36*, 57–62 (In Chinese with English abstract).

Korboulewsky, N., Tétégan, M., Samouelian, A., & Cousin, I. (2020). Plants use water in the pores of rock fragments during drought. *Plant and Soil*, *454*(1-2), 35–47. https://doi.org/10.1007/s11104-020-04425-3

Kou, L., Jiang, L., Fu, X., Dai, X., Wang, H., & Li, S. (2018). Nitrogen deposition increases root production and turnover but slows root decomposition in *Pinus elliottii* plantations. *New Phytologist*, *218*(4), 1450–1461. https://doi.org/10.1111/nph.15066

Kowaljow, E., & Fernández, R. J. (2011). Differential utilization of a shallow-water pulse by six shrub species in the Patagonian steppe. *Journal of Arid Environment*, *75*(2), 211–214. https://doi.org/10.1016/j.jaridenv.2010.10.004

Kulmatiski, A., Beard, K. H., Verweij, R. J. T., & February, E. C. (2010). A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytologist*, *188*(1), 199–209. https://doi.org/10.1111/j.1469-8137.2010.03338.x

Le Roux, X., Bariac, T., & Mariotti, A. (1995). Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia*, *104*(2), 147–155. https://doi.org/10.1007/BF00328579

Lee, J. E., Oliveira, R. S., Dawson, T. E., & Fung, I. (2005). Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(49), 17576–17581. https://doi.org/10.1073/pnas.0508785102

Leffler, A. J., & Caldwell, M. M. (2005). Shifts in depth of water extraction and photosynthetic capacity inferred from stable isotope proxies across an ecotone of *Juniperus osteosperma* (Utah juniper) and *Artemisia tridentata* (big sagebrush). *Journal of Ecology*, *93*(4), 783–793. https://doi.org/10.1111/j.1365-2745.2005.01014.x

Li, B., Zhang, W., Li, S., Wang, J., Liu, G., & Xu, M. (2021). Severe depletion of available deep soil water induced by revegetation on the arid and semiarid Loess Plateau. *Forest Ecology and Management*, *491*, 119156. https://doi.org/10.1016/j.foreco.2021.119156

Limousin, J.-M., Yepez, E. A., McDowell, N. G., & Pockman, W. T. (2015). Convergence in resource use efficiency across trees with differing hydraulic strategies in response to ecosystem precipitation manipulation. *Functional Ecology*, *29*(9), 1125–1136. https://doi.org/10.1111/1365-2435.12426

Liu, L., Gudmundsson, L., Hauser, M., Qin, D. H., Li, S. C., & Seneviratne, S. I. (2020). Soil moisture dominates dryness stress on ecosystem production globally. *Nature Communication*, *11*(1), 4892. https://doi.org/10.1038/s41467-020-18631-1

Liu, W., Li, P., Duan, W., & Liu, W. (2014). Dry-season water utilization by trees growing on thin karst soils in a seasonal tropical rainforest of Xishuangbanna, Southwest China. *Ecohydrology*, *7*(3), 927–935. https://doi.org/10.1002/eco.1419

Liu, W., Liu, W., Li, P., Duan, W., & Li, H. (2010). Dry season water uptake by two dominant canopy tree species in a tropical seasonal rainforest of Xishuangbanna, SW China. *Agricultural and Forest Meteorology*, *150*(3), 380–388. https://doi.org/10.1016/j.agrformet.2009.12.006

Markewitz, D., Devine, S., Davidson, E. A., Brando, P., & Nepstad, D. C. (2010). Soil moisture depletion under simulated drought in the Amazon: Impacts on deep root uptake. *New Phytologist*, *187*(3), 592–607. https://doi.org/10.1111/j.1469-8137.2010.03391.x

Martínez-Vilalta, J., & García-Forner, N. (2017). Water potential regulation, stomatal behaviour and hydraulic transport under

drought: Deconstructing the iso/anisohydric concept. *Plant, Cell & Environment*, *40*(6), 962–976. https://doi.org/10.1111/pce.12846

Maseyk, K. S., Lin, T., Rotenberg, E., Grunzweig, J. M., Schwartz, A., & Yakir, D. (2010). Physiology-phenology interactions in a productive semi-arid pine forest. *New Phytologist*, *178*(3), 603–616. https://doi.org/10.1111/j.1469-8137.2008.02391.x

McCole, A. A., & Stern, L. A. (2007). Seasonal water use patterns of *Juniperus ashei* on the Edwards Plateau, Texas, based on stable isotopes in water. *Journal of Hydrology*, *342*(3-4), 238–248. https://doi.org/10.1016/j.jhydrol.2007.05.024

McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*, *26*(10), 523–532. https://doi.org/10.1016/j.tree.2011.06.003

McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, *23*(8), 2941–2961. https://doi.org/10.1111/gcb.13629

Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, M. N., Cavelier, J., & Wright, S. J. (1999). Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia*, *121*(3), 293–301. https://doi.org/10.1007/s004420050931

Meinzer, F. C., James, S. A., & Goldstein, G. (2004). Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. *Tree Physiology*, *24*(8), 901–909. https://doi.org/10.1093/treephys/24.8.901

Midgley, G. F., Aranibar, J. N., Mantlana, K. B., & Macko, S. (2004). Photosynthetic and gas exchange characteristics of dominant woody plants on a moisture gradient in an African savanna. *Global Change Biology*, *10*(3), 309–317. https://doi.org/10.1111/j.1365-2486.2003.00696.x

Miller, J. M., Williams, R. J., & Farquhar, G. D. (2001). Carbon isotope discrimination by a sequence of Eucalyptus species along a subcontinental rainfall gradient in Australia. *Functional Ecology*, *15*(2), 222–232. https://doi.org/10.1046/j.1365-2435.2001.00508.x

Montenegro, S., & Ragab, R. (2012). Impact of possible climate and land use changes in the semi arid regions: A case study from North Eastern Brazil. *Journal of Hydrology*, *434*, 55–68. https://doi.org/10.1016/j.jhydrol.2012.02.036

Muler, A. L., van Etten, E. J. B., Stock, W. D., Howard, K., & Froend, R. H. (2018). Can hydraulically redistributed water assist surrounding seedlings during summer drought? *Oecologia*, *187*(3), 625–641. https://doi.org/10.1007/s00442-018-4158-7

Nie, Y. P., Chen, H. S., Wang, K. L., & Ding, Y. L. (2014). Seasonal variations in leaf $\delta^{13}C$ values: Implications for different water-use strategies among species growing on continuous dolomite outcrops in subtropical China. *Acta Physiologiae Plantarum*, *36*(10), 2571–2579. https://doi.org/10.1007/s11738-014-1628-3

Nie, Y. P., Chen, H. S., Wang, K. L., Tan, W., Deng, P. Y., & Yang, J. (2011). Seasonal water use patterns of woody species growing on the continuous dolostone outcrops and nearby thin soils in subtropical China. *Plant and Soil*, *341*(1–2), 399–412. https://doi.org/10.1007/s11104-010-0653-2

Nilsson, M. C., & Wardle, D. A. (2005). Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, *3*(8), 421–428. https://doi.org/10.2307/3868658

Oliva Carrasco, L., Bucci, S. J., Di Francescantonio, D., Lezcano, O. A., Campanello, P. I., Scholz, F. G., et al. (2015). Water storage dynamics in the main stem of subtropical tree species differing in wood density, growth rate and life history traits. *Tree Physiology*, *35*(4), 354–365. https://doi.org/10.1093/treephys/tpu087

Pederson, N., Dyer, J. M., McEwan, R. W., Hessl, A. E., Mock, C. J., Orwig, D. A., Rieder, H. E., & Cook, B. I. (2014). The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*, *84*(4), 599–620. https://doi.org/10.1890/13-1025.1

Phillips, D. L., & Gregg, J. W. (2003). Source partitioning using stable isotopes: Coping with too many sources. *Oecologia*, *136*(2), 261–269. https://doi.org/10.1007/s00442-003-1218-3

Phillips, D. L., Newsome, S. D., & Gregg, J. W. (2005). Combining sources in stable isotope mixing models: Alternative methods. *Oecologia*, *144*(4), 520–527. https://doi.org/10.1007/s00442-004-1816-8

Phillips, N., Ryan, M. G., Bond, B. J., McDowell, N. G., Hinckley, T. M., & Cermak, J. (2003). Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology*, *23*(4), 237–245. https://doi.org/10.1093/treephys/23.4.237

Prieto, I., Padilla, F. M., Armas, C., & Pugnaire, F. I. (2011). The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology Evolution and Systematics*, *13*(3), 181–187. https://doi.org/10.1016/j.ppees.2011.05.002

Querejeta, J. I., Estrada-Medina, H., Allen, M. F., & Jimenez-Osornio, J. J. (2007). Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia*, *152*(1), 26–36. https://doi.org/10.1007/s00442-006-0629-3

Riegel, G. M., Miller, R. F., & Krueger, W. C. (1992). Competition for resources between understory vegetation and overstory *Pinus ponderosa* in Northeastern Oregon. *Ecological Applications*, *2*(1), 71–85. https://doi.org/10.2307/1941890

Ripullone, F., Camarero, J. J., Colangelo, M., & Voltas, J. (2020). Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of Mediterranean oaks. *Tree Physiology*, *40*(5), 591–604. https://doi.org/10.1093/treephys/tpaa026

Rolo, V., & Moreno, G. (2012). Interspecific competition induces asymmetrical rooting profile adjustments in shrub-encroached open oak woodlands. *Trees-Structure and Function*, *26*(3), 997–1006. https://doi.org/10.1007/s00468-012-0677-8

Sabo, K., Hart, S., Sieg, C., & Bailey, J. (2008). Tradeoffs in overstory and understory aboveground net primary productivity in southwestern ponderosa pine stands. *Forest Science*, *54*(4), 408–416. https://doi.org/10.1016/j.forpol.2008.02.002

Sabo, K. E., Sieg, C. H., Hart, S. C., & Bailey, J. D. (2009). The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. *Forest Ecology and Management*, *257*(8), 1656–1662. https://doi.org/10.1016/j.foreco.2009.01.006

Scholz, F. G., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., & Miralles-Wilhelm, F. (2007). Biophysical properties and functional significance of stem water storage tissues in neotropical savanna trees. *Plant, Cell & Environment*, *30*(2), 236–248. https://doi.org/10.1111/j.1365-3040.2006.01623.x

Schwinning, S. (2008). The water relations of two evergreen tree species in a karst savanna. *Oecologia*, *158*(3), 373–383. https://doi.org/10.1007/s00442-008-1147-2

Sheffield, J., Wood, E. F., & Roderick, M. L. (2012). Little change in global drought over the past 60 years. *Nature*, *491*(7424), 435–438. https://doi.org/10.1038/nature11575

Sigurdsson, B. D., Magnusson, B., Elmarsdottir, A., & Bjarnadottir, B. (2005). Biomass and composition of understory vegetation and the forest floor carbon stock across Siberian larch and mountain birch chronosequences in Iceland. *Annuals of Forest Science*, *62*(8), 881–888. https://doi.org/10.1051/forest:2005079

Stratton, L. C., Goldstein, G., & Meinzer, F. C. (2000). Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia*, *124*(3), 309–317. https://doi.org/10.1007/s004420000384

Tetegan, M., Korboulewsky, N., Bouthier, A., Samouëlian, A., & Cousin, I. (2015). The role of pebbles in the water dynamics of a stony soil

cultivated with young poplars. *Plant and Soil*, *391*(1–2), 307–320. https://doi.org/10.1007/s11104-015-2429-1

Thomas, A., Yadav, B. K., & Šimůnek, J. (2020). Root water uptake under heterogeneous soil moisture conditions: An experimental study for unraveling compensatory root water uptake and hydraulic redistribution. *Plant and Soil*, *457*(1-2), 421–435. https://doi.org/10.1007/s11104-020-04738-3

Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, *4*(1), 17–22. https://doi.org/10.1038/nclimate2067

Valentini, R., Scarascia Mugnozza, G. E., & Ehleringer, J. R. (1992). Hydrogen and carbon isotope ratios in selected species of a Mediterranean macchia ecosystem. *Functional Ecology*, *6*(6), 627–631. https://doi.org/10.2307/2389955

Wallrup, E., Saetre, P., & Rydin, H. (2006). Deciduous trees affect small-scale floristic diversity and tree regeneration in conifer forests. *Scandinavian Journal of Forest Research*, *21*(5), 399–404. https://doi.org/10.1080/02827580600917387

Wang, P., Huang, K., & Hu, S. (2020). Distinct fine-root responses to precipitation changes in herbaceous and woody plants: A meta-analysis. *New Phytologist*, *225*(4), 1491–1499. https://doi.org/10.1111/nph.16266

Wang, S., An, J., Zhao, X., Gao, X., Wu, P., Huo, G., & Robinson, B. H. (2020). Age- and climate- related water use patterns of apple trees on China's Loess Plateau. *Journal of Hydrology*, *582*, 124462. https://doi.org/10.1016/j.jhydrol.2019.124462

Wang, Y., Hu, W., Zhu, Y. J., Shao, M., Xiao, S., & Zhang, C. (2015). Vertical distribution and temporal stability of soil water in 21-m profiles under different land uses on the Loess Plateau in China. *Journal of Hydrology*, *527*, 543–554. https://doi.org/10.1016/j.jhydrol.2015.05.010

Ward, D., Wiegand, K., & Getzin, S. (2013). Walter's two-layer hypothesis revisited: Back to the roots! *Oecologia*, *172*(3), 617–630. https://doi.org/10.1007/s00442-012-2538-y

Warren, C. R., & Adams, M. A. (2004). What determines rates of photosynthesis per unit nitrogen in Eucalyptus seedlings? *Functional Plant Biology*, *31*(12), 1169–1178. https://doi.org/10.1071/FP04115

Wen, X., Lee, X., Sun, X., Wang, J., Hu, Z., Li, S., & Yu, G. (2012). Dew water isotopic ratios and their relationships to ecosystem water pools and fluxes in a cropland and a grassland in China. *Oecologia*, *168*(2), 549–561. https://doi.org/10.1007/s00442-011-2091-0

Wu, Y., Zhou, H., Zheng, X.-J., Li, Y., & Tang, L. S. (2014). Seasonal changes in the water use strategies of three co-occurring desert shrubs. *Hydrology Processes*, *28*(26), 6265–6275. https://doi.org/10.1002/hyp.10114

Wu, Z., Behzad, H. M., He, Q., Wu, C., Bai, Y., & Jiang, Y. (2021). Seasonal transpiration dynamics of evergreen *Ligustrum lucidum* linked with water source and water-use strategy in a limestone karst area, southwest China. *Journal of Hydrology*, *597*, 126199. https://doi.org/10.1016/j.jhydrol.2021.126199

Xu, Q., Li, H., Chen, J. Q., Cheng, X. L., Liu, S. R., & An, S. Q. (2011). Water use patterns of three species in subalpine forest, Southwest China: the deuterium isotope approach. *Ecohydrology*, *4*(2), 236–244. https://doi.org/10.1002/eco.179

Yang, B., Wen, X., & Sun, X. (2015). Seasonal variations in depth of water uptake for a subtropical coniferous plantation subjected to drought in an East Asian monsoon region. *Agricultural and Forest Meteorology*, *201*, 218–228. https://doi.org/10.1016/j.agrformet.2014.11.020

Yang, F., Feng, Z., Wang, H., Dai, X., & Fu, X. (2017). Deep soil water extraction helps to drought avoidance but shallow soil water uptake during dry season controls the inter-annual variation in tree growth in four subtropical plantations. *Agricultural and Forest Meteorology*, *234*, 106–114. https://doi.org/10.1016/j.agrformet.2016.12.020

Yang, Y., Wang, L., Yang, Z., Xu, C., Xie, J., Chen, G., Lin, C., Guo, J., Liu, X., Xiong, D., Lin, W., Chen, S., He, Z., Lin, K., Jiang, M., & Lin, T. C. (2018). Large ecosystem service benefits of assisted natural regeneration. *Journal of Geophysical Research-Biogeosciences*, *123*(2), 676–687. https://doi.org/10.1002/2017JG004267

Yu, K. L., & D'Odorico, P. (2015). Hydraulic lift as a determinant of tree-grass coexistence on savannas. *New Phytologist*, *207*(4), 1038–1051. https://doi.org/10.1111/nph.13431

Zhang, T., Xu, M. J., Zhang, Y. J., Zhao, T. H., An, T. T., Li, Y. G., Sun, Y., Chen, N., Zhao, T. T., Zhu, J. T., & Yu, G. R. (2019). Grazing-induced increases in soil moisture maintain higher productivity during droughts in alpine meadows on the Tibetan Plateau. *Agricultural and Forest Meteorology*, *269*, 249–256. https://doi.org/10.1016/j.agrformet.2019.02.022

Zhu, Y.-J., Wang, G.-J., & Xin, Z.-M. (2020). Water use strategy of *Ammopiptanthus mongolicus* community in a drought year on the Mongolian Plateau. *Journal of Plant Ecology*, *13*(6), 793–800. https://doi.org/10.1093/jpe/rtaa064

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Jiang, P., Meinzer, F. C., Wang, H., Dai, X., Meng, S., Kou, L., Chen, Y., & Fu, X. (2022). Spatio-temporal variation in deep soil water use patterns of overstorey and understorey layers in subtropical plantations predicts community assembly. *Journal of Ecology*, *110*, 2998–3011. https://doi.org/10.1111/1365-2745.14007