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Disentangling the Effects of Tree and Soil Properties on the Water Uptake of a Waterlogging Tolerant Tree in the Yangtze River Delta, China

Beibei Zhang [1], Jing Jiang [2], Qing Xu [1,*], Deqiang Gao [1], Haijun Zuo [1] and Ranran Ren [1]

1 Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China; zhangbb@caf.ac.cn (B.Z.); gaodeqiang@caf.ac.cn (D.G.); zuohaijun2003@163.com (H.Z.); xiaoran2822@163.com (R.R.)

2 Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; jing007@student.ubc.ca

* Correspondence: xuqing@caf.ac.cn; Tel.: +86-10-6288-9549

Abstract: Waterlogging tolerant tree species exert a critical role in forest preservation and the associated water conservation in flood prone areas. Clarifying the patterns and drivers of water uptake by waterlogging tolerant trees is crucial for forest management in flood-prone areas, especially in the scenario of precipitation changes in the estuary delta. Here, we uploaded the values of δD and δ^{18}O obtained from soil and xylem waters to a Bayesian mixed model (MixSIAR) to determine the water use pattern of *Taxodium distichum*, a waterlogging tolerant tree, following different magnitudes of rainfall events in three sites of the Yangtze River Delta, China. We further conducted variation partitioning analysis and a random forest model to discern the dominant factor driving plant water uptake. Our results indicated that *T. distichum* mainly absorbed soil water from shallow soil layers (0–40 cm, 43.63%–74.70%), while the percentage of water uptake from deep soil layers was lower in the Yangtze River Delta (60–100 cm, 13.43%–35.90%), whether in light, moderate, or heavy rainfall conditions. Furthermore, our results demonstrated that tree traits, such as fine root biomass, are dominantly driving plant water uptake. These findings imply that waterlogging tolerant tree species could increase the percentage of water uptake from shallow soils by changing their plant attributes, which would effectively improve the water conservation of forests in the estuary delta.

Keywords: soil properties; stable isotope; tree traits; water uptake; Yangtze River Delta

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1. Introduction

Changes in global precipitation increase the frequency and intensity of extreme precipitation in humid areas, subsequently leading to frequent floods [1–3]. Floods induced by extreme precipitation expose trees to waterlogging stress, and cause root hypoxia and inhibit plant respiration, ultimately increasing the tree mortality [4–6]. This phenomenon is particularly universal in the river basins and estuarine deltas of tropical/subtropical areas [7–9]. In order to alleviate the large-scale tree death caused by frequent floods, tree species owning waterlogging resistance have been cultivated in some estuarine deltas in recent years. Under the excessive soil moisture condition, waterlogging resistance trees could transport the oxygen to the root system and rhizosphere soils to ensure plant water absorption through changing their morphology, such as the formation of adventitious root, aerial root, or aerenchyma [10]. Therefore, trees with waterlogging resistance could optimize plant water uptake by adjusting root distribution, finally adapting to waterlogging stress. Collectively, knowledge on water use pattern of waterlogging tolerant tree species is thus of importance for forest management in flood-prone areas.

However, our understanding on the water uptake of waterlogging tolerant trees is still limited by the following two aspects. First, previous studies primarily concentrated on the water use pattern of waterlogging tolerant trees in coastal delta hummocks, while ignored that in the alluvial plain of the estuary delta. It has been reported that, *Taxodium distichum* and *Pterocarpus officinalis* in coastal forest hummocks mainly absorbed the water accessed from unsaturated soil in the hummock top [11,12]. Nevertheless, this phenomenon might not occur in waterlogging tolerant trees in the alluvial plain of the estuarine delta. Given the influences of salinity and tide, the water consumption of trees in coastal delta hummocks is lower [13], while trees in estuarine deltas are less affected by these above factors. Therefore, the tree water use patterns in estuarine deltas could then differ from those observed in coastal delta hummocks. More importantly, compared with coastal delta hummocks, the alluvial plain of estuarine delta has a flatter terrain and poorer drainage capacity, and therefore trees in the alluvial plain are more vulnerable to waterlogging stress. Based on such reasons, their water use patterns may also be different from those observed in hummocks. Especially in the scenario of changing precipitation, frequent occurrence of extreme precipitation may aggravate waterlogging stress in the estuarine alluvial plain. Taken together, it is necessary to study the water use patterns of waterlogging tolerant trees in the alluvial plain of the estuarine delta under different magnitudes of precipitation.

Second, it remains unclear which factor mainly affects the water absorption of waterlogging tolerant trees in the alluvial plain of the estuary delta. Generally, tree traits and soil properties are considered as two main factors influencing water use patterns of trees [14–16]. It has been reported that, the larger the fine root biomass distributed in a soil layer, the greater the water absorption from the soil layer by trees [17,18]. Besides the fine roots, both leaf biomass and diameter at breast height of trees could also affect the plant water absorption by regulating the transpiration [19,20]. Moreover, soil properties also exert a critical role in driving tree water uptake. Previous studies have illustrated that the soil with smaller bulk density and larger field water capacity could store more water [21,22], and subsequently enhance the tree water uptake. Distinguished from common trees, the water uptake of waterlogging tolerant trees is also influenced by soil aeration since the soil with better aeration is conducive to root respiration that could stimulate plant water absorption [23,24]. Nevertheless, the relative contributions of the above factors to water uptake patterns of waterlogging tolerant trees remain unknown, largely due to the lack of comprehensive studies at a regional scale.

To address these issues, we selected three *T. distichum* plantations in the Yangtze River Delta, China. Then we employed stable hydrogen and oxygen isotopes (δD and δ^{18}O) coupled with the Bayesian mixed model (MixSIAR) to explore the water use patterns of *T. distichum* [25,26]. Furthermore, we examined both tree traits and soil properties in each plantation, and explored which factor dominantly drives the *T. distichum* water uptake. This study primarily tests the following two hypotheses: (i) The water use patterns of *T. distichum* were different following light, moderate, and heavy rainfall events. (ii) Compared with soil properties, tree traits are the dominant factor affecting the *T. distichum* water absorption.

2. Materials and Methods

2.1. Study Site

Three study sites, such as Chizhou in Anhui Province (CZ, 117°2′33″ E, 30°8′4″ N), Gaoyou in Jiangsu Province (GY, 119°27′34″ E, 32°53′21″ N) and Shaoxing in Zhejiang Province (SX, 120°40′20″ E, 29°47′32″ N), were selected in the Yangtze River Delta (Figure 1). The mean average temperature in the three study sites is 16.5, 15, and 16.5 °C, and the mean average precipitation is 1800, 1030, and 1400 mm, respectively. In the *T. distichum* plantation of the CZ site, the soil type is sandy loam, and the understory vegetation mainly includes *Camellia oleifera*, *Rubus parvifolius*, *Oenanthe javanica*, and *Cyclosorus acuminatus*. In the GY site, the soil belongs to sandy loam, and the understory chiefly consists of *Bromus japonicus*, *Duchesnea indica*, and *Geranium wilfordii*. In the SX site, the soil type is regarded as red-yellow soil, and the understory vegetation is composed of *Poa annua* and *Zoysia japonica*.

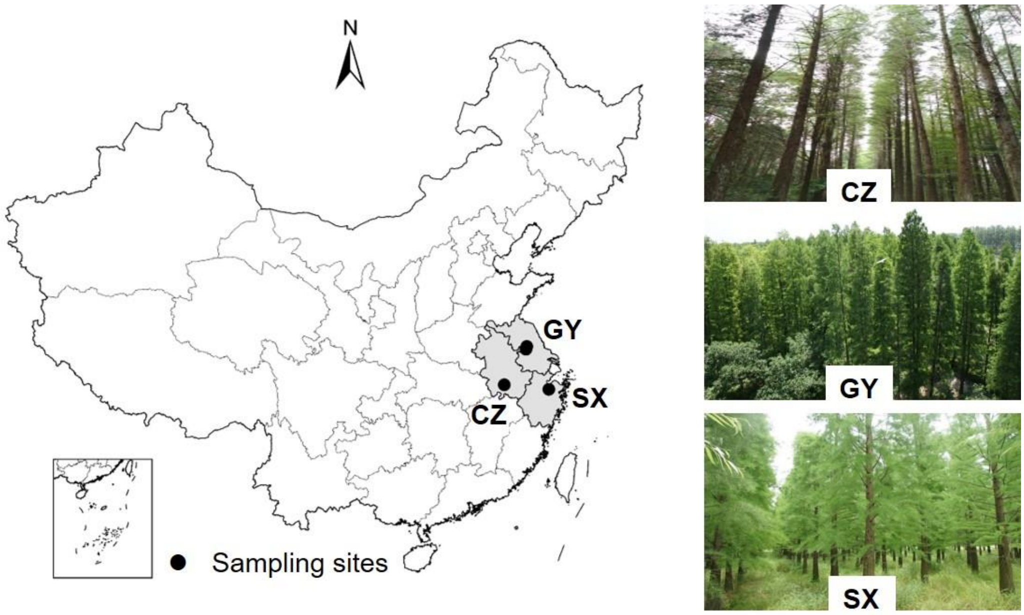

Figure 1. Sampling sites and sceneries in the three *Taxodium distichum* plantations in the Yangtze River Delta of China. The black dots labeled as CZ, GY, and SX denote the site location at Chizhou, Gaoyou, and Shaoxing, respectively.

2.2. Sample Collection

Based on the classification standard of precipitation issued by China Meteorological Administration, three magnitudes of precipitations were selected in each study site, including light (precipitation: 5–10 mm), moderate (precipitation: 10–25 mm), and heavy rainfalls (precipitation > 25 mm) (Table 1). Within 8–9 days after each rainfall event (before the occurrence of another rainfall), samples of rainfall, groundwater, soil and tree stems (xylem) were collected in each site.

Table 1. Characteristics of three rainfall events that occurred at the three study sites.

Site	Rainfall Event I		Rainfall Event II		Rainfall Event III	
	Time	Precipitation (mm)	Time	Precipitation (mm)	Time	Precipitation (mm)
CZ	11 July 2018	8.7	14 December 2017	14.5	4 September 2018	27.0
GY	27 November 2017	9.3	8 November 2016	19.5	8 October 2016	29.2
SX	10 July 2017	7.5	22 May 2017	14.5	16 September 2016	35.5

CZ, GY, and SX indicate the site located at Chizhou, Gaoyou, and Shaoxing, respectively.

For rainfall sampling, three rain gauges with a built-in funnel were randomly placed in an open space adjacent to the study site, and a table tennis ball was put into the funnel to prevent rainfall evaporation. After each rainfall event, three rainfall samples were collected from the rain gauges, then mixed as one sample (about 3 mL). The sampling time ranged from 7:00 a.m. to 8:00 a.m. Regarding tree stems (xylem) sampling, three healthy trees with similar diameter at breast height and crown width were selected from the *T. distichum* plantation as standard trees used in this study (Table S1). Then 3–5 tree stem (xylem) samples with a length of 3–4 cm were collected on the sunny side of each standard tree. For soil collection, three soil profiles with 100 cm depth were randomly excavated in the *T. distichum* plantation in each site. In each soil profile of each site, ~5 g soil samples were collected with a knife at 0–20, 20–40, 40–60, 60–80, and 80–100 cm soil layers, respectively.

With respect to shallow groundwater, a well was selected nearby the *T. distichum* plantation and then the groundwater samples were collected from this well.

After each rainfall event, xylem, soil, and groundwater samples were gathered once a day from 8:00 a.m. to 10:00 a.m. All samples were immediately put into glass bottles, tightened with caps, and sealed with parafilm. Glass bottles containing samples were stored in an incubator (−5–0 °C) in the field and in a refrigerator at −18 °C after being transported to the laboratory.

2.3. Determining Water Isotopes and Calculating Water Uptake Pattern of T. distichum

The water in soil and tree stem (xylem) samples was extracted by water vacuum extraction system [27]. Both δD and δ^{18}O in the soil water, xylem water, rainfall, and groundwater were assayed by isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Inc., Waltham, MA, USA) coupled with an element analyzer (Flash 2000 HT, Thermo Fisher Scientific, Inc., Waltham, MA, USA). The δD and δ^{18}O were calculated based on Equation (1):

$$\delta X\ (‰) = [(R_s/R_d) - 1] \times 1000‰ \quad (1)$$

where R_s was the D/H or ^{18}O/^{16}O molar ratios in the sample, and R_d was the D/H or ^{18}O/^{16}O molar ratios in the standard (V-SMOW, Vienna standard mean ocean water).

Then the δD and δ^{18}O of precipitation in each site were linearly fitted to obtain the local meteoric water line (LMWL). If the values of δD and δ^{18}O from other sources of water (including soil and xylem water and groundwater) were distributed on the LMWL, these waters were not affected by evaporation. When the δD and δ^{18}O of these waters were located on the right side of LMWL, they were enriched by evaporation during the transformation process. As the δD and δ^{18}O in any two of the three water bodies were similar, they had similar water sources.

We further used the Bayesian mixed model MixSIAR (version 3.1.7) to calculate the percentage of water uptake by *T. distichum* to each soil layer. This analysis was performed by the "MixSIAR" package using R 4.0.3. Detailed data analysis process was conducted with the following three steps. First, the obtained data was uploaded to the MixSIAR interface. In detail, the values of δD and δ^{18}O from xylem water, soil water in each layer, and fractionation coefficient were loaded into the model as "Mixture data", "Source data", and "Discrimination data", respectively. Second, other related parameters were set on the MixSIAR interface. Specifically, we set "MCMC (Markon chain Monte Carlo) run long", "error structure" and "specify priority" to "long", "residual only", and "uninformative prior", respectively. Third, we tested the convergence of the model through "Gelman-Rubin" and "Geweke" [26].

2.4. Determination of Tree Traits and Soil Properties

To evaluate the factors affecting *T. distichum* water uptake, we measured both tree traits and soil properties in each site. The tree traits mainly include fine root biomass (FB), diameter at breast height (DBH), and leaf biomass (LB). For the measurement of FB, soils were collected with a root drill (10 cm diameter) at 60° intervals on a circle with the trunk as the center and 1 m as the radius. Soil sampling depth was the same as that in Section 2.2. Fine roots ($\leq$2 mm) were then screened from the collected soils, dried, and weighed to obtain FB. With regard to the determination of DBH, the diameter of standard wood was measured at 1.3 m from the ground. For the examination of LB, we first measured the DBH and tree height of *T. distichum*, and then substituted these two parameters to the allometric equation of *T. distichum* in each site, and finally calculated the LB of *T. distichum*.

Furthermore, we analyzed the soil properties of *T. distichum* plantation to evaluate their impacts on plant water absorption, including bulk density (BD), field capacity (FC) and soil water-filled pore space (WFPS). For the BD, undisturbed soil was collected with a cutting ring of 100 cm^3, and then dried and weighed. The ratio of dried-soil weight to cutting ring volume is the BD. Regarding the FC, the specific analysis procedure is as follows: first, soil was collected with a cutting ring. Second, the cutting ring containing soil was soaked in water for 12 h. Third, the soaked cutting ring was placed in a flat bottom plate covered with sand for 72 h and weighed. Finally, soil was dried at 105 °C and weighed. The FC was calculated by the ratio of soil weight after standing for 72 h to the dried soil weight minus one [28]. The WFPS was calculated by Equation (2) [29]:

$$\mathrm{WFPS} = \frac{\mathrm{SWC} \times \mathrm{BD}}{1 - \mathrm{BD}/\mathrm{PD}} \quad (2)$$

where SWC represents soil water content (%), BD is bulk density (g cm^{-3}), PD denotes particle density of soil (2.65 g cm^{-3}).

2.5. Statistical Analyses

To explore factors affecting *T. distichum* water uptake, we used ordinary least squares (OLS) regression analyses to examine the relationships between the percentage of water uptake by *T. distichum* in each soil layer and tree traits/soil properties. Furthermore, we employed variation partitioning analysis to evaluate the pure and joint effects of tree traits and soil properties on water absorption of *T. distichum*. To verify the results based on variation partitioning analysis, we further used the random forest model to clarify the dominant driver regulating the water use of *T. distichum*. Variation partitioning analysis and random forest model were performed using R software with the "vegan" and "randomForest" packages, respectively [30,31].

3. Results

3.1. Characteristics of δD and δ^{18}O in Soil Water, Xylem Water, and Groundwater

The δD and δ^{18}O of soil and xylem water were located on the right side of local meteoric water line (LMWL) (Figure 2), suggesting that they were enriched by evaporation during the transformation process. In addition, the δD and δ^{18}O of xylem water in *T. distichum* were close to that of soil water in each site (Figure 2), indicating that the xylem water of *T. distichum* mainly originated from soil water in the Yangtze River Delta. By contrast, the δD and δ^{18}O of shallow groundwater in the *T. distichum* plantations were distributed on the LMWL, whether in CZ, GY, or SX sites (Figure 2).

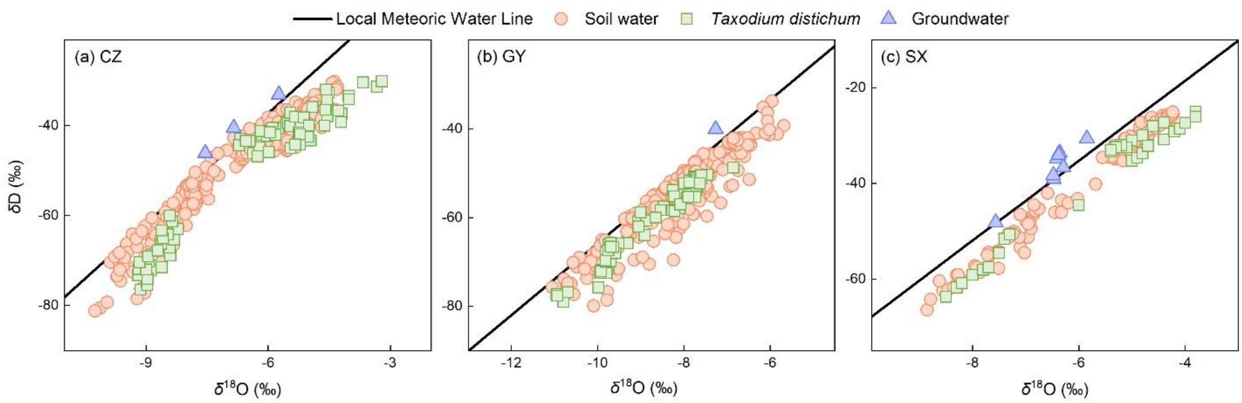

Figure 2. Isotopes (δ^{18}O and δD) in soil water, tree xylem water, and groundwater from *Taxodium distichum* plantations in (**a**) Chizhou, (**b**) Gaoyou, and (**c**) Shaoxing. CZ, GY, and SX indicate the sites located at Chizhou, Gaoyou, and Shaoxing, respectively.

3.2. Water Uptake Patterns of T. distichum under Light, Moderate, and Heavy Rainfalls

After light rainfall, *T. distichum* absorbed a higher percentage of water in shallow soil layers (0–40 cm) while a lower percentage of water in deep soil layers (60–100 cm), accounting for 71.53%–74.70% and 13.43%–17.03%, respectively (Figure 3a). Similarly, after moderate and heavy rainfalls, the percentage of water uptake from shallow soil layers by

T. distichum was higher than that from deep soil layers (43.63%–62.73% vs. 21.8%–35.9% after moderate rainfall, 58.77%–66.67% vs. 18.33%–23.3% after heavy rainfall) (Figure 3b,c).

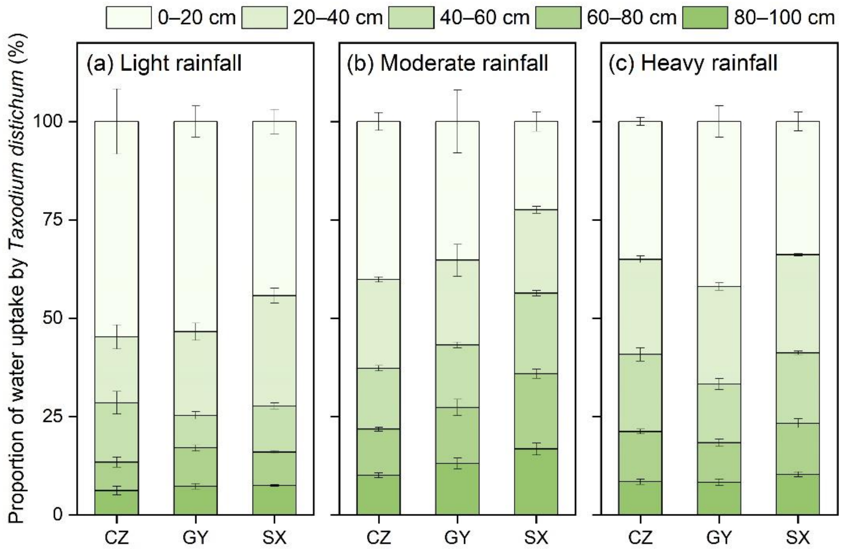

Figure 3. Percentage of water uptake from different soil layers (0–20, 20–40, 40–60, 60–80, 80–100 cm) by *Taxodium distichum* in Chizhou (CZ), Gaoyou (GY), and Shaoxing (SX) following light, moderate, and heavy rainfalls.

3.3. Dominant Drivers Influencing T. distichum Water Uptake

Variation partitioning analysis revealed that tree traits and soil properties jointly explained 77.2%, 72.0%, and 75.8% of variations in *T. distichum* water uptake under the light, moderate, and heavy rainfall events. Specifically, tree traits explained 36.0%, 45.3%, and 35.0% of the variability in *T. distichum* water uptake, while soil properties explained 6.3%, 1.1%, and 8.0% of the variability (Figure 4), respectively. Tree traits have higher pure effects on *T. distichum* water absorption than soil properties (Figure 4).

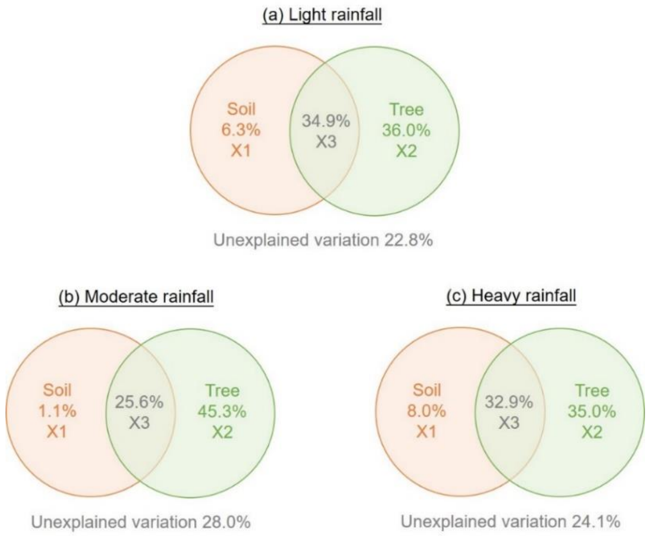

Figure 4. Variation partitioning analysis for percentage of water uptake by *Taxodium distichum* following (**a**) light, (**b**) moderate, and (**c**) heavy rainfalls. The variation is divided into the following four fractions: pure effect of soil properties (X1), pure effect of tree traits (X2), joint effects of soil and tree properties (X3), and unexplained variation.

The random forest model further showed that FB explained 25.63%, 19.46%, and 34.10% of variations in *T. distichum* water absorption, respectively (Figure 5a,d,g), suggesting that tree traits were the dominant driver influencing water use patterns of *T. distichum*. Besides the FB, soil properties, such as WFPS, also exerted an important role in regulating *T. distichum* water uptake, accounting for 11.02%, 12.96%, and 10.99% of variations for plant water uptake under light, moderate, and heavy rainfalls, respectively (Figure 5a,d,g). Specifically, *T. distichum* water uptake was positively correlated with FB (Figure 5b,e,h), while negatively related to WFPS (Figure 5c,f,i), whether in light, moderate, or heavy rainfall events.

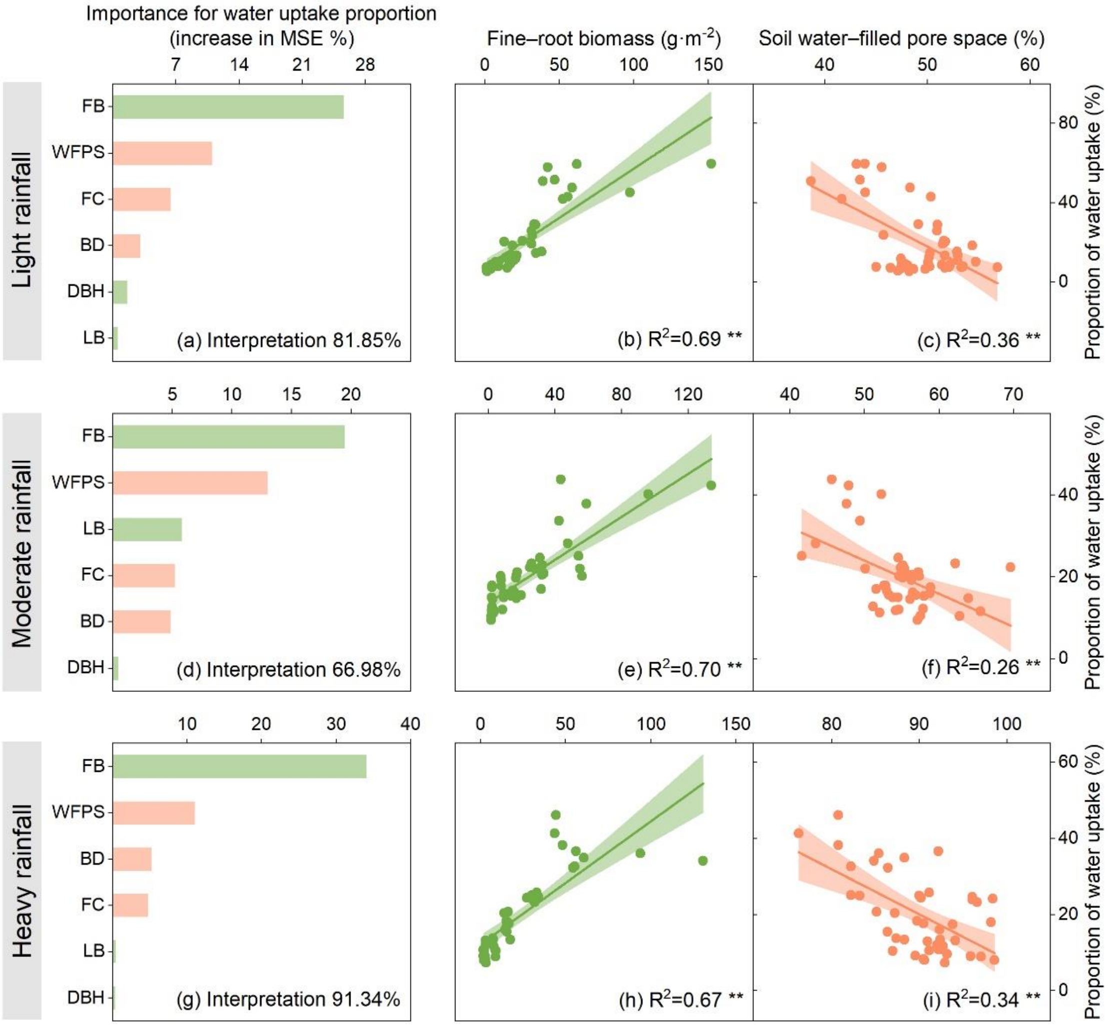

Figure 5. Importance of tree and soil properties to the proportion of water uptake by *Taxodium distichum* and relationships of plant water uptake proportion with fine root biomass and total porosity following (**a**–**c**) light, (**d**–**f**) moderate, and (**g**–**i**) heavy rainfall by mean percent increase in mean squared error (MSE). The solid lines represent the fitted ordinary least-squares model, and the shaded areas represent the 95% confidence intervals. LB, leaf biomass; FB, fine root biomass; DBH, diameter at breast height; BD, bulk density; WFPS, soil water-filled pore space; FC, field capacity. ** denotes significant correlation between tree water uptake and the corresponding variables at $p < 0.01$.

4. Discussion

4.1. Soil Water Was the Dominant Water Source of T. distichum

Our results revealed that δD and δ^{18}O in shallow groundwater were distributed on the LMWL, while those in soil and xylem water were located on the right side of the LMWL in the *T. distichum* plantations of the Yangtze River Delta, indicating that both xylem and soil water did not exchange with groundwater. Thus, the "ecohydrological separation" phenomenon between plant transpiration and groundwater, observed in Mediterranean mountain forest [32], temperate forest [33], and tropical forest [34], also exists in the plantation of the estuarine delta. Moreover, our results also showed that the δD and δ^{18}O of xylem water were close to those of soil water, illustrating that soil water was the dominating water source of *T. distichum* in the Yangtze River Delta. This observation was distinct to previous studies reporting that the water sources of many tree species are not only derived from soil water but also groundwater, such as *Quercus ilex*, *Arbutus unedo*, *Phillyrea latifolia*, *Fagus sylvatica*, and *Abies alba* [35,36]. This contradiction may be ascribed to the differences of precipitation in these study areas. Specifically, due to the low annual average precipitation (610 mm) [35] or simulated precipitation reduction experiment [36] conducted in their sites, soil moisture was relatively lower, which was not enough for water requirement of trees. Therefore, these trees not only absorbed soil water, but also acquired groundwater to satisfy their water requirements. However, in this study, the mean annual precipitation of the three sites ranged from 1030 to 1800 mm, which was sufficient for trees. Hence, *T. distichum* plantations conducted in this study did not need to absorb groundwater to maintain their growth.

4.2. Tree Traits Primarily Regulated the Water Uptake of T. distichum

Our results demonstrated that *T. distichum* mainly absorbed shallow soil water, while the percentage of water uptake from deep soil layer was relatively lower, whether in light, moderate, or heavy rainfall, supporting our first hypothesis. The water use pattern of *T. distichum* is opposite to that of *Cunninghamia lanceolata* and *Populus deltoides* [26,37]. This discrepancy may be attributed to the following two reasons. First, *T. distichum* is a shallow-rooted tree species, and its roots are mostly distributed within shallow soil layers. Thus, it tends to absorb shallow soil water in the absence of water competition with other tree species. On the contrary, *C. lanceolata* and *P. deltoides* belong to deep-rooted tree species, their roots are generally distributed in deep soil layers, and their xylem water is mainly originated from deep soil water [15,38,39]. Second, *T. distichum* generally grows in humid areas with high or even excessive soil moisture, and thus its water absorption would be largely influenced by soil aeration. In this study, the aeration in shallow soils was better than that in deep soils (Table 2), and consequently *T. distichum* tended to absorb shallow soil water. Contrary to the growth environment of *T. distichum*, *C. lanceolata* and *P. deltoides* grow in habitats with moderate soil water content, and their water absorption was mainly affected by field capacity rather than soil aeration [40]. Given the higher water storage in the deep soil layer than the shallow layer, *C. lanceolata* and *P. deltoides* mainly adsorbed deep soil water. Taken together, both tree traits (such as root distribution) and soil properties (such as soil water-filled pore space) could affect the water use patterns of *T. distichum* living in the estuarine deltas.

However, it remains unclear which kind of factor dominantly drives the *T. distichum* water uptake. Based on variation partitioning analysis and random forest model, our results illustrated that *T. distichum* water uptake was mainly regulated by tree traits such as FB, LB, and DBH (Figure 4), which supported our second hypothesis. Among the tree traits, FB was one of the most important tree properties in influencing the water use of *T. distichum*. It is well known that trees mainly absorb soil water through fine roots, despite the environment and soil water status. The more fine roots distributed in a soil layer, the greater the percentage of water uptake from the soil layer [21,41]. In these three study sites of the Yangtze River Delta, the FB of *T. distichum* distributed in 0–40 cm soil layers was significantly higher than that in 60–100 cm soil layers (Table 2). Therefore, *T. distichum* mainly absorbed shallow soil water, while obtained less from deep soils. Besides the FB, LB also exhibited a critical role in affecting *T. distichum* water uptake. This may be due to the fact that leaves are the major apparatus for tree transpiration, while transpiration is the driving force for tree water uptake. Hence, the larger LB has stronger tree transpiration, which could in turn absorb more water to maintain metabolism [19]. Moreover, DBH also affected the *T. distichum* water absorption. Given that DBH could reflect the tree growth status, the higher DBH represents a more flourishing tree that needs more water applied for plant metabolism [42]. Although both LB and DBH could influence the *T. distichum* water absorption, these two factors had less effect than FB (Figure 5). Such a phenomenon could be explained by the fact that although LF and DBH could play an important role in affecting the total water absorption of *T. distichum*, they cannot directly influence the percentage of water uptake from each soil layer. By comparison, the distribution of fine root biomass in each soil layer could regulate the water uptake proportion because the root is the main apparatus of water absorption. Therefore, FB exerted greater effects on the water uptake of *T. distichum* than LB and DBH.

Table 2. Dynamics of fine root biomass (FB) and soil water-filled pore space (WFPS) in each soil layer within CZ, GY, and SX sites after light, moderate, and heavy rainfall events.

Trait	Site	Rainfall Event	0–20 cm	20–40 cm	40–60 cm	60–80 cm	80–100 cm
FB	CZ	Light	103.7 ± 26.2 b	28.3 ± 7.8 a	19.3 ± 1.1 a	3.7 ± 0.4 a	1.3 ± 0.2 a
		Moderate	96.4 ± 21.7 b	26.1 ± 0.8 a	17.5 ± 1.2 a	3.1 ± 0.2 a	1.7 ± 0.1 a
		Heavy	95.0 ± 20.2 b	30.5 ± 0.6 a	15.5 ± 0.9 a	2.9 ± 0.1 a	1.8 ± 0.1 a
	GY	Light	42.6 ± 2.3 e	29.5 ± 2.2 d	15.9 ± 0.6 c	8.3 ± 0.7 b	2.9 ± 0.5 a
		Moderate	44.6 ± 1.6 e	31.7 ± 0.4 d	14.2 ± 0.3 c	9.0 ± 0.3 b	2.1 ± 0.2 a
		Heavy	45.3 ± 1.4 e	30.3 ± 1.7 d	15.7 ± 0.9 c	8.7 ± 0.2 b	2.8 ± 0.1 a
	SX	Light	55.5 ± 1.7 e	32.8 ± 0.8 d	18.0 ± 1.9 c	8.3 ± 0.3 b	2.4 ± 0.3 a
		Moderate	55.2 ± 0.6 e	32.2 ± 0.6 d	16.9 ± 0.3 c	7.6 ± 0.1 b	2.1 ± 0.1 a
		Heavy	55.2 ± 0.6 e	32.5 ± 1.1 d	15.3 ± 0.1c	7.4 ± 0.1 b	1.9 ± 0.2 a
WFPS	CZ	Light	43.6 ± 0.3 a	51.6 ± 0.8 b	53.0 ± 0.8 b	49.9 ± 0.8 b	50.7 ± 3.1 b
		Moderate	49.2 ± 1.5 a	62.4 ± 4.1 b	59.1 ± 2.4 ab	58.5 ± 3.9 ab	59.1 ± 1.8 ab
		Heavy	86.2 ± 1.1 a	95.0 ± 2.6 c	87.6 ± 1.6 ab	92.4 ± 0.9 abc	92.9 ± 2.9 bc
	GY	Light	42.5 ± 2.0 a	49.6 ± 1.9 b	49.2 ± 1.3 b	50.7 ± 2.1 b	49.1 ± 2.2 b
		Moderate	46.1 ± 1.8 a	53.7 ± 1.1 b	54.7 ± 1.6 b	55.9 ± 1.4 b	53.8 ± 1.5 b
		Heavy	79.2 ± 1.5 a	92.5 ± 1.8 b	90.3 ± 2.0 b	92.2 ± 2.9 b	93.1 ± 1.5 b
	SX	Light	46.8 ± 2.6 a	50.3 ± 0.6 a	50.2 ± 1.6 a	50.8 ± 0.7 a	50.1 ± 2.6 a
		Moderate	48.8 ± 3.8 a	55.5 ± 0.5 ab	56.2 ± 0.6 a	55.4 ± 1.4 a	55.2 ± 1.8 a
		Heavy	86.9 ± 2.9 a	87.1 ± 4.5 a	93.9 ± 2.4 ab	89.5 ± 1.7 b	92.2 ± 0.6 ab

Values are means ± SE (n = 3). Significant differences in independent variables among different soil layers are denoted by different lowercase letters ($p < 0.05$).

Our results also showed that soil properties had less effect on *T. distichum* water uptake compared with tree traits (Figure 4). Although the soil with lower BD and higher FC has greater water holding capacity that finally supplied more water for trees [40,43,44], the amount of water absorption largely depends on fine roots of *T. distichum*. Hence, soil properties (BD and FC) could only indirectly affect the water use pattern of *T. distichum* by influencing tree traits. Besides the above two soil properties, WFPS, an indicator representing soil aeration [28], also had an effect on the water absorption of *T. distichum*. This may be because soil with lower WFPS has higher aeration, which is conducive to the growth of tree fine roots. Given that fine roots mainly perform the process of water absorption [25,45], WFPS could also impact plant water uptake. Taken together, soil properties, including BD, FC, and WFPS, indirectly regulated the water absorption of *T. distichum* via affecting tree traits.

5. Conclusions

In conclusion, based on the δD and δ^{18}O coupled with the Bayesian mixed model, our study revealed that *T. distichum*, a waterlogging tolerant tree species, mainly absorbed shallow soil water in the Yangtze River Delta of China, whether in light, moderate, or heavy rainfalls. The main factor affecting the water uptake of *T. distichum* was tree traits. These findings provide us with one important implication. Under the scenario of global precipitation changes, extreme precipitation events occur frequently in humid areas, and the forests in the estuary delta with flat terrain usually suffer from floods induced by extreme precipitation. Some waterlogging tolerant tree species such as *T. distichum* could improve the percentage of water uptake from shallow soils by altering their fine root distribution, which could effectively improve water conservation in the estuary delta. In the future, when we conduct vegetation restoration and structural optimization in humid areas, more attention should be paid on the selection of waterlogging tolerant tree species to resist floods. However, given the limitations of workload and cost, only three study sites were selected in our case. Further studies on water uptake of waterlogging tolerant trees should be conducted in more field sites to improve the reliability of our observations and advance our understanding on this issue.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12111547/s1, Table S1 Diameter at breast height and crown width of selected *Taxodium distichum* used in this study.

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