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Changes in Water Utilization Characteristics of Trees in Forests across a Successional Gradient in Southern China

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Abstract: Elucidating the water utilization strategy of trees during forest succession is a prerequisite for predicting the direction of forest succession. However, the water utilization characteristics of trees in forests across a successional gradient remain unclear. Here, we utilized the hydrogen and oxygen stable isotopes combined with the Bayesian mixed model (MixSIAR) to analyze the water utilization of dominant trees (*Pinus massoniana*, *Castanea henryi*, and *Schima superba*) in forests along a successional gradient in the Dinghushan Biosphere Reserve of China. Furthermore, we determined the primary factor affecting the water utilization of various trees based on variation partitioning analysis and a random forest model. Our results illustrated that in the early-successional forest, the water utilization ratios from shallow soil layers by *P. massoniana* were significantly lower than that in the mid-successional forest (51.3%–61.7% vs. 75.3%–81.4%), while its water utilization ratios from deep soil layers exhibited the opposite pattern (26.1%–30.1% vs. 9.0%–15.0%). Similarly, the ratios of water utilization from shallow soil layers by *C. henryi* (18.9%–29.5% vs. 32.4%–45.9%) and *S. superba* (10.0%–25.7% vs. 29.2%–66.4%) in the mid-successional forest were relatively lower than in the late-successional forest, whereas their water utilization ratios from deep soil layers showed the contrary tendency. Moreover, our results demonstrated that the diverse water utilization of each tree in different successional forests was mainly attributed to their distinct plant properties. Our findings highlight the increased percentage of water utilization of trees from shallow soil layers with forest succession, providing new insights for predicting the direction of forest succession under changing environments.

Keywords: forest succession; plant water utilization; stable isotopes; plant and soil properties

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1. Introduction

Forest succession is an essential process for the self-recovery of forest ecosystems to adapt to external disturbances, including global climate change, species invasion, and human interference [1–3]. During forest succession, species structure, plant phenology, morphology, and physiological characteristics would change to maintain the community stability [4]. In addition, forest succession could also affect the plant water utilization strategy due to the different water and light conditions at various stages of succession [5]. The plant water utilization strategy, one of the important hydrological processes in forest ecosystems, plays a decisive role in the succession direction and ecological function of soil-vegetation systems [6,7]. Especially under climate change, the shifts in precipitation could affect plant water use strategies and thereby alter forest hydrological processes, which ultimately change the direction of forest succession and disrupt forest stability. Therefore, exploring the plant water utilization strategy along a successional gradient is necessary for a comprehensive understanding of the hydrological processes in vegetation restoration and the direction of vegetation succession under climate change.

Despite its importance, the plant water utilization strategy across a successional gradient remains uncertain. Specifically, previous studies mainly focused on plant water use efficiency at different successional stages, with limited studies involving the water utilization pattern of plants [8–10]. More importantly, the results from these studies are divergent. It was reported that *Pinus densiflora* mainly used shallow soil water in the early-successional forest in Tsukuba, Japan, while it shifted to utilize deep soil water in the mid-successional forest [11]. Similarly, Chang et al. [7] indicated that vegetation in the abandoned land from the Loess Plateau used soil water at 0–20 cm depth in the early-successional forest. By comparison, in the mid- and late-successional forests, the depth of plant water absorption extended to 0–100 cm soil. The above results illustrate that the depth of vegetation water uptake deepens with progressing forest succession. In contrast, other studies found that the *Ocotea samosa* (30–70 cm), *Eugenia* spp. (30–70 cm), and *Juniperus occidentalis* (0–80 cm) in the early-, mid- and late-successional forests primarily used water from a similar soil layer [12–14]. These different observations imply that the water utilization characteristics of plants at different succession stages need further exploration.

Additionally, it is still unclear which factor primarily affects the plant water utilization across a successional gradient. Generally, environment, soil, and plant properties were supposed to be the drivers influencing tree water utilization [15–19]. Environmental factors, such as air temperature, solar radiation, and vapor pressure deficit, could indirectly affect plant water uptake by regulating transpiration [19–21]. However, given the minor variations in environmental factors in the same region, soils and plants rather than the environment should be the main factors mediating plant water absorption. It has been reported that soils with lower bulk density, higher total porosity, and field capacity possess more pores, which could store more water for tree utilization [22,23] and thereby improve tree water utilization. Other studies also illustrated that soils with higher moisture exhibit greater water availability, which is more conducive to plant water absorption [24]. Meanwhile, a lower soil temperature could increase the water viscosity and thus reduce the water diffusion rate and inhibit plant water absorption [25]. In addition, soil texture and soil organic matter could indirectly affect plant water utilization by adjusting soil water holding capacity [26,27]. Besides the above-mentioned soil properties, plant properties may also affect the water utilization of trees. Specifically, given that fine roots are the main organ for water utilization by trees [28,29], the fine root biomass distributed in the soil layer directly affects the tree water utilization ratio from this soil layer. Apart from fine root biomass, trees with higher leaf biomass have a stronger transpiration pull, thereby promoting their water utilization [30,31]. Additionally, a higher leaf water potential indicates less water stress on the tree, resulting in greater water absorption by the tree [32,33]. Plant physiological indicators could affect plant water utilization characteristics by regulating photosynthesis, transpiration, and leaf stomatal conductance [34]. However, it remains obscure which factor mainly regulates the water utilization of trees across a successional gradient.

To resolve this gap, we selected forests along successional gradients, including a coniferous forest (early-successional forest), a mixed coniferous broad-leaved forest (mid-successional forest), and a monsoon evergreen broad-leaved forest (late-successional forest) in the Dinghushan Biosphere Reserve in Guangdong province, China. Then, by using the hydrogen and oxygen stable isotopes combined with the Bayesian mixed model (MixSIAR), we analyzed the water utilization characteristics of dominant trees (*Pinus massoniana*, *Castanea henryi*, and *Schima superba*) in each forest following different magnitudes of precipitation. Furthermore, we measured the plant and soil variables in the study area to reveal the primary factors mediating the water utilization of various trees. It should be noted that *P. massoniana*, the dominant tree species in early- and mid-successional forests, is suitable as a pioneer tree species due to its lower water consumption compared to other coniferous tree species [35]. Both *C. henryi* and *S. superba*, the zonal tree species in the mid- and late-successional forests, have higher water consumption than *P. massoniana* [36]. This study seeks to answer the following two questions: (1) Is there a difference in the water utilization characteristics of *P. massoniana*/*C. henryi*/*S. superba* in different successional forests? (2) Which factor is the dominant driver affecting the water utilization of various trees in forests along successional gradients?

2. Materials and Methods

2.1. Study Area

Our study site is located at the Dinghushan Biosphere Reserve, Guangdong Province of China (112°30′39″–112°33′41″ E, 23°09′21″–23°11′30″ N, Figure 1). The mean annual temperature, mean annual precipitation, and relative humidity in the area are 21.0 °C, 1956 mm, and 77.7%, respectively [37]. The climate type belongs to the South Asian tropical monsoon, and the soil type is lateritic soil. Three typical forests along successional gradients, a coniferous forest (CF, early-successional forest), a mixed coniferous and broad-leaved forest (MCBF, mid-successional forest), and a monsoon evergreen broad-leaved forest (MEBF, late-successional forest), are distributed across the site [38]. Of the three forest types, the CF is mainly dominated by *P. massoniana* in the arbor layer and *Psychotria rubra* and *Blechnum orientale* in the understory, which has a topsoil containing 20.3% clay, 23.7% silt, and 56.0% sand. The MCBF primarily consists of *P. massoniana*, *C. henryi*, and *S. superba* in the arbor layer and *P. rubra* and *Pteris multifida* in the understory. Its topsoil is composed of 22.9% clay, 21.8% silt, and 55.3% sand. In addition, the MEBF is dominated by *C. henryi* and *S. superba* in the arbor layer and *Psychotria asiatica* and *Blechnum orientale* in the understory [39]. Its topsoil consists of 25.7% clay, 33.7% silt, and 40.6% sand. The content of the topsoil's organic matter is 24.17 g/kg, 29.76 g/kg, and 32.81 g/kg in CF, MCBF, and MEBF, respectively.

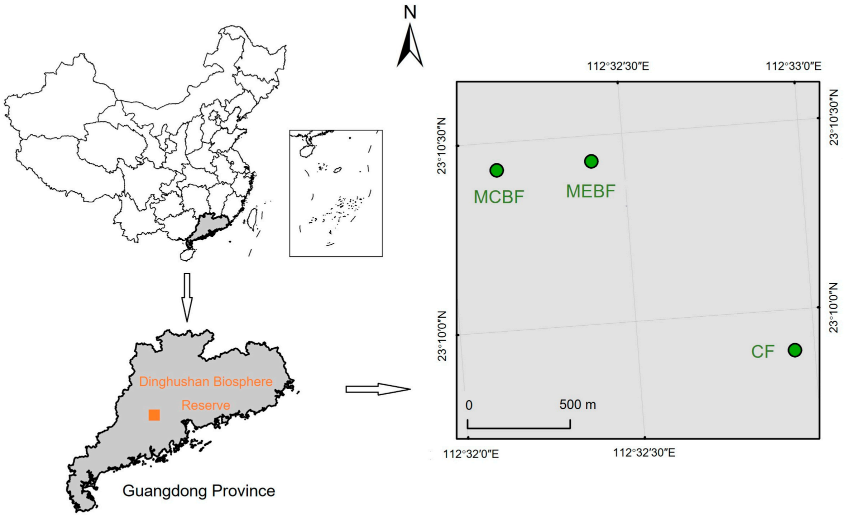


Figure 1. Location of the study site, including coniferous forest (CF), mixed coniferous and broad-leaved forest (MCBF), and monsoon evergreen broad-leaved forest (MEBF) in the Dinghushan Biosphere Reserve, Guangdong Province of China.

2.2. Field Sampling

According to the standard of light (5–10 mm/24 h), moderate (10–25 mm/24 h), and heavy precipitation (>25 mm/24 h), three magnitudes of precipitation events were collected from the rainfalls that occurred in the study area. The three rainfall events occurred on 1 October 2013, 7 September 2013, and 18 December 2013, with precipitation of 5.4 mm, 20.0 mm, and 45.8 mm, respectively. When rainfall events occurred, we rapidly selected samples from the precipitation, soil, and tree stem (xylem) within five days.

Before collecting precipitation, three rain gauges (Figure S1) embedded into funnels were randomly placed on the vacant land outside the forest, and a table tennis ball was put inside the funnels to inhibit water evaporation. The distances between the rain gauges and each forest were about 500–1000 m. When each rainfall event occurred, we gathered three precipitation samples from three rain gauges, respectively.

Regarding soil sample collection, we set up three soil profiles (100 cm depth), which were randomly excavated from each forest (CF, MCBF, and MEBF) in the study area. The distance between these three soil profiles was approximately 20–25 m. After each rainfall event, new soil profiles were excavated again. We sampled soils at depths of 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm, respectively. In total, 45 soil samples were collected once a day after precipitation.

For collecting tree stem (xylem) samples, we selected three healthy trees with diameters and heights (Table S1) close to the average value of the dominant trees in each forest as the standard trees. Specifically, three *P. massoniana* in the CF, three *P. massoniana*, three *C. henryi* and three *S. superba* in the MCBF, and three *S. superba* and three *C. henryi* in the MEBF were selected as standard trees. We collected 3–5 segments of biennial branches with a length of 3–4 cm on the sunny side of each standard tree. Then, we removed the phloem of the branch and retained the xylem as an experimental sample. Similar to soil samples, the collection frequency of xylem samples was also once a day after precipitation.

All the above-mentioned samples were immediately packed into bottles. Then, the caps of the bottles were quickly tightened and sealed with parafilm. The collected samples were stored in a −18 °C refrigerator.

2.3. Sample Treatment and Isotope Analysis

We extracted the soil and xylem water through a vacuum extraction system using the evaporative cooling method [40]. The water derived from soils and xylems and the precipitation were measured for δD and δ^{18}O using a mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Inc., Waltham, MA, USA) combined with an element analyzer (Flash 2000 HT, Thermo Fisher Scientific, Inc., Waltham, MA, USA). Both the δD and δ^{18}O were expressed relative to the Vienna Standard Mean Ocean Water (VSMOW) as follows:

$$\delta \mathrm{X}\ (‰) = [(\mathrm{R_s}/\mathrm{R_d}) - 1] \times 1000‰ \tag{1}$$

where δX represents δD (δ^{18}O), Rs denotes ^{2}H/^{1}H (^{18}O/^{16}O) in the sample, and $\mathrm{R_d}$ is ^{2}H/^{1}H (^{18}O/^{16}O) in VSMOW.

2.4. Calculation of Water Utilization Characteristics of Trees

We further employed the Bayesian mixed model (MixSIAR) to calculate the water utilization ratio by the trees from each soil layer (*P. massoniana*, *C. henryi*, and *S. superba*) across a successional gradient. The calculation includes the following steps. First, the δD (δ^{18}O) of water from tree xylems and soils were imported into the "Mixture data" and "Source data" in the MixSIAR interface, respectively. Second, given that isotopic values do not undergo fractionation during the process of root water absorption [41], the "Discrimination data" was set to 0 in the MixSIAR interface. Finally, the running length of "Markon chain Monte Carlo, MCMC" was set as "long" (chain length = 300,000; burn = 200,000; thin = 100; chains = 3); "Error structure" and "Specify prior" were set as "Residual only" and "Uninformative prior", respectively. In addition, the model was tested for convergence through "Gelman Rubin" and "Geweke" tests [42]. This above analysis was performed using "MixSIAR" in the R software (v 3.6.0).

2.5. Examination of Soil and Plant Properties

Soil properties, such as bulk density (BD), total porosity (TP), and field capacity (FC), were measured to evaluate their impacts on the water utilization of the dominant trees at different successional stages (Table S2). Regarding the determination of the BD, the undisturbed soil was first collected using a 100 cm^3 ring cutter, then the collected soil was oven-dried at 105 °C, and the soil weight was measured. The ratio of dried soil to the volume of the ring cutter was the BD. The TP was determined using the ring cutter method [43]. To determine the FC, a 100 cm^3 ring cutter containing undisturbed soil was immersed in water for 12 h, and then it was put on a platform covered with sand for 72 h before being weighed. Furthermore, the soil was dried and weighed at 105 °C. The difference between the soil weight after standing for 72 h and the dry soil weight divided by the dry soil weight was the FC.

Meanwhile, we also determined the plant properties of dominant trees in each successional forest to analyze their effects on water utilization characteristics. The plant properties mainly included leaf biomass (LB, Table S3), fine root biomass (FB, Table S4), and predawn leaf water potential (Ψ_{PLWP}, Table S3). Of them, the LB was calculated by introducing the measured height and diameter of each tree into the known allometric growth equation in the study area [44,45]. Before measuring the FB, the soil was first collected with a 10 cm root drill at intervals of 60° at 1 m from the tree trunk. The soil depth was consistent with that in Section 2.2. Fine roots ($\leq$2 mm) were selected from the soil samples, then oven-dried and weighed to calculate the FB. Additionally, the Ψ_{PLWP} was determined using a dew point water potential meter (WP4C, Meter, Decagon, Pullman, WA, USA) between 5:00 am and 6:30 am.

2.6. Statistical Analyses

To test the difference in the water utilization ratio from each soil layer (R) by *P. massoniana* in the early- and mid-successional forests, we compared the R of *P. massoniana* between the two forests using a one-way ANOVA. Similarly, we also used this method to examine the differences in the R of *C. henryi*/*S. superba* between the mid- and late-successional forests. To explore the factors affecting the R of each tree, we established the Pearson correlation between the P and soil properties (BD, TP, and FC)/plant (LB, FB, and Ψ_{PLWP}). Furthermore, to determine the primary driver of the R, we employed variation partitioning analysis to examine the pure and combined effects of vegetation and soil properties on R. To verify the results obtained from the variation partitioning analysis, we also used a random forest model to screen for the primary factors of R. The "ntree" included in the model was set to 1000, and default parameters were used for other parameters. The variation partitioning analysis and random forest model were implemented with "vegan" and "randomForest" packages in the R software, respectively.

3. Results

3.1. δ^{18}O and δD of Soil and Xylem Water in Forests along Successional Gradients

Whether in the CF, MCBF, or MEBF, the δ^{18}O and δD of the water derived from soil and xylem were distributed on the right side of the local meteoric water line (Figure 2a–c), indicating the occurrence of hydrogen and oxygen isotope fractionation with the conversion of precipitation into soil water and xylem water in the three forests. In addition, in the three above-mentioned forests along the successional gradients, the δ^{18}O and δD of xylem water in each tree were close to those of soil water (Figure 2a–c), demonstrating that the xylem water in this area originated from soil water.

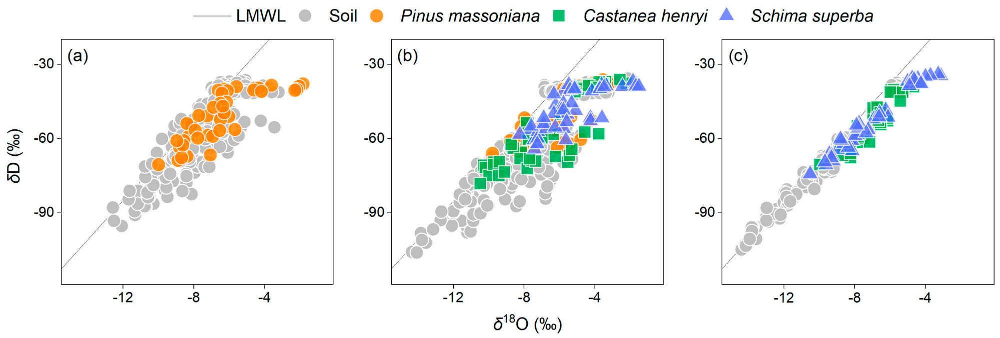


Figure 2. δ^{18}O and δD in soil water and xylem water (*Pinus massoniana*, *Castanea henryi*, and *Schima superba*) from the Coniferous Forest ((**a**), CF), Mixed Coniferous Broad-leaved Forest ((**b**), MCBF) and Monsoon Evergreen Broad-Leaved Forest ((**c**), MEBF). LMWL is the local meteoric water line (y = 7.88x + 9.41).

3.2. Water Utilization Characteristics of Dominant Trees in Forests at Different Successional Stages

The results based on a one-way ANOVA showed that, after light, moderate, and heavy rainfall, the water utilization ratios from the 0–20 cm and 20–40 cm soil layers by *P. massoniana* in the MCBF were significantly higher than that in the CF (77.6% vs. 56.2%), while those from the 60–80 cm and 80–100 cm soil layers in the MCBF were significantly lower than that in the CF (12.6% vs. 28.6%, Figure 3a–c). Additionally, after light rainfall, there was no difference in the water utilization ratio from the 40–60 cm soil layer by *P. massoniana* between the CF and MCBF. By comparison, after moderate and heavy rainfall, the water utilization ratio from the 40–60 cm soil layer by *P. massoniana* in the MCBF was significantly lower than that in the CF.

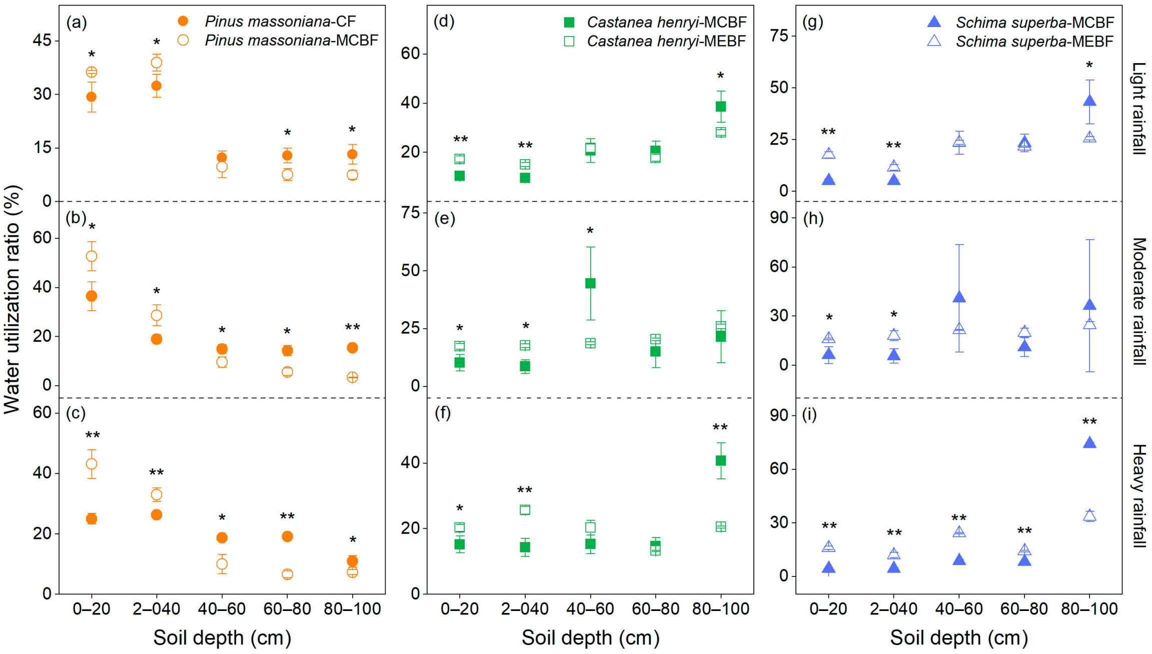


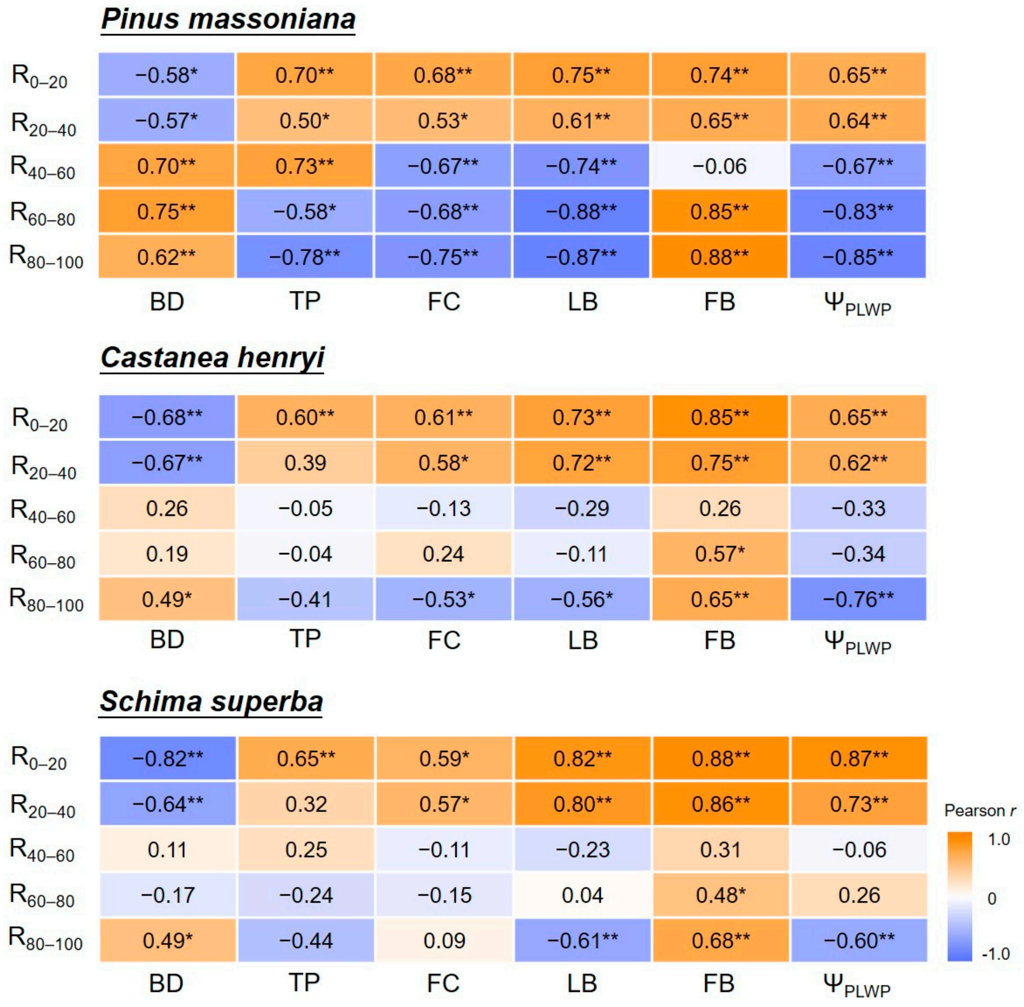
Figure 3. Water utilization ratio from each soil layer by trees in the Coniferous Forest (CF), Mixed Coniferous Broad-leaved Forest (MCBF), and Monsoon Evergreen Broad-Leaved Forest (MEBF) following light (**a**,**d**,**g**), moderate (**b**,**e**,**h**), and heavy (**c**,**f**,**i**) rainfall events. The dots, squares, and triangles represent the water utilization ratio by *Pinus massoniana* (**a**–**c**), *Castanea henryi* (**d**–**f**), and *Schima superba* (**g**,**h**,**i**), respectively. The error bar represents the standard error. * $p < 0.05$; ** $p < 0.01$.

Similar to *P. massoniana*, following light, moderate, and heavy rainfall events, the water utilization ratios from the 0–20 cm and 20–40 cm soil layers by *C. henryi* in the MEBF were significantly higher than that in the MCBF (37.8% vs. 22.8%, Figure 3d–f). Nevertheless, no difference existed in the water utilization ratio from the 40–100 cm layers between the MCBF and MEBF, except for that from the 80–100 cm layer after light and heavy rainfall and that from the 40–60 cm layer after moderate rainfall.

After light and moderate rainfall, the water utilization ratios by *S. superba* from the 0–20 cm and 20–40 cm soil layers in the MEBF were significantly higher than that in the MCBF (31.6% vs. 10.9%), while there was no difference in the water utilization ratios from the 40–100 cm soil layers by *S. superba* between the MCBF and MEBF except for the ratio from the 80–100 cm soil layer after a light rainfall event (Figure 3g,h). After a heavy rainfall event, the water utilization ratios from the 0–20 cm, 20–40 cm, 40–60 cm, and 60–80 cm soil layers by *S. superba* in the MEBF were significantly higher than that in the MCBF (66.4% vs. 25.7%), whereas the ratio from the 80–100 cm soil layer in the MEBF was significantly lower than that in the MCBF (33.6% vs. 74.3%, Figure 3i).

3.3. Factors Affecting Water Utilization Characteristics of Trees in Forests along Successional Gradients

The correlation analysis showed that the water utilization ratios (R) from the 0–20 cm and 20–40 cm soil layers ($R_{0–20}$ and $R_{20–40}$) from each type of tree were significantly correlated with soil/plant properties (Figure 4; Tables S2–S4), indicating that both factors may affect the $R_{0–20}$ and $R_{20–40}$. Specifically, the $R_{0–20}$ and $R_{20–40}$ of *P. massoniana*/*C. henryi*/*S. superba* were negatively associated with bulk density ($p < 0.05$), while they were positively related to other soil (total porosity and field capacity) and plant properties (leaf biomass, fine root biomass, and predawn leaf water potential). By contrast, the difference existed in the correlation between the R from the 60–100 cm soil layer and the soil/plant properties among various trees. Concretely, the R from the 60–100 cm soil layers ($R_{60–80}$ and $R_{80–100}$) of *P. massoniana* were significantly correlated with soil and plant properties ($p < 0.05$; Figure 4), suggesting that the two properties may affect the $R_{60–80}$ and $R_{80–100}$ of *P. massoniana*. The $R_{60–80}$ of *S. superba* and *C. henryi* were not related to soil and plant properties ($p > 0.05$), except for fine root biomass ($p < 0.05$; Figure 4). On the contrary, the $R_{80–100}$ of *S. superba* and *C. henryi* were significantly correlated with all plant properties and some soil properties ($p < 0.05$; Figure 4), implying that both the two properties may affect the $R_{80–100}$ of *S. superba* and *C. henryi*.



Pinus massoniana

	BD	TP	FC	LB	FB	Ψ_{PLWP}
$R_{0–20}$	−0.58*	0.70**	0.68**	0.75**	0.74**	0.65**
$R_{20–40}$	−0.57*	0.50*	0.53*	0.61**	0.65**	0.64**
$R_{40–60}$	0.70**	0.73**	−0.67**	−0.74**	−0.06	−0.67**
$R_{60–80}$	0.75**	−0.58*	−0.68**	−0.88**	0.85**	−0.83**
$R_{80–100}$	0.62**	−0.78**	−0.75**	−0.87**	0.88**	−0.85**

Castanea henryi

	BD	TP	FC	LB	FB	Ψ_{PLWP}
$R_{0–20}$	−0.68**	0.60**	0.61**	0.73**	0.85**	0.65**
$R_{20–40}$	−0.67**	0.39	0.58*	0.72**	0.75**	0.62**
$R_{40–60}$	0.26	−0.05	−0.13	−0.29	0.26	−0.33
$R_{60–80}$	0.19	−0.04	0.24	−0.11	0.57*	−0.34
$R_{80–100}$	0.49*	−0.41	−0.53*	−0.56*	0.65**	−0.76**

Schima superba

	BD	TP	FC	LB	FB	Ψ_{PLWP}
$R_{0–20}$	−0.82**	0.65**	0.59*	0.82**	0.88**	0.87**
$R_{20–40}$	−0.64**	0.32	0.57*	0.80**	0.86**	0.73**
$R_{40–60}$	0.11	0.25	−0.11	−0.23	0.31	−0.06
$R_{60–80}$	−0.17	−0.24	−0.15	0.04	0.48*	0.26
$R_{80–100}$	0.49*	−0.44	0.09	−0.61**	0.68**	−0.60**

Figure 4. Correlations between the water utilization ratio of trees from each soil layer and predictors. $R_{0–20}$, $R_{20–40}$, $R_{40–60}$, $R_{60–80}$, and $R_{80–100}$ refer to the water utilization ratios from 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm soil depths, respectively. BD, TP, FC, LB, FB, and Ψ_{PLWP} represent bulk density, total porosity, field capacity, leaf biomass, fine root biomass, and predawn leaf water potential, respectively. The color and numbers correspond to the strength of the correlation (decrease/increase of color intensity = loss of/gain of correlation). * $p < 0.05$; ** $p < 0.01$.

3.4. Primary Drivers of Water Utilization of Trees in Different Successional Forests

To clarify the drivers influencing the water utilization of trees, this study introduced two statistical methods, including a variation partitioning analysis and a random forest model, to determine the relative importance of soil and plant properties on the water utilization of each tree. Variation partitioning analysis showed that plant properties explained 19.0%, 18.0%, 9.1%, 25.4%, and 5.5% of the variation in the $R_{0–20}$, $R_{20–40}$, $R_{40–60}$, $R_{60–80}$, and $R_{80–100}$ of *P. massoniana*, respectively, while soil properties only explained 6.3%, 11.3%, 3.6%, 3.9%, and 3.7% of the variation (Figure 5a–e). Similarly, the pure effect of plant properties on the water utilization of *C. henryi*/*S. superba* was higher than that of soil properties (Figure 5f–o). These results indicated that plant properties were the primary driver influencing the water utilization characteristics of various trees. The random forest model also confirmed that plant properties were the primary factor in the water utilization of each tree. Specifically, the $R_{0–20}$ and $R_{20–40}$ of *P. massoniana*/*C. henryi*/*S. superba* and the $R_{40–60}$, $R_{60–80}$, and $R_{80–100}$ of *P. massoniana* were mainly influenced by vegetation such as fine root biomass, leaf biomass, and predawn leaf water potential (Figure 6a–g,k,l). Taken together, the water utilization of various trees was mainly regulated by plant properties.

Figure 5. Relative contribution of soil and plant factors to the water utilization ratio of trees from the (**a**,**f**,**k**) 0–20 cm, (**b**,**g**,**l**) 20–40 cm, (**c**,**h**,**m**) 40–60 cm, (**d**,**i**,**n**) 60–80 cm, and (**e**,**j**,**o**) 80–100 cm soil layers.

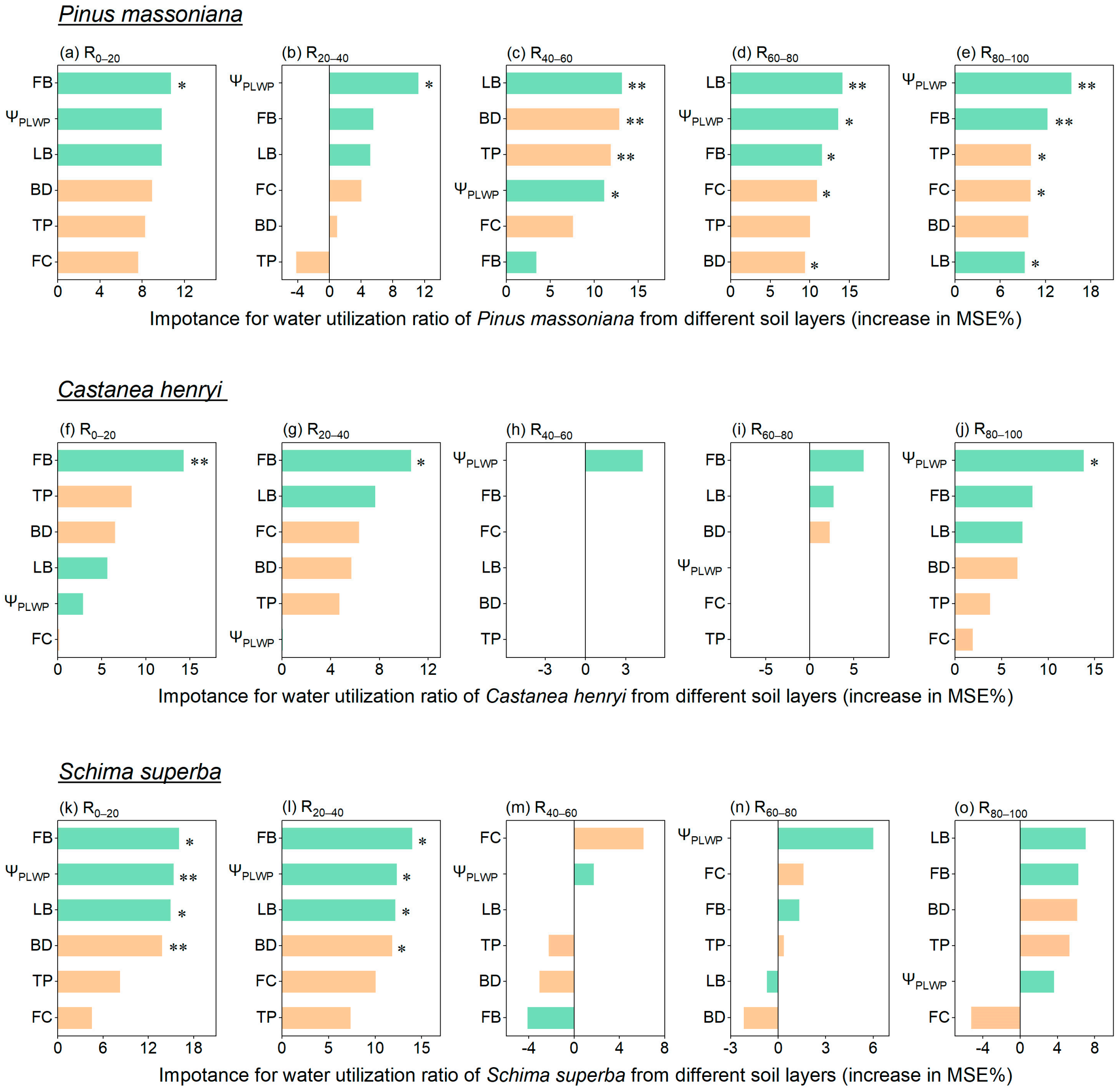


Figure 6. Importance of soil and plant properties to the water utilization ratio of trees conducted using random forest models in the (**a**,**f**,**k**) 0–20 cm, (**b**,**g**,**l**) 20–40 cm, (**c**,**h**,**m**) 40–60 cm, (**d**,**i**,**n**), 60–80 cm and (**e**,**j**,**o**) 80–100 cm soil layers. BD, bulk density; TP, total porosity; FC, field capacity; LB, leaf biomass; FB, fine root biomass; Ψ_{PLWP}, predawn leaf water potential. Orange and green bars represent soil and plant attributes, respectively. ** and * indicate $p < 0.01$ and $p < 0.05$, respectively.

4. Discussion

4.1. Differences in Water Utilization of Each Tree in Forests Along Successional Gradients

This study indicated that in both the early- (CF) and mid-successional (MCBF) forests, *P. massoniana* mainly absorbed water from shallow soil layers (0–40 cm, Figure 3a–c), while in the mid- and late-successional (MEBF) forests, zonal vegetation such as *C. henryi* and *S. superba* primarily used water from middle and deep soil layers (40–100 cm, Figure 3d–i). Such a phenomenon could be ascribed to the root distribution characteristics of various trees [46–48]. Specifically, the root of *P. massoniana* is mainly distributed in shallow soil layers, while that of *C. hystrix* and *S. superba* is mainly distributed in deep soil layers. Therefore, regardless of the successional stage, *P. massoniana* mainly utilized shallow soil water, yet *C. hystrix* and *S. superba* mainly absorbed deep soil water.

Our results also illustrated that from the early to the mid-successional stage, the water utilization ratio of *P. massoniana* from shallow soil layers (0–40 cm) significantly improved, while that from deep soil layers (60–100 cm) significantly decreased (Figure 3a–c). Similarly, from the middle to the late-successional stage, the water utilization ratio of *C. henryi* and *S. superba* from the shallow soil layer significantly increased, whereas that from the deep soil layer significantly declined (Figure 3d–i). The above observations indicate that with progressing forest succession, some dominant trees increase their water utilization ratio for the shallow soil layer, which may be caused by the following two reasons. On the one hand, the differences in root distribution among various trees lead to changes in their water utilization characteristics at different successional stages. Specifically, given that the root of *P. massoniana* and zonal broad-leaved tree species (*C. henryi* and *S. superba*) were mainly distributed in the soil layers 0–40 cm and 60–100 cm, respectively (Table S4), in the mid-successional stage, the three trees exhibited different water absorption niches after zonal broad-leaved tree species entering the *P. massoniana* forest. That is, shallow-root trees (*P. massoniana*) tend to use water from shallow soil layers, while deep-root trees (*C. henryi* and *S. superba*) utilize deep soil water [49,50]. Therefore, compared with *P. massoniana* in the early-successional forest, *P. massoniana* in the mid-successional forest had an increased water utilization ratio from the shallow soil layer. In the late-successional forest, *P. massoniana* disappeared, and its original water absorption niche, shallow soil water, was also released. *C. henryi* and *S. superba*, which originally had the deep soil water absorption niche, increased their water utilization ratio from the shallow soil layer. On the other hand, shifts in soil properties of forests along successional gradients induce changes in the water absorption of each tree. In our study, the field capacity and total porosity in the 0–40 cm soil layers in the mid-successional forest (MCBF) were significantly higher than those in the early-successional forest (CF, Table S2). Similarly, these two soil properties from the 0–40 cm soil layers in the late-successional forest (MEBF) were significantly higher than those in the mid-successional forest (Table S2). The above-mentioned differences in soil properties of forests at different successional stages may result in a higher soil water storage in the mid-successional forest compared to the early-successional forest and also lead to a higher soil water storage in the late-successional forest than the mid-successional forest. As a result, *P. massoniana* absorbed more water from the 0–40 cm soil layers in the mid-successional forest compared to the early-successional forest, while *C. henryi* and *S. superba* utilized more water from the 0–40 cm soil layers in the late-successional forest than in the mid-successional forest. Taken together, both vegetation and soil properties may cause changes in the water utilization characteristics of *P. massoniana*, *C. henryi*, and *S. superba* among different successional forests.

4.2. Primary Factors Affecting the Water Utilization Characteristics of Various Trees in Different Successional Forests

The observation based on the random forest model and variation partitioning analysis showed that the water utilization of *P. massoniana*, *C. henryi*, and *S. superba* was mainly regulated by plant properties (Figures 5 and 6). Among plant properties, fine root biomass was a critical factor regulating the water utilization of trees, which was attributed to the correlation between plant water absorption depth and fine root distribution [51,52]. Thus, a larger fine root biomass within soil layers led to a higher ratio of water utilization from soil layers [53,54]. This phenomenon has also been found in previous studies, revealing that the higher water utilization rate from the deep soil layer by Mediterranean species was mainly attributed to the more fine root biomass in this soil layer [55]. In our case, the fine root biomass of *P. massoniana* from the shallow soil layers in the early-successional forest (CF) was significantly lower than that in the mid-successional forest (MCBF), while that in deep soil layers in the former was significantly higher than in the latter (Table S4). Hence, *P. massoniana* in the MCBF had a significantly higher water utilization ratio from shallow soil layers than in the CF and a significantly lower water absorption percentage from deep soil layers than in the CF. Similarly, in the mid-successional forest, the fine root biomass of *C. henryi* and *S. superba* distributed in the shallow soil layer was significantly lower than that in the late-successional forest (MEBF), whereas the fine root biomass from the deep soil layer in MCBF was significantly higher than that from the MEBF (Table S4). Therefore, the water utilization ratio from shallow soil layers of *C. henryi* and *S. superba* in the latter was significantly higher than that in the former, and the water absorption percentage from the deep soil layer in the latter was significantly lower than that in the former. Besides fine root biomass regulation, leaf biomass could modulate the water utilization characteristics of trees through leaf transpiration regulation, as transpiration is the power source of tree water absorption [56,57]. Therefore, higher leaf biomass induces stronger tree transpiration, subsequently leading to trees absorbing more water to maintain metabolism [30,31]. In this study, the leaf biomass of *P. massoniana* in the MCBF was significantly higher than that in the CF (Table S3). Thus, its water absorption was also greater than that in the CF. Similarly, the leaf biomasses of *C. henryi* and *S. superba* in MEBF were significantly higher than those in the MCBF (Table S3), indicating their higher water absorptions in the MEBF compared to the MCBF. In addition, leaf water potential could regulate the water utilization of trees. It has been confirmed that leaf water potential could be used to evaluate the water use status of plants [32,33]. Specifically, a lower leaf water potential denotes more severe drought stress on plants, while conversely, it indicates that plants absorb more water [58,59]. Such an opinion has also been confirmed by Bello et al. [60] and Wu et al. [61] for *Quercus petraea* and *Myricaria squamosa*, respectively. In this study, the predawn leaf water potential of *P. massoniana* in the MCBF was significantly higher than that in the CF (Table S3), and the predawn leaf water potential of *C. henryi* and *S. superba* in the MEBF was significantly higher than that in the MCBF (Table S3). This indicates that the water absorption of *P. massoniana* in the MCBF was greater than that in the CF, and the water absorption of *C. henryi* and *S. superba* in the MEBF was smaller than that in the MCBF.

Compared with vegetation, soil properties, including bulk density, total porosity, and field capacity, had less pure effects on the water utilization of trees, but they had a larger overlap with plant properties. Such a phenomenon could be attributed to the following two aspects. First, although soil with a lower bulk density, higher total porosity, and field capacity has stronger water storage capacity [22,23], the main organ for tree water absorption is fine roots. Therefore, soil properties exert a small direct impact on the water utilization of trees, which could only indirectly affect the water utilization by influencing plant properties. This result is also supported by previous research, demonstrating that compared to plant parameters, soil properties exhibit a smaller effect on the water utilization of *Cunninghamia lanceolata*, but they can indirectly affect its water utilization by regulating plant factors [34]. In this study, the bulk density of the 0–80 cm soil layers in the MCBF was significantly lower than that in the CF, and the bulk density of the 0–100 cm soil layers in the MEBF was significantly lower than that in the MCBF (Table S2). Hence, the soil properties of the MCBF and MEBF were conducive to fine root growth, thereby indirectly affecting the water utilization of trees. Second, the sampling periods in this study were after the occurrence of rainfall events rather than the seasonal drought period, and thus, water was not a limiting factor for tree growth during the study period. Consequently, although soil properties could affect water storage capacity, they could not directly impact plant water utilization. Taken together, the direct impact of soil properties on the water utilization of trees was lower than that of plant properties, but they could exert indirect effects by influencing vegetation.

It should be noted that in our case, the explained variations of soil and plant factors on the tree water utilization ratio in some soil layers are relatively low (Figure 5h,m,n). This phenomenon may be due to the fact that the effect of other soil (such as soil texture and soil organic matter) and plant (physiological indicators) parameters on tree water utilization were ignored in this study. For example, it has been reported that soil texture and soil organic matter could indirectly affect plant water utilization by regulating soil porosity and soil water holding capacity [26,27]. In addition, plant physiological indicators could influence plant water utilization by impacting photosynthesis, transpiration, and leaf stomatal conductance [34]. Therefore, in future research, it is necessary to explore the effects of the above-mentioned factors on tree water utilization to improve the explained variation in the model.

4.3. Implications

Our results demonstrate that, with progressing forest succession, the water utilization ratio from shallow soil layers by dominant trees increased, while that from deep soil layers decreased. This phenomenon is contrary to the conventional view that the plant water utilization ratio from deep soil layers would increase during the succession process accompanied by root distribution deepening. These inconsistent observations may be attributed to the following explanation. Specifically, previous studies mainly concentrated on the root distribution of single species, neglecting the root distribution relationships among multiple types of plants. In fact, with the development of succession, various plants in the same habitat may exhibit two types of ecological niche relationships, including competition and complementation. If several plants exhibit a competitive relationship, their root distribution will deepen, and their water utilization rate from the deep soil layer will increase. However, if they display a complementary relationship, some plants' root systems become shallower, and their water utilization rate from shallow soil layers could increase, while other plants show the opposite pattern. Therefore, in the future, we should pay more attention to exploring the differences in water utilization of dominant trees in forests along successional gradients rather than simply inferring the water utilization of a single species based on its root distribution.

5. Conclusions

In summary, based on the stable hydrogen and oxygen isotopes coupled with the Bayesian mixed model (MixSIAR), our study found that in the early-successional forest (CF), the water utilization ratio to shallow soil layers by *P. massoniana* was significantly lower than that in the mid-successional forest (MCBF), while its water utilization ratio to deep soil layers in the CF was significantly higher than that in the MCBF. Similarly, the water utilization ratio from shallow soil layers of *C. henryi* and *S. superba* in the mid-successional forest (MCBF) was significantly lower than that in the late-successional forest (MEBF), whereas their water utilization ratio from deep soil layers in the MCBF was significantly higher than that in the MEBF. Furthermore, the variation partitioning analysis and random forest model indicated that the difference in the water utilization characteristics of each tree in different successional forests was mainly attributed to their distinct plant properties. The above results challenged the traditional view that the water utilization ratio of plants from deep soil layers increased during the succession process and provided new insights for understanding the direction of forest succession.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15081329/s1, Figure S1: Rain gauge; Table S1: Average diameter, crown width, and tree height of dominant species in forests with different successional stages; Table S2: Soil properties (mean ± SD, n = 3) of forests in different successional stages; Table S3: Plant properties (mean ± SD, n = 3) of dominant species in forests with different successional stages; Table S4: Fine root biomass ($g \cdot m^{-2}$, mean ± SE, n = 3) of dominant species in forests with different successional stages.

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