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ARTICLE

Relationship of Water Uptake Depth with Tree Height and Resource-Use Strategies in a Warm-Temperate Secondary Forest in Central Japan

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ABSTRACT

Understanding water uptake depth and its relationship with functional traits offers valuable insights into resource-use partitioning among coexisting tree species as well as forest responses to drought. However, knowledge about water uptake patterns in vertical soil layers, especially among increasingly widespread secondary forest tree species, remains limited. In this study, we investigated interspecific and seasonal variations in water uptake depth among seven coexisting tree species over a 2-year period in a warm-temperate secondary forest in central Japan. We also analyzed the relationships of water uptake depth with tree height and functional traits, including specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (N) content, and wood density (WD), to discern resource-use and -acquisition strategies. Results revealed that taller trees, especially when soil water is scarce, tend to access deeper soil water sources, indicating that water source partitioning is correlated with tree height. This interspecific and temporal variation in water sources likely stratifies trees to facilitate coexistence within the forest. Water uptake depth was primarily associated with WD and LDMC: trees absorbing more water from shallow soils during dry conditions exhibited lower WD and LDMC, indicating a proactive resource-use strategy. Conversely, SLA and leaf N content were orthogonal to water uptake depth, suggesting that strategies for acquiring belowground and aboveground resources may differ. Considering the alternation of tree species composition during secondary forest succession, our study highlights the importance of further data collection regarding root water uptake depth along successional stages to understand dynamic shifts in water uptake sources.

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1. Introduction

Global climate change is expected to increase drought intensity and frequency[1], altering soil water availability patterns at various depths, thereby impacting forest ecosystems. Hence, studies assessing root water uptake depth are garnering substantial attention[2]. Compared with shallow-rooted trees, deep-rooted trees may access more stable soil water sources during droughts[3]. In a severe European drought in 2018, trees relying on shallow soil water exhibited heightened drought vulnerability[4]. Such trees were also damaged more severely in a rainfall exclusion experiment[5]. These results highlight the importance of understanding water uptake depth for predicting forest hydrological responses to drought. However, tree water use patterns, especially in increasingly widespread secondary forests[6], remain poorly understood[7, 8].

Co-occurring tree species exhibit varying water uptake depths[9–11], with trees of varying size coexisting in multilayered forests potentially vertically partitioning soil water sources. Larger trees typically access deeper water[5, 12–14]. On the other hand, a global review indicates that the water uptake depth of evergreen trees tends to be greater than that of deciduous trees[15]. In warm secondary forests where deciduous and evergreen trees grow in the canopy and subcanopy layers, respectively[16], it is interesting to see which (size or life form) has the greater effect on tree water uptake depth. Although diameter at breast height (DBH) is often used as a tree size parameter, tree height, closely linked to hydraulic traits[17, 18], may better predict the relationship with water source depth. Temporal variation in soil water availability likely influences seasonal patterns of water uptake depth. Trees mainly tap shallow soil water during rainy seasons, shifting to deeper soil layers during dry seasons when water in upper layers is scarce[19, 20]. Such spatial and temporal water resource partitioning among co-occurring tree species could facilitate their coexistence by reducing competition for these resources[21].

Water uptake is associated with soil nutrient acquisition and aboveground water resource use; thus, water uptake depth may reflect interspecific variation in growth-related resource requirements and uses[22]. In Mediterranean shrublands, species using shallow soil water tend to exhibit a higher specific leaf area (SLA) and leaf nitrogen (N) concentration, indicating a more resource-acquisitive and nutrient-utilizing strategy[9]. Song et al.[21] reported similar trends, although the relationship varied with soil water availability. In addition to SLA, leaf dry matter content (LDMC) is a key trait correlated with resource use[23]; however, its relationship with water uptake depth remains unclear. In an Australian tropical forest, trees using shallower water sources tended to exhibit higher wood density (WD), associated with water storage capacity, growth rate, and drought tolerance[24–26], although such correlation was not detected in other forests[27, 28]. Data on the coordination between whole-plant functional traits provide valuable insights into ecological strategies[29, 30]; however, limited empirical data hinder our understanding of the relationship between water uptake depth and resource-use and -acquisition strategies, which serve as key indicators for estimating water uptake depth.

This study quantified water uptake depth for seven co-occurring broadleaved tree species across the canopy, subcanopy, and understory layers in a warm-temperate secondary forest. To identify interspecific and temporal variations in tree water sources, we measured isotopic vertical soil water profiles and xylem water isotopic composition (stable oxygen isotope) in three seasons over 2 years[31, 32]. We also measured leaf traits (SLA, leaf N concentration, and LDMC) and wood density, indicative of resource-use and -acquisition strategies, to determine their relationship with root water uptake depth. Specifically, we addressed the following questions: (1) Is tree height related to vertical partitioning of soil water sources? (2) Do interspecific water uptake depth patterns differ according to soil water availability? (3) Do relationships exist between root water uptake depth and aboveground functional traits?

2. Material and Methods

2.1. Study Site and Field Survey

Our field survey was conducted in a warm-temperate secondary forest situated at Higashiyama Campus, Nagoya

University, Nagoya, central Japan (35°15′ N, 136°97′ E, 135–150 m a.s.l.). The forest canopy is predominantly comprised of deciduous *Quercus variabilis* and *Quercus serrata* (Fagaceae), with evergreen *Quercus glauca* (Fagaceae), *Ilex pedunculosa* (Aquifoliaceae), and *Cleyera japonica* (Pentaphylacaceae) in the subcanopy layer, and evergreen *Eurya japonica* (Pentaphylacaceae) and deciduous *Lyonia ovalifolia* (Ericaceae) in the understory[33]. Meteorological data from the nearby Nagoya weather station collected during 1991–2020 indicate an annual mean temperature of 16.2 °C, with monthly mean temperatures ranging from 4.8°C in January to 28.2 °C in August[34]. Mean annual precipitation is 1578.9 mm, with mean monthly precipitation exceeding 50 mm throughout the year and surpassing 100 mm during March–October. The soil type is yellowish-brown forest soil formed on the Yagoto diluvial formation.

We sampled eight or nine individuals per species for dominant trees in the canopy and subcanopy layers in 2020 (5 species and 42 individuals in total) and in all three layers in 2021 (7 species and 58 individuals in total; **Table 1**). All individuals sampled in 2020 were resampled in 2021. These broadleaved trees were distributed within an 80 × 45 m area with a gentle slope. Plant and soil samples were collected during pre- (late May or early June), mid- (August), and post-summer (October or early November) periods in both 2020 and 2021, with each census completed within a single day. Total precipitation 30 days prior to each sampling date was 198.5, 104.5, and 269.0 during pre-, mid-, and post-summer periods in 2020, and 260.0, 139.5, and 129.0 mm in these periods during 2021, respectively. Mean daily temperature was 20.9 °C, 29.1 °C, and 17.5 °C during pre-, mid-, and post-summer periods in 2020, and 18.9 °C, 28.7 °C, and 24.1 °C in these periods during 2021, respectively. Sampling was conducted during relatively dry spells in each season, with no precipitation occurring more than 5 days prior to the sampling date (**Figure 1**), ensuring a distinct isotopic gradient of vertical soil water.

Tree xylem samples were obtained by cutting suberized twigs approximately 1 cm in diameter, with bark promptly removed. Soil samples were collected at five points near selected individuals using a hand auger, with samples taken every 10 cm to a depth of 100 cm. Owing to extreme hardness, especially in mid-summer, soil samples below 60 cm in depth could not be fully collected. The collected samples were immediately stored in screw-cap 20 mL glass vials, maintained in a cool box during fieldwork, and then frozen in the laboratory at –20 °C until analysis.

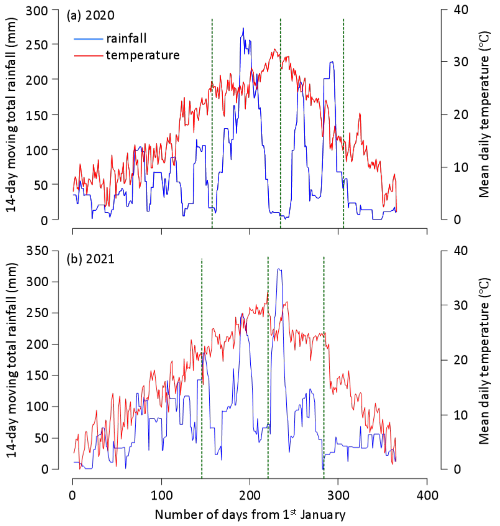

Figure 1. Time series of 14-day moving total rainfall (mm) and mean daily temperature (°C) in (**a**) 2020 and (**b**) 2021.

Note: Dotted vertical lines indicate sampling dates in each year's pre-, mid-, and post-summer periods.

Fully developed and healthy leaves were harvested from all trees during mid-summer in 2022 and stored at 4 °C for subsequent leaf trait measurements. Wood density was obtained by collecting wood cores approximately 5–15 cm in length from all trees at breast height (approximately 1.3 m from the ground) using an increment borer with a 5.15 mm radius. Tree height was measured using a TruPulse 200 (Laser Tech) for trees in the canopy and subcanopy layers, whereas a telescopic pole was used for those in the understory layer during the defoliated season in early 2023, when maximum tree height could be accurately determined.

2.2. Isotopic Analysis and Trait Measurement

We used the cryogenic vacuum distillation method to extract water from xylem and soil samples[32]. Soil water content (g g^{-1}) was determined by comparing sample weights before and after water extraction to assess soil drought levels during each census. Due to uncertainties regarding hydrogen stable isotope ratio depletion in xylem water compared with soil water, we focused solely on quantifying the oxygen stable isotope ratio to estimate water sources, consistent with previous studies[4, 9, 12, 35]. Oxygen stable isotopes in extracted water were analyzed at Mie University,

Table 1. Species information, sample number (N), and mean tree size (±SD) for each studied species.

Species	Abbreviation	Layer*	Life Form**	N	DBH (cm)		Height (m)	
Quercus variabilis	Qv	C	DB	9	34.5	(4.7)	17.7	(2.3)a
Quercus serrata	Qs	C	DB	8	35.7	(5.1)	15.8	(4.1)a
Quercus glauca	Qg	S	EB	8	10.4	(2.1)	8.9	(1.0)b
Ilex pedunculosa	Ip	S	EB	8	10.9	(2.4)	8.0	(1.3)b
Cleyera japonica	Cj	S	EB	9	9.4	(1.6)	7.5	(1.8)b
Lyonia ovalifolia***	Lo	U	DB	8	4.9	(1.2)	4.5	(0.7)c
Eurya japonica***	Ej	U	EB	8	5.4	(0.4)	4.5	(0.7)c

* C: canopy layer, S: subcanopy layer, U: understory layer.

** DB: deciduous broadleaved trees, EB: evergreen broadleaved trees.

*** Sampling was conducted in 2021.

Note: Different letters indicate significant differences in tree height among species.

Japan, using the GasBench II system connected to a Delta V isotope-ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA, USA), with a mean precision of ±0.21‰. The oxygen stable isotope ratio ($\delta^{18}O$) is expressed in standard delta notation (‰) relative to the Vienna Standard Mean Ocean Water as follows:

$$\delta^{18}\mathrm{O}\ (‰) = 1,000 \times \frac{(\mathrm{R}_{\mathrm{sample}} - \mathrm{R}_{\mathrm{standard}})}{\mathrm{R}_{\mathrm{standard}}} \quad (1)$$

where R_{sample} and $_{standard}$ represent the $^{18}O/^{16}O$ of the sample and standard, respectively.

Leaf traits, including SLA, leaf N content, and LDMC, were assessed using 10 intact, well-lit leaves from each individual. Leaf area was measured on scanned leaf images using freely available LIA32 software[36]. Fresh weights were recorded for each leaf, followed by drying in an 80 ℃ dry oven for 48 h to obtain dry weights. SLA (cm^2 g^{-1}) and LDMC (g g^{-1}) were calculated as leaf area divided by dry weight and dry weight divided by fresh weight, respectively. Two or three dried leaves from the same individual were ground together into a fine powder using a bead mill (TissueLyser QA-85200, Qiagen), and the leaf N concentration (%) for three samples per individual was measured using a C–N analyzer (Macro corder JM1000CN, J-Science Lab, Japan). For WD measurements, the fresh volume of wood cores was determined based on their length and diameter. Cores were subsequently oven-dried at 80 °C for at least 72 h until reaching a constant weight, with WD (g cm^{-3}) calculated as dry weight divided by fresh volume.

2.3. Data Analyses

We employed an isotopic mixing model within a Bayesian framework, implemented via the MixSIAR package[37] in R (version 4.1.2)[38], to estimate the proportions of different water sources used by each individual. This model estimated the contribution of each soil layer to the observed xylem water isotope ratio. Soil depth was categorized as shallow (0–20 cm) or mid-deep (20–100 cm), as the isotopic soil water gradient was most prominent between these depths across several censuses (refer to Results). Means and standard deviations (SDs) of soil water $\delta^{18}O$ at depths of 0–20 and 20–100 cm from five soil sampling points in each census served as source data, whereas the xylem water $\delta^{18}O$ of individual trees served as mixture data. Discrimination data were set to zero, and the model was run with three chains and 100,000 iterations (burn-in: 50,000; thin: 50).

Differences in soil water content among sampling periods within each year and soil $\delta^{18}O$ between shallow and mid-deep sources in each census were assessed via one-way analysis of variance (ANOVA), followed by a t-test with Bonferroni correction and Weltch's t-test, respectively. To compare proportions of mid-deep water sources among tree species, we used the Kruskal–Wallis test followed by the pairwise Wilcoxon rank sum test with Holm correction for multiple *post-hoc* comparisons. The relationship between tree height and mid-deep water source proportion was evaluated using the standardized major axis (SMA) method via the *smatr* package in R[39], which is preferred over type I regression for describing relationships between variables with error[40]. Seasonal differences among SMAs for each year were assessed using the test for common slopes[41].

Interspecific variations in leaf traits, wood density, and tree height were examined using the Kruskal–Wallis test followed by the pairwise Wilcoxon rank sum test with Holm correction. Principal component analysis (PCA) was conducted to determine whether water uptake depth correlated with leaf traits and wood density. Xylem water δ^{18}O in mid-summer of each year was employed for PCA, as water resource partitioning was pronounced during mid-summer in both years (refer to Results). PCA was performed on individual values using the *prcomp* function in R.

3. Results

3.1. Interspecific Variation in Water Uptake Depth and Its Seasonal Pattern

Mid-summer soil water content was 0.105 ± 0.018 and 0.126 ± 0.022 g g^{-1} in 2020 and 2021, respectively, and was significantly lower than that in the pre- (0.127 ± 0.018 and 0.155 ± 0.017 g g^{-1}, respectively) and post-summer (0.128 ± 0.023 and 0.117 ± 0.019 g g^{-1}, respectively) periods in both years ($P < 0.001$), except post-summer 2021 (**Figure 2**). Despite minor vertical gradients, soil water δ^{18}O profiles generally decreased from shallow to deeper soil layers across censuses (**Figure 3**). Shallow soil water (0–20 cm) exhibited higher δ^{18}O values compared with mid-deep soil water, with significant differences observed between depths in mid- and post summer 2020 (Welch's t test, $P < 0.01$).

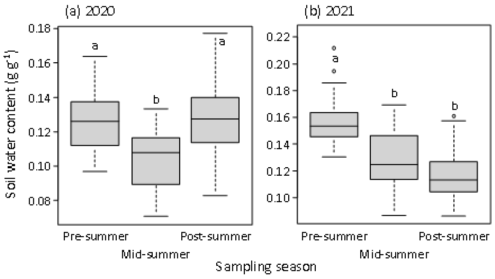

Figure 2. Soil water content (g g^{-1}) for each sampling season in (**a**) 2020 and (**b**) 2021.

Note: Different letters indicate significant differences.

Xylem water δ^{18}O variations among individuals across censuses ranged from 2.36‰ in mid-summer 2020 to 4.73‰ in post-summer 2021. Tree species exhibited differing water source proportions in pre-summer in 2020, mid-summer in both years, and post-summer in 2021 (**Figures 4** and **5**).

Notably, during mid-summer in both years, substantial differences in water proportions from the two soil layers were observed between species: *Q. variabilis* and *Q. serrata* in the canopy layer absorbed more mid-deep soil water compared with *I. pedunculosa* and *C. japonica* in the subcanopy layer in 2020 (**Figure 4**), whereas *E. japonica* in the understory relied more on shallow soil water compared with other species, except *C. japonica*, in 2021 (**Figure 5**). Although interspecific differences in water source proportions were not significant in post-summer 2021 (based on multiple *post-hoc* comparisons), each species exhibited water uptake patterns similar to those observed in mid-summer 2021. In pre-summer 2020, the proportion of mid-deep soil water in *Q. variabilis* was higher than that in *Q. glauca* in the subcanopy layer. Furthermore, trees within the same layer always exhibited similar water source proportions in each census.

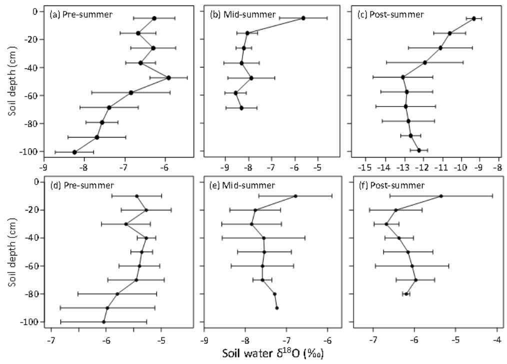

Figure 3. Soil water δ^{18}O (‰) along the vertical soil profile for each sampling season in (**a–c**) 2020 and (**d–f**) 2021.

Note: Values are means ± SDs.

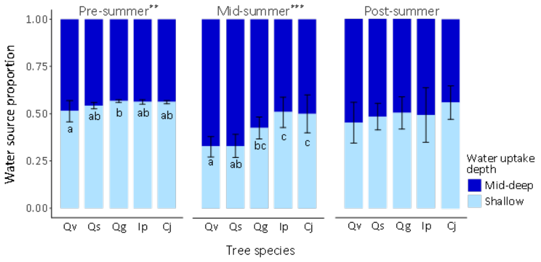

Figure 4. Proportions (mean ± SD) of two water sources (shallow: 0–20 cm; mid-deep: 20–100 cm) for each sampling season in 2020.

Note: Tree species are ordered by height, with different letters indicating significant interspecific differences in each season. Refer to **Table 1** for species codes.
**: $P < 0.01$, ***: $P < 0.001$ (Kruskal–Wallis test).

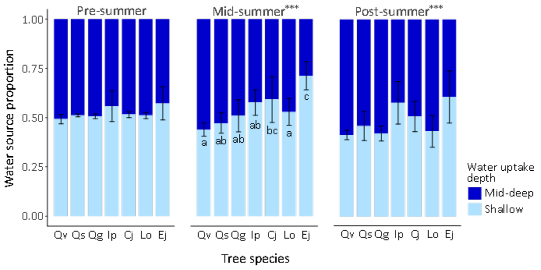

Figure 5. Proportions (mean ± SD) of two water sources (shallow: 0–20 cm; mid-deep: 20–100 cm) for each sampling season in 2021.

Note: Tree species are ordered by height, with different letters indicating significant interspecific differences in each season. Refer to **Table 1** for species codes.
**: $P < 0.01$, ***: $P < 0.001$ (Kruskal–Wallis test).

3.2. Tree Traits and Their Relationships with Water Uptake Depth

Mean height of tree species varied significantly among the canopy, subcanopy, and understory layers (15.8–17.7, 7.5–8.9, and 4.5 m, respectively; **Table 1**). The proportion of mid-deep water sources increased with tree height across all censuses, except post-summer 2020 (**Figure 6**). SMA regression analysis revealed significantly different slopes in the relationship between tree height and mid-deep water source proportion among sampling periods ($P < 0.001$ in both years): taller trees relied more on mid-deep water during drier mid-summer conditions in both years as well as in post-summer 2021, when soil water content resembled that in mid-summer 2021.

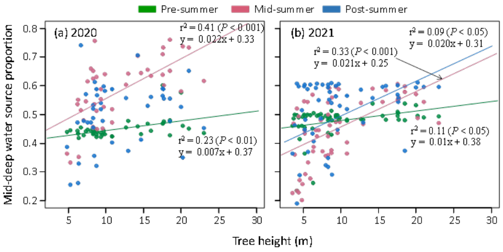

Figure 6. Relationship between tree height and the proportion of mid-deep water sources in the pre-, mid-, and post-summer periods of (**a**) 2020 and (**b**) 2021.

Note: Significant regression lines and their regression equations with r^2 values derived from the SMA method are shown.

Interspecific variations were observed in leaf traits and wood density. Species' mean values of SLA, leaf N content, LDMC, and WD were in the ranges of 98.3–247.7 $cm^2 g^{-1}$, 1.04%–1.95%, 0.35–0.49 $g g^{-1}$, and 0.54–0.74 $g cm^{-3}$, respectively (**Table 2**). The first two PCA axes based on xylem water δ18O, leaf traits, and WD accounted for 82.0% and 83.9% of the total variation in 2020 and 2021, respectively (**Figure 7**). The first axis (PC1) was mainly related to LDMC and WD, reflecting resource-use strategies, with species exhibiting higher LDMC and WD values indicative of slower growth and efficient resource conservation within well-protected tissues. Xylem water $\delta^{18}O$ was negatively related to PC1, suggesting that species tending to use shallow soil water adopt a more consumptive resource-use strategy. The second axis (PC2) was primarily associated with SLA; it was negatively correlated with WD in 2020 and positively correlated with leaf N content in 2021. Species with higher SLA and leaf N content generally adopted a more carbon-acquisitive strategy.

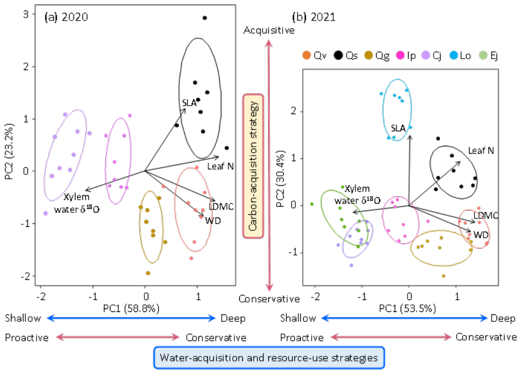

Figure 7. Biplot of the first two PCA axes for (**a**) 2020 and (**b**) 2021.

Note: Refer to **Table 1** for species codes.

4. Discussion

4.1. Interspecific and Temporal Water Source Partitioning among Stratified Trees

Our findings reveal that co-occurring tree species use soil water from varying depths, with taller trees showing a greater reliance on deep soil water, a trend consistent with previous studies conducted in tropical [11, 12, 42, 43] and temperate forests [14, 44]. This pattern may partly reflect positive allometry between aboveground plant size and root system size [45]: taller trees, with enhanced light interception, may allocate more photosynthates for deeper root growth [46]. However, even tall trees exhibited some reliance on shallow soil water, possibly due to higher nutrient concentrations typically found in shallower soil layers, which markedly decline with soil depth [47, 48]. Root water absorption appears to be governed by both water and nutrient availability.

Water source segregation was more pronounced during periods of low soil water availability. In 2020, during mid-summer when soil water content was lowest, canopy trees exhibited increased water uptake depth. Taller canopy trees, exposed to intense sunshine, higher wind speeds, and lower humidity, may compensate for higher evaporative demand [18, 49]. In 2021, when understory trees were also examined, clearer partitioning was observed during mid-summer, characterized by a decrease in water uptake depth among shorter trees. Under drier and hotter conditions, understory trees may proactively avoid competition with taller trees for deeper soil water. Such temporal variation in water sources, responding to fluctuating soil water availability, likely aids the coexistence of stratified trees within warm-temperate

Table 2. Aboveground traits (mean ± SD) across seven coexisting tree species.

Species	SLA (cm^2 g^{-1})		Leaf N (%)		LDMC (g g^{-1})		Wood density (g cm^{-3})	
Quercus variabilis	110.9	(12.2)a	1.73	(0.15)a	0.49	(0.03)a	0.74	(0.03)a
Quercus serrata	167.6	(18.6)b	1.95	(0.17)a	0.47	(0.03)a	0.66	(0.05)bd
Quercus glauca	98.3	(10.4)a	1.46	(0.08)b	0.47	(0.02)a	0.71	(0.03)ab
Ilex pedunculosa	121.5	(17.5)a	1.43	(0.13)b	0.43	(0.03)c	0.60	(0.02)d
Cleyera japonica	99.7	(12.3)a	1.04	(0.08)c	0.36	(0.02)b	0.56	(0.02)c
Lyonia ovalifolia	247.7	(19.5)c	1.82	(0.14)a	0.38	(0.03)b	0.55	(0.03)c
Eurya japonica	117.4	(13.6)a	1.21	(0.17)bc	0.35	(0.02)b	0.54	(0.03)c

Note: Different letters indicate significant differences in each trait among species.

secondary forests. Similar temporal partitioning of limited water sources has been observed in diverse forest ecosystems[13, 15, 19, 50, 51]. However, root water uptake depth may play a crucial role in determining hydraulic vulnerability for temperate tree species during severe drought spells[4]. Climate models predict that a reduction in rainfall events could result in decreased soil water moisture in northern temperate regions[52, 53]. Understory trees, typically reliant on shallow soil water, may face heightened susceptibility to drought, potentially altering tree species composition in warm-temperate forests.

Conversely, soil water partitioning among trees within the same layer was not observed in the present study, except for understory trees in mid-summer 2021. In each layer, trees consistently exhibited similar water uptake proportions from both soil sources across all seasons, indicating ongoing competition for water resources, particularly during periods of low water availability. Such intense water resource competition may be mitigated in part by differences in resource-use strategies[9]. Trees within the same layer were distinctly separated in the PCA ordination (**Figure 7**), highlighting how resource-use and -acquisition strategies collectively contribute to the coexistence of trees in forest ecosystems.

Greater uptake depth in evergreen trees was not detected in this study, indicating small effect of life form on tree water uptake depth as noted in the global review[15]. In the understory layer, where both deciduous and evergreen broadleaved trees were investigated in 2021, the pattern opposite to the global pattern was detected in mid-summer[16]: deciduous *L. ovalifolia* relied more on deeper soil water compared with evergreen *E. japonica*. Prior studies have also reported that deciduous trees rely on deeper water sources relative to evergreen trees[20, 54]. However, over a prolonged period, the expected replacement of deciduous canopy trees by evergreen trees, such as *Q. glauca* currently growing in the subcanopy layer of warm-temperate secondary forests[55], may alter water cycling in forest ecosystems. Although the water uptake depth of large *Q. glauca* trees remains unclear, some trees in old secondary forests have shown deeper water uptake depths during dry seasons compared with trees in young secondary forests[7]. Consequently, the water absorption pattern may differ from that of current deciduous canopy trees, potentially influencing forest ecosystem water dynamics. To better understand changes in water absorption patterns through succession, which will aid to improve local ecohydrological models, further data collection on root water uptake depth across successional stages in secondary forest is essential.

4.2. Linking Water Acquisition and Resource-Use Strategies

Given that LDMC and WD serve as indicators of plants' resource-use strategies, reflecting a trade-off relationship between consumptive resource use for rapid assimilation and growth and resource conservation[24, 56–58], our PCA results indicate that trees absorbing more water from shallow soils during dry conditions tend to exhibit a more proactive resource-use strategy with a higher growth rate. As nutrient content is generally higher in the soil surface layer[47, 48], it is reasonable to assume that trees actively using resources rely more on shallow soil water. This pattern aligns with findings showing that trees obtaining more water from deeper soils exhibit high wood density and grow slowly in Patagonian[59]. Conversely, it has been reported that trees with fast-growth strategies (i.e., low wood density) use deeper soil water[12] or show plasticity in their deep root mode[28]. Soil temperature offers one explanation for the observed differences, as prior studies were conducted in tropical or subtropical forests lacking seasonal winters with their low temperatures. Indeed, a global-scale review of tree water uptake across climatic zones supports this notion, indicating that trees in cold and temperate zones tend to exploit shallower soil water compared with those in arid and tropical zones[60, 61], as fine root production is promoted by higher soil temperatures in shallow depth after cold winter[62, 63].

Given that trees with higher WD possess greater water storage capacity and lower hydraulic conductivity[24, 55, 59], PC1 may reflect both water-acquisition and water-use strategies. Contrastingly, PC2 was associated with SLA (as well as leaf N content in 2021), which typically reflects a carbon capture strategy, suggesting a strategic divergence for acquiring belowground and aboveground resources. These findings contrast with a study of Mediterranean shrub communities, in which water uptake depth and SLA were aligned on the same PCA axis[9]. Similarly, water uptake from shallow soils and SLA were situated on the same axis in a subtropical evergreen tree study performed in a drought year but aligned on different axes during a normal, non-drought year[21]. Thus, the relationship between water acquisition and resource-acquisition/use strategies may vary among biomes and years with different soil water availability[15, 28].

5. Conclusions

Evaluation of water uptake depth for seven coexisting tree species in a warm-temperate secondary forest across three seasons revealed evidence of interspecific partitioning for water resources. Water source partitioning was correlated with tree height: taller trees accessed deeper water sources, especially when soil water availability was low. In the understory layer, deciduous trees relied more on deeper soil water compared with evergreen ones in mid-summer. In addition, this study highlights the relationship between water acquisition depth and resource-use strategies, orthogonal to aboveground resource (carbon) capture strategies, likely facilitating tree coexistence in forests through mitigation of constant competition for water resources among trees in the same layer. Considering the expected change in tree species composition through succession, such as the increase in evergreen broadleaved trees across all layers, continuous and repeated monitoring of water uptake depth in secondary forests is imperative to elucidate dynamic shifts in water uptake sources through succession. This insight will be essential for informing forest management practices that account for the water cycle. Finally, this study underscores the need for further investigation of trees' water uptake depths in secondary forests, given the increasing worldwide prevalence of these forests and the potential for major changes in water uptake patterns.

Author Contributions

Conceptualization, methodology, field work, data curation, data analysis, writing—review and editing, writing original draft, supervision, M.N.; stable isotopic experiment, writing—review, N.M.; field work, data analysis, writing—review, C.; field work, data analysis, writing—review, K.H.

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Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

Data will be available on appropriate request.

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Conflicts of Interest

The authors declare that there are no known competing financial interests or personal relationships capable of influencing the work reported in this paper.

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