Matching root water uptake patterns to fine root and soil water distributions

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Research Article

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Abstract

Aims

Exploring the relationships between water uptake, fine root, and soil water is essential for many fields, such as plant physiology, ecological hydrology, and water conservancy.

Methods

In four Populus tomentosa stands with different ages (young and mature) and stand structures (low and high stand density), we matched root water uptake patterns obtained from stable isotope techniques with fine root and soil water distributions, respectively. The effects of soil water content and meteorological factors on these matching degrees were further explored.

Results

It was found that the water uptake pattern was closer to soil water distribution than to fine root distribution in mature stands, while water uptake pattern matched both fine root and soil water distribution closely in young stands. Increased competition intensity within a stand would suppress the matching degree between water uptake patterns and fine root distribution, but would have little effect on the matching degree between water uptake patterns and soil water distribution. There is a relatively high positive or negative correlation between these two matching degrees in all four stands. Compared with the direct effect of soil water content, the influence of meteorological factors on matching degrees was relatively weak.

Conclusion

The results indicate that the expression of water uptake function of the young stand depends on a combination of root structure and available water resources, while the water uptake function of mature stands is driven more by available water resources rather than root structure.

1 Introduction

Root water uptake is a key ecohydrological process and an essential component in the terrestrial biosphere model (Fan et al., 2017; Feddes et al., 2001; Jackson et al., 2000; Kleidon and Heimann, 1998). The spatial distribution of the root system is generally considered to be the primary factor in determining plant water uptake, principally because the placement of roots in the soil delineates the zone of soil exploration and restricts the potential amount of available water (Jackson et al., 1996; Nippert and Knapp, 2007; Warren et al., 2015). In addition, the distribution and quantity of water uptake by roots are also affected by the distribution and amount of available soil water (Gardner, 1964; Lobet et al., 2014).
Therefore, the relationships between root water uptake, spatial root distribution, and soil water have been the subject of concern in many fields such as plant physiology, ecohydrology, and water conservancy (Fan et al., 2017; Feddes et al., 1976; Jackson et al., 2000).

Accurately predicting root water uptake remains a critical conundrum in ecological, hydrological, and climate models. Most previous models calculated root water uptake according to the soil water availability and root distribution proportion in different layers within the root zone (Albasha et al., 2015; Fan et al., 2017; Foley et al., 1996; Jing et al., 2014; Zhu et al., 2017). However, an increasing number of studies showed that root water uptake would shift to wet root zones to meet the transpiration demand under water stress and heterogeneous soil moisture (i.e., compensatory root water uptake), which gave rise to spatial differences between root water uptake and root distribution (Green and Clothier, 1999; Jarvis, 1976; Šimůnek and Hopmans, 2009; Thomas et al., 2020). Further, some studies suggested that root water uptake pattern may be more associated with the spatial distribution of soil water than the root system (Kühnhammer et al., 2020; Kulmatiski et al., 2017). The compensatory water uptake function has received more attention and has been incorporated into the water uptake model (Cai et al., 2018; Šimůnek and Hopmans, 2009; Zhu et al., 2017). To our knowledge, however, studies which have quantified the relationship between root water uptake pattern and root or soil water distributions were mainly investigated in crops or herbaceous rather than large root system (Doussan et al., 2006; Javaux et al., 2013; Schnepf et al., 2020). Compared with herbaceous, the root system of trees is more complex, extensive, and deep, and their water uptake sources are more abundant and diverse (e.g., groundwater, deep soil water) (Drake et al., 2011; Geng et al., 2022; Huo et al., 2018). Therefore, understanding the information about trees is beneficial for the further improvement of functional structural root models.

Parameterization of root water uptake models in ecological, hydrological, and climate research has often been limited to the relatively shallow soil layers (Doussan et al., 2006; Gardner, 1991; Vrugt et al., 2001). However, deep roots, usually defined as root systems in the soil below 1 m depth, are a common trait among a wide range of plant species and biomes (Maeght et al., 2013; Pierret et al., 2016). The functions of deep roots, such as absorbing deep soil water or groundwater and hydraulic redistribution, are critical for maintaining physiological and ecological functions of plants when shallow soil becomes dry and precipitation is insufficient (Bleby et al., 2010; Caldwell et al., 1998; Christina et al., 2017; Dawson, 1996; Yang et al., 2017). Despite the increasing recognition of the functional significance of deep roots in multiple fields, current research efforts allocated to the study of deep roots remained disproportionate to those devoted to shallow roots. Better understanding deep roots and their functions in water uptake associated with soil water will help reassess the role of shallow roots and improve the performance of various ecological, hydrological, and climate models.

Quantifying root water uptake is the basis for revealing the interaction between root activity and soil resource availability. Previous studies usually related the spatial distribution of root water uptake to the variation of soil water content (Belmans et al., 1983; Green and Clothier, 1999; Panigrahi and Panda, 2003; Zhang et al., 2020). However, the limitation of this method is its difficulty to obtain information on changes in deep soil water, resulting in its inability to obtain root uptake in the complete root zone under
natural conditions in the field (Aggarwal et al., 2017; Belmans et al., 1983; Green et al., 2006; Janik et al., 2021). Advances in stable isotope techniques have facilitated the study of root water uptake. Now, stable isotope techniques are widely applied in the study of plant-water relationships (Dawson et al., 2020; Rothfuss and Javaux, 2017; Volkman et al., 2016; Yang et al., 2017). Several studies have obtained the distribution of root water uptake using stable isotope methods and compared it with the fine root distribution. They found that the fine root distribution was a weak predictor of root water uptake patterns (Ellsworth and Sternberg, 2015; Fruleux et al., 2020; Gao et al., 2018; Kühnhammer et al., 2020). However, the relationships between root water uptake pattern (determined by isotopic analysis), root distribution, and soil water distribution need rigorous quantitative testing.

The root water uptake patterns, fine root distribution, and soil water distribution in this study refer to distribution curves that vary with soil depth. We need an index to quantify their relationship. Pianka's standardized overlap value offers the possibility of achieving quantification, which is commonly used to describe the degree of overlap of ecological niches between different species (Pianka, 1973). In this study, this index was used to calculate the matching degree between water uptake patterns and fine root or soil water distribution curves.

Stand age and stand structure affect root water uptake (Drake et al., 2011; O'Keefe et al., 2019; Trogisch et al., 2016), root distribution (Ma and Chen, 2016; Yuan and Chen, 2012), and soil water status (Bucci et al., 2008; Liu et al., 2022; Tao et al., 2021; Wei and Liang, 2021). Therefore, stand age and structure should also affect the relationships between root water uptake and root distribution and soil water distribution. However, this speculation needs to be examined. To fill the knowledge gaps mentioned above, we investigated the distribution characteristics of root water uptake, fine roots, and soil water in four *Populus tomentosa* stands during the growing season in 2019. The objectives of this study were (1) to explore the dynamics of the matching degree between root water uptake pattern and fine root or soil water distribution over the growing season in four stands, and (2) to identify factors (e.g., gravimetric soil water content, vertical spatial heterogeneity of soil water, precipitation, and reference evapotranspiration) that affect the matching degree. We hypothesized that (a) with the increase of soil water, the matching degree between root water uptake pattern and soil water distribution gradually decreased, while the matching degree between root water uptake pattern and fine root distribution gradually increased; (b) seasonal changes in soil water will regulate the matching degree more effectively than climatic drivers.

2 Materials and methods

2.1 Study description

The study was conducted on a state-owned forest farm in the North China Plain, located in Gaotang County, LiaoCheng City, Shandong Province, China (36°48′ N, 116°05′ E; about 30 m above sea level). The region has a warm temperate monsoon climate, with an annual mean temperature of 13.9°C, annual precipitation of 553 mm, and potential evapotranspiration of 1880 mm. The groundwater level fluctuates between a depth of 6 to 9 m in this experimental site, which has a very flat terrain. The soil profile from 0
to 140 cm has a sandy loam texture, while the profile below 140 cm depth alternates silty loam and silty soil. The other soil physical and chemical properties can be found in Li et al. (2020) and He et al. (2021).

During the growing season (April–September) of 2019, we monthly investigated four *P. tomentosa* stands (YP<sub>LC</sub>, YP<sub>HC</sub>, MP<sub>LC</sub>, and MP<sub>HC</sub>; Fig. 1). Among them, YP<sub>LC</sub> and YP<sub>HC</sub> stands were young stands (3 years old), and MP<sub>LC</sub> and MP<sub>HC</sub> stands were mature stands (40 years old). The YP<sub>LC</sub> (6 m × 6 m; 277 trees ha<sup>−1</sup>), YP<sub>HC</sub> (3 m × 3 m; 1111 trees ha<sup>−1</sup>), and MP<sub>LC</sub> (6 m × 6 m; 277 trees ha<sup>−1</sup>) were all pure stands of *P. tomentosa* with different planting densities. The MP<sub>HC</sub> was a mixed stand of *P. tomentosa* and *Robinia pseudoacacia* with a planting density of 555 tree ha<sup>−1</sup> (3 m × 6 m). Information on the dimensions and location of the four forest stands can be found in Zhu et al. (2022).

The facilitative effects such as niche differentiation generated by mixing different tree species may alleviate the intensity of competition among trees (Brassard et al., 2011; Case et al., 2020; Rodríguez-Robles et al., 2020; Silvertown et al., 2015; Sun et al., 2017). Nonetheless, under the premise of high stand densities, resource competition may still outweigh potential facilitation in species-diverse ecosystems (Forrester, 2014). Therefore, in this study, we considered that the YP<sub>LC</sub> and MP<sub>LC</sub> stand had a low-density stand structure, while the YP<sub>HC</sub> and MP<sub>HC</sub> were stands with a high-density stand structure.

### 2.2 Measurement of meteorological factors

A weather station (Delta-T Devices Ltd, Cambridge, UK) was installed approximately 2.2 km away from the experimental stands to measure meteorological factors every 10 minutes from April to October 2019. These factors included precipitation, air temperature, relative humidity, wind speed and direction, solar radiation, and photosynthetically active radiation. Using the measured meteorological data, reference evapotranspiration was calculated using the Penman-Monteith (FAO 56 PM) method (Allen et al., 1998).

The experimental period was divided into three phases (Zhu et al., 2022) based on the distribution of precipitation during the growing season of 2019 (total: 459 mm): period I - drought period from April 1 to July 15 (accounting for 18% of the total precipitation), period II - wet period from July 16 to August 31 (accounting for 76% of the total precipitation), and period III - autumn drought period from September 1 to September 30 (accounting for 6% of the total precipitation). Daily reference evapotranspiration increased and then decreased during the growing season (total: 487 mm), reaching the peak point in June (Zhu et al., 2022).

### 2.3 Xylem and soil sampling

The xylem and soil samplings were conducted in the middle of each month from April to September 2019. During each sampling event, three average-sized trees of *P. tomentosa* in each stand were selected for xylem sampling before dawn. In the young stands (YP<sub>LC</sub> and YP<sub>HC</sub> stands), xylem samples (n = 3) were taken from 1-year-old branches in the middle canopy of each sample tree, and their bark and phloem were removed immediately after sampling. Mature trees of *P. tomentosa* are too tall to obtain xylem samples from the branches, so the xylem samples (n = 3) in the mature stands (MP<sub>LC</sub> and MP<sub>HC</sub> stands)
were collected from the tree trunk at 1.3 m height above the ground using a growth cone. It is assumed that no oxygen-18 ($^{18}$O) and deuterium ($^2$H) fractionation occurs during root water uptake and sap transfer within the xylem tissue (Ehleringer and Dawson, 1992; Zimmermann et al., 1968). Therefore, the difference in the locations of xylem sampled in mature and young stands should not affect the final determination of the source of root water uptake (De Deurwaerder et al., 2018). All xylem samples for isotope ratios determination were transferred to 8 ml glass vials and then sealed with parafilm.

Paired with xylem sampling, soil samples were collected near the sample trees. The soil sample was divided into two parts: one was placed directly in vials sealed with the parafilm for isotope ratios determination, and the other was placed in an aluminum box for gravimetric soil water content (SWC, %) determination. Soil sampling was performed at a spot of 50 cm away from each of the three sampled trees in the YP$_{LC}$ and YP$_{HC}$ stands and 100 cm away from each of the three sampled trees in MP$_{LC}$ stand. In the mixed stand (MP$_{HC}$), three sampling points were between the *P. tomentosa* and *R. pseudoacacia*, i.e., 150 cm distance from the sample trees of *P. tomentosa*. We measured the depth of root systems and found that the average rooting depth of 3-year-old trees and 40-year-old trees was 2.19 and 6.4 m, respectively. Therefore, at each spot, six samples were taken in 0–200 cm soil layer (i.e., 0–30, 30–50, 50–70, 70–100, 100–150, 150–200 cm) in the YP$_{LC}$ and YP$_{HC}$ stands, and in the MP$_{LC}$ and MP$_{HC}$ stands, eight samples were collected in 0–600 cm soil layer (i.e., 0–30, 30–50, 50–70, 70–100, 100–150, 150–200, 200–400, 400–600 cm). Uniform sampling was conducted for thick soil layers, for instance, when sampling the 400–600 cm soil layer, the soil layer was divided into four equal parts, i.e., 400–450 cm, 450–500 cm, 500–550 cm, and 550–600 cm. The four parts of the soil sample were then mixed and loaded into 8 ml glass vial.

Totally, 504 soil samples were collected for SWC determination, and 504 soil samples and 90 xylem samples were collected for isotope ratio determination. All these xylem and soil samples for isotope analyses were taken back to the laboratory and stored in a freezer (−20°C) until water extraction.

### 2.4 Fine roots sampling

Fine root sampling was conducted with a hand drill (diameter of 8 cm) in four stands at the end of September 2019. The fine root sampling was performed at the same spot as the soil sampling but at different soil depth intervals. In YP$_{LC}$ and YP$_{HC}$ stands, fine roots were sampled in the top 200 cm of the soil profile in 10-cm increments. In the MP$_{LC}$ and MP$_{HC}$ stands, fine roots were sampled in the top 600 cm of the soil profile in 10-cm intervals in the 0-140 cm soil layer and 20-cm intervals below the 140 cm depth. Ultimately, a total of 624 soil samples were collected for fine roots. Each soil sample was carefully hand-washed with tap water through a sieve with 0.104 mm mesh size to separate the roots from soil particles and organic matter. After washing, the roots are placed in water to select live roots manually. Live roots are lighter in color and more elastic than dead roots. These live roots were then placed in marked ziplock bags and kept frozen until root characteristics were measured.
The roots samples were carefully spread out on a transparent plastic sheet without overlapping and then scanned by a high-quality scanner (Epson Perfection V800 Photo, Epson, Japan). Both the root length and diameter were determined using the automatic image analysis software (WinRHIZO, Regent Instruments Inc., Quebec, Canada). In this study, fine roots were defined as all roots ≤ 2 mm in diameter (Block et al., 2006), which contain a mix of large-diameter transport roots and absorbing roots. The fine root length density (FRLD, cm cm\(^{-3}\)) was calculated as the total fine root length of a soil core (sample) volume.

### 2.5 Determination of root water uptake source

An automatic vacuum condensation extraction system (LI-2100, LICA, China) was used for xylem water and soil water extraction with > 98% water extraction efficiency and 99%-101% recovery rate (Li et al., 2023; Qiu et al., 2016; Wang et al., 2019a; Wang et al., 2017; Wang et al., 2019b; Xiao et al., 2020). Then the hydrogen and oxygen isotopic composition of all water samples were determined using the DLT-100 Liquid-Water Isotope Analyzer (LWIA, Los Gatos Research Inc., Mountain View, CA, USA) with a δ\(2^H\) precision of 0.40‰ and a δ\(18^O\) precision of 0.10‰. Spectral correction was utilized to remove the impact of methanol, by employing calibration curves with \(R^2 > 0.99\), following the analysis of water samples extracted from plants. All δ\(2^H\) and δ\(18^O\) values were calculated by Eq. (1) and reported in "δ", which expresses the isotopic composition of a material relative to that of an accepted standard (Vienna Standard Mean Ocean Water, V-SMOW) on a per mil (‰) basis.

\[
δ = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where δ is the isotope ratio and \(R\) is the molar ratio of heavy to light isotopes.

The contribution of each water source (i.e. different soil layers above mentioned) to root water uptake (RWU) was determined using a Bayesian isotope mixing model (R-package "MixSIAR", version 3.1), which considers uncertainties associated with discrimination factors and multiple source values (Stock et al., 2018). Specifically, an "id" column was created (with each "id" corresponding to one sample tree) in the raw data of xylem isotopic values (δ\(2^H\) and δ\(18^O\)) to assess the source of water uptake for each sample tree (refer to the official case of MixSIAR: Ex 6 Cladocera, https://brianstock.github.io/MixSIAR/articles/cladocera_ex.html). The raw data of xylem isotopic values were then added into the model, treating the "id" as a fixed effect. Next, the raw data of isotopic values from each water source were added into the model. Previous studies have shown that a common dryland riparian tree species, *Populus euphratica* Oliv., does not exhibit δ\(18^O\) δ\(2^H\) fractionation during water uptake (Zhao et al., 2016). Therefore, in this study, we assumed that *P. tomentosa* would also not exhibit δ\(18^O\) δ\(2^H\) fractionation during water uptake, and thus the discrimination data for both δ\(18^O\) δ\(2^H\) were set to zero. The model was run using the Markov Chain Monte Carlo (MCMC) option 'normal' (with a chain length of 100,000, burn-in of 50,000, thin of 50, and three chains) and 'Process only' error structure.
Gelman-Rubin and Geweke diagnostic tests were employed to assess whether the model had converged before accepting the output of “MixSIAR” (Stock et al., 2018).

2.6 Data analysis

The root water uptake generated from the Bayesian isotope mixing model represents the proportion of each water source to the total water uptake of the tree. As a result, the fine root length density and soil water content in each soil layer were converted into proportional values. To determine the degree of match between the vertical root water uptake pattern and the vertical fine root distribution or soil water distribution, Pianka’s overlap index (Pianka, 1973) was used (Eqs. 2, 3).

\[
M_{FR} = \frac{\sum_{i=1}^{n} P_{IF} P_{IR}}{\sqrt{\sum_{i=1}^{n} P_{IF}^2 \sum_{i=1}^{n} P_{IR}^2}}
\]

\[
M_{SR} = \frac{\sum_{i=1}^{n} P_{IS} P_{IR}}{\sqrt{\sum_{i=1}^{n} P_{IS}^2 \sum_{i=1}^{n} P_{IR}^2}}
\]

Where \( M_{FR} \) refers to a measure of matching degree between FRLD and RWU, \( M_{SR} \) refers to a measure of matching degree between SWC and RWU. \( P_{IF}, P_{IS}, \) and \( P_{IR} \) represent the proportions of FRLD, SWC, and RWU in the soil layer \( i \) to all soil layers, respectively. Pianka’s index values range between 0 (no match) and 1 (complete match).

To analyze the effects of stands or soil layers on the isotopic value, a one-way ANOVA was conducted. Post-hoc analysis was performed using the least significant difference (LSD) test at \( \alpha = 0.05 \). The relationship between various drivers and the degree of match was explored using Pearson’s correlation coefficient. All statistical analyses and graphical illustrations were conducted using R software (v.4.0.2, R Core Team, 2020).

3 Results

3.1 Environmental conditions

During period I, the average soil water content across the soil profile (SWC\text{profile}) tended to increase and then decrease in the YP\text{HC} stand, while it tends to decrease gradually in the other three stands (Fig. 2A, B, C, D). The SWC\text{profile} increased in period II and decreased in period III for all four stands. The seasonal dynamics of the coefficient of variation of soil water content across the soil profile (CV\text{SWC}) were not completely consistent among the four stands. In period I and period II, the CV\text{SWC} showed a trend of
increasing and then decreasing in all stands (Fig. 2E, F, G, H), with a peak in June for the YP_{LC} stand, in June and July for the YP_{HC} stand, and in May for both MP_{LC} and MP_{HC} stands (Fig. 2E, F, G, H). In period III, all stands showed an increasing trend in CV_{SWC}.

### 3.2 Isotopic characteristics

The changes in isotopic values over the growing season had similar patterns in all four stands, regardless of soil layer (shallow, middle, or deep) or xylem (Fig. 3). The isotopic values in shallow soil water showed a decreasing then increasing, and then decreasing pattern in period I, a decreasing pattern in period II, and an increased pattern in period III (Fig. 3). The isotopic values in middle and deep soil water fluctuated relatively steadily throughout the growing season (Fig. 3). The trend of fluctuations in xylem isotopic values during the growing season differed significantly among the four stands (Fig. 3). There was a significant decrease in xylem isotopic values in period II (wet season) in the young stands (YP_{LC} and YP_{HC}) (Fig. 3A, B, E, F), while xylem isotopic values in the mature stands (MP_{LC} and MP_{HC}) were relatively stable over the growing season (Fig. 3C, D, G, H).

Regarding the isotopic values averaged over the growing season, there were no significant differences between shallow and deep soil water in both YP_{LC} and YP_{HC} stands ($P > 0.05$; Table 1). The average isotopic values were significantly higher in shallow and deep soil layers than in the middle soil layer ($P < 0.05$; Table 1). In contrast, in the MP_{LC} and MP_{HC} stands, there were significant differences in the average isotopic values among the three soil layers, with the lowest values in the middle soil layer and the highest values in the shallow soil layer ($P < 0.05$; Table 1).
Table 1
Isotopic values of soil water averaged over the growing season in different soil layers of the four stands.

<table>
<thead>
<tr>
<th>Isotope ratio</th>
<th>Stands</th>
<th>Shallow soil layer (0–30 cm)</th>
<th>Middle soil layer (30–100 cm)</th>
<th>Deep soil layer (&gt; 100 cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>δ²H (‰)</td>
<td>YP&lt;sub&gt;LC&lt;/sub&gt;</td>
<td>-63.77 ± 18.97 aA</td>
<td>-73.51 ± 9.30 bB</td>
<td>-57.33 ± 3.75 aA</td>
</tr>
<tr>
<td></td>
<td>YP&lt;sub&gt;HC&lt;/sub&gt;</td>
<td>-62.29 ± 20.19 aAB</td>
<td>-67.15 ± 9.04 aB</td>
<td>-57.47 ± 3.67 aA</td>
</tr>
<tr>
<td></td>
<td>MP&lt;sub&gt;LC&lt;/sub&gt;</td>
<td>-59.13 ± 18.74 aA</td>
<td>-75.91 ± 11.9 bC</td>
<td>-68.51 ± 9.18 bB</td>
</tr>
<tr>
<td></td>
<td>MP&lt;sub&gt;HC&lt;/sub&gt;</td>
<td>-51.86 ± 18.58 aA</td>
<td>-76.80 ± 7.75 bC</td>
<td>-66.55 ± 4.92 bB</td>
</tr>
<tr>
<td>δ¹⁸O (‰)</td>
<td>YP&lt;sub&gt;LC&lt;/sub&gt;</td>
<td>-7.41 ± 3.32 aA</td>
<td>-9.70 ± 1.33 bB</td>
<td>-7.80 ± 0.52 aA</td>
</tr>
<tr>
<td></td>
<td>YP&lt;sub&gt;HC&lt;/sub&gt;</td>
<td>-7.54 ± 3.27 aA</td>
<td>-9.07 ± 1.23 aB</td>
<td>-7.86 ± 0.45 aA</td>
</tr>
<tr>
<td></td>
<td>MP&lt;sub&gt;LC&lt;/sub&gt;</td>
<td>-6.89 ± 2.94 aA</td>
<td>-9.99 ± 1.60 bC</td>
<td>-9.06 ± 1.26 bB</td>
</tr>
<tr>
<td></td>
<td>MP&lt;sub&gt;HC&lt;/sub&gt;</td>
<td>-6.38 ± 2.59 aA</td>
<td>-10.1 ± 1.10 bC</td>
<td>-8.80 ± 0.77 bB</td>
</tr>
</tbody>
</table>

For a given soil layer, different lowercase letters indicate significant differences in isotopic values at \( \alpha = 0.05 \) among stands; for a given stand, different uppercase letters indicate significant differences in isotopic values at \( \alpha = 0.05 \) among soil layers. Data shown are mean ± SD.

3.3 Matching degree between root water uptake pattern and fine root distribution

Root water uptake patterns changed continuously during the growing season, resulting in a change in the match between root water uptake pattern and fine root distribution \( M_{FR} \) over the growing season (Fig. 4; Fig. 5). From April to August, the \( M_{FR} \) in different stands showed a general trend of decreasing and then increasing, but with varying magnitudes of change and turning points (Fig. 5). From August to September, the \( M_{FR} \) showed a decreasing trend in YP<sub>LC</sub>, YP<sub>HC</sub> and MP<sub>LC</sub> stands (Fig. 5). The average \( M_{FR} \) within the growing season varied among different stands, with the ranking order of YP<sub>LC</sub> (0.91) > YP<sub>HC</sub> (0.82) > MP<sub>LC</sub> (0.76) > MP<sub>HC</sub> (0.60) (Fig. 5).

The \( M_{FR} \) was not significantly related to SWC<sub>deep</sub>, monthly precipitation (\( P \)), or monthly reference evapotranspiration (ET<sub>0</sub>) in all stands (Fig. 6). The \( M_{FR} \) was significantly and positively related to both SWC<sub>profile</sub> and SWC<sub>middle</sub> in the YP<sub>HC</sub> stand and was positively related to SWC<sub>shallow</sub> and negatively related to CV<sub>SWC</sub> in the MP<sub>HC</sub> stand (Fig. 6). The \( M_{FR} \) in the MP<sub>LC</sub> stand decreased significantly with increasing monthly average air temperature \( (T) \) (Fig. 6).

3.4 Matching degree between root water uptake pattern and soil water distribution
The matching degree between root water uptake pattern and soil water distribution ($M_{SR}$) also changed over the growing season (Fig. 4; Fig. 5). The $M_{SR}$ in YP$_{LC}$ and YP$_{HC}$ stands showed a similar trend of increasing then decreasing, and then increasing again since August (Fig. 5E, F). The $M_{SR}$ in MP$_{LC}$ stand increased gradually with the season, while the $M_{SR}$ in MP$_{HC}$ stand showed a trough in May and then leveled off (Fig. 5G, H). The average $M_{SR}$ of the four stands did not differ significantly (from 0.84 to 0.91) during the growing season (Fig. 5).

The SWC$_{profile}$, SWC$_{deep}$, $P$, $T$, and ET$_0$ were not significantly related to $M_{SR}$ in all four stands (Fig. 7). The SWC$_{shallow}$, SWC$_{middle}$, and CV$_{SWC}$ were significantly related to $M_{SR}$ in both MP$_{LC}$ and YP$_{HC}$ stands. The $M_{SR}$ increased with increasing SWC$_{shallow}$ but decreased with increasing CV$_{SWC}$ in the MP$_{LC}$ stand, and decreased with increasing SWC$_{middle}$ in the YP$_{HC}$ stand (Fig. 7).

### 3.5 The relationship between $M_{FR}$ and $M_{SR}$

In MP$_{LC}$ and MP$_{HC}$ stands, the average $M_{SR}$ across the growing season were 0.90 and 0.87, respectively, higher than the average $M_{FR}$ (0.76 and 0.60, respectively) (Fig. 4; Fig. 5). The difference between average $M_{FR}$ and $M_{SR}$ values was slight in both YP$_{LC}$ (0.91 and 0.87) and YP$_{HC}$ (0.82 and 0.84) stands (Fig. 5).

There was no significant correlation between $M_{SR}$ and $M_{FR}$ in YP$_{LC}$ and MP$_{LC}$ stands (Fig. 8). The $M_{SR}$ and $M_{FR}$ were significantly negatively related in the YP$_{HC}$ stand but positively related in the MP$_{HC}$ stand.

### 4 Discussion

Fine root sampling is a highly intricate and challenging process, particularly for deep soils. The task of separating and morphologically scanning fine roots from the soil requires an enormous amount of effort. Consequently, deep root studies have been conducted only in a few regions globally, such as the Loess Plateau, the sandy regions of northern China, and south-western Australia (Drake et al., 2011; Li et al., 2019; Nan et al., 2019; Song et al., 2020; Wang et al., 2021; Zhou et al., 2019). Most studies have been limited to sampling depths above 1 m of soil layer (Finér et al., 2007; Finér et al., 2011; Jagodzinski et al., 2016; Yuan and Chen, 2012). In order to obtain deep (1–6 m) fine roots, our study was conducted with fine root sampling only at the end of the growing season. To investigate the seasonal dynamics of fine roots, micro root tubes provide a more convenient sampling method than root augers (Coleman and Aubrey, 2018). However, the use of micro root tubes does not allow for observations of roots at deeper soil depths. Although we conducted only one sampling during the growing season, the data we collected could reflect the general vertical distribution pattern of fine roots in that year. Specifically, our findings indicate that fine roots gradually decreased with increasing soil depth, and a higher abundance of fine roots was present in the shallow layer. This distribution pattern is representative of the global fine root distribution pattern, as shown in previous studies (Jackson et al., 1996; Zou et al., 2022). However, our investigation highlights that this distribution pattern is only representative of water uptake during specific times of the growing season. This finding underscores the significance of directly examining root uptake.
Unfortunately, we were unable to establish the relationship between actual absorbing roots and root water uptake. This limitation is due to the fact that the commonly defined fine root diameter (≤ 2 mm) far exceeds that of absorbing roots (McCormack et al., 2015; Pregitzer et al., 2002). Therefore, our fine root samples contain a mix of large-diameter transport roots and absorbing roots.

Understanding the relationships between plant structure or morphology, function, and environment is an enduring area of ecological research (Freschet et al., 2021; Sack and Buckley, 2020). Researchers have long recognized that roots can alter resource uptake based on resource availability (Javot and Maurel, 2002; Lauter et al., 1996). However, in most field-based studies, root length density is commonly measured as a representative of water uptake function. For instance, research aimed at the subdivision of subsurface ecological niches relies on evaluating root length density at varying depths. This approach suggests that root distribution can reflect the ability to absorb resources (Brassard et al., 2011; Brassard et al., 2013; Sun et al., 2017; Zeng et al., 2021). Our results showed that fine root distribution did not match systematically the water uptake pattern over the whole growing season (Fig. 4). Recently, stable isotope methods have been increasingly used to determine root water uptake patterns (Dawson et al., 2020; Rothfuss and Javaux, 2017; Volkmann et al., 2016; Yang et al., 2017). The simultaneous use of an isotope in-situ measurement system and a liquid flow measurement system enables monitoring of root uptake patterns with high temporal resolution (Gessler et al., 2022; Kühnhammer et al., 2020). The resultant data could be directly used to develop temporally dynamic eco-hydrological models, rather than using root and/or soil water distribution data (Kühnhammer et al., 2020; Kulmatiski et al., 2017; Mazzacavallo and Kulmatiski, 2015; Seeger et al., 2020). In our current study, root water uptake patterns were determined using the stable isotope technology, and then were linked with fine root or soil water distribution. The results obtained in this study will provide data support and reference value for future development of related models.

When water deficit occurred at shallow soil layer, water uptake in deeper or wetter soil layers increased, resulting in mismatched distribution of fine roots and root water uptake patterns (Green and Clothier, 1999; Jarvis, 1976; Šimůnek and Hopmans, 2009; Thomas et al., 2020). Our results showed that the matching degree between the water uptake pattern and fine root distribution increased with soil water content significantly in high-density stands, but this correlation was insignificant in stands with low-density stand structures (Fig. 6A, B, C, D). This suggests that soil water content should be the primary factor responsible for variations in the degree of matching between water uptake patterns and fine root distribution in stands with high-density structures. However, other factors such as soil texture, soil compaction, and intra-forest interactions also contribute to the degree of matching in stands with low-density structures. When roots move to areas with higher soil moisture content due to water stress, the water uptake pattern may become more closely aligned with the distribution of soil water (Ellsworth and Sternberg, 2015; Gao et al., 2018; Kühnhammer et al., 2020; Kulmatiski et al., 2017). In the present study, however, the matching degree between the water uptake pattern and soil water distribution was found to increase gradually with increasing water stress (i.e., decreasing soil water) only in young stands (Fig. 7A, B, C, D). In contrast, in mature stands, the water uptake pattern deviated more from the soil water distribution pattern as water stress increased (Fig. 7A, B, C, D). This may be due to the fact that deeper
soil water in mature stands has been over-consumed during stand development resulting in low soil water potential at deep soil layers (Liu et al., 2022), this can also be demonstrated by our soil water data (Fig. 2). It would be more difficult for mature stands to uptake water from deeper soil layers with increasing water stress (Christina et al., 2017; Davidson et al., 2011; Gardner, 1991; Yang et al., 2017), causing the stands to change their root uptake strategy and absorb water from relatively shallow soil layers alternatively.

In general, as the soil water content increased, the root water uptake pattern in the young stands tended to be closer to the fine root distribution pattern and far away from the soil water distribution, while the matching of the root water uptake pattern with both the fine root and soil water distributions became closer in the mature stands (Fig. 6; Fig. 7). Therefore, our first hypothesis was partially supported by the results.

The matching degree between water uptake pattern and soil water distribution was higher than the matching degree between the water uptake pattern and fine root distribution in mature stands (Fig. 5), suggesting that water uptake pattern matched more closely with soil water distribution than with fine root distribution in mature stands. However, the water uptake pattern matched closely with both soil water distribution and fine root distribution in young stands (Fig. 5). This evidence indicates that water uptake functions in young stands are driven by both root structure and available water resources, while water uptake in mature forests with larger and more complex root system is better associated with soil water availability than root structure. Mature trees have deeper roots and more complex root system than young trees (Coleman and Aubrey, 2018; Finér et al., 2007; Geng et al., 2022; Yuan and Chen, 2010, 2012). Therefore, mature trees are able to absorb soil water from deeper, wetter, and more stable water sources to meet transpiration requirements (Drake et al., 2011; Feild and Dawson, 1998; Finér et al., 2007; Geng et al., 2022; Huo et al., 2018), resulting in their water uptake pattern being closer to the soil water distribution and farther away from the fine root distribution. Given the stand age, the matching degree between the water uptake pattern and fine root distribution was lower in high-density stands than in low-density stands during the growing season, but the difference in the matching degree between the water uptake pattern and soil water distribution was minimal (Fig. 5). This indicates that the relationship between root water uptake pattern and fine root distribution is more affected by stand structure compared to the relationship between root water uptake pattern and soil water distribution.

Previous studies have found that root uptake patterns may be closer to soil water distribution patterns than to fine root distribution patterns (Kühnhammer et al., 2020; Kulmatiski et al., 2017). This holds true only for mature stands in our study. However, in young stands, our results showed that root water uptake patterns closely matched both soil water distribution and fine root distribution patterns, as indicated by their high matching degrees with little difference (Fig. 5). The reason for the variability between the current and previous results may be due to the fact that the material of previous study was herbaceous perennial while this study was based on trees in stands, as well as their neglect of the seasonal dynamics of root uptake. Additionally, it is interesting that these two matching degrees were significantly related in high-density stands but positively in the mature stand and negatively in the young stand (Fig. 8). In low-
density stands, regardless of young or mature stands, their correlations were negative, although not significant (Fig. 8). This intriguing result implies that while the fine root distribution drives root uptake, the soil water distribution also drives root uptake in a synergistic or trade-off manner.

In addition to the variables related to soil water content, other factors that influence the matching degree between water uptake pattern and fine root or soil water distributions were also identified (Fig. 6; Fig. 7). For example, we found that higher soil water heterogeneity (as represented by the coefficient of variation of soil water content across the soil profile) significantly decreased the matching degree between the water uptake pattern and fine root distribution in the mature high-density stand (Fig. 6E) and the matching degree between the water uptake pattern and soil water distribution in the mature low-density stand (Fig. 7E). Previous studies have shown that the soil water heterogeneity was the cause of compensatory root water uptake, which changed the matching degree between root water uptake and fine root distribution or soil water distribution (Ellsworth and Sternberg, 2015; Green and Clothier, 1999). Additionally, of the three meteorological factors, only temperature was found to have a significant inhibitory effect on the matching degree between fine root distribution and root water uptake in the mature low-density stand. This indicates that the meteorological factors have a relatively weak modulation on the matching degree of between water uptake pattern and fine root or soil water distribution, compared to the direct effect of soil water content. That is, our second hypothesis was also supported by the results.

5 Conclusions

In this study, stable isotope techniques were used to understand root water uptake pattern, then the relationships between root water uptake patterns and fine root distributions and soil water distributions were quantified. The matching degree between the root water uptake pattern and fine root distribution increased with the soil water content in both young and mature stands. However, the matching degree between the root water uptake pattern and soil water distribution decreased in the young stands and increased in the mature stands with increasing soil water content. Compared with the direct effect of soil water content, the influence of meteorological factors on the matching degree was relatively weak. In addition, the water uptake function is driven by both root structure and available water resource in young stands with incompletely developed root systems. In mature stands with large and complex root systems, however, the water uptake function is driven more by available water resource rather than root structure. More competitive intensity within stand would suppress the matching degree between the root water uptake pattern and fine root distribution but had little influence on the matching degree between the root water uptake pattern and soil water distribution. Finally, we found that there is a relatively high positive or negative correlation between these two matching degrees in all four stands.

Declarations

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**Author Contributions**

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Wei Zhu, Dehai Zhao, Ou Zhou, Liming Jia and Benye Xi. The first draft of the manuscript was written by Wei Zhu and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data Availability**

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Competing Interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figures
Figure 1

Tree layout of four experimental forest stands.
Seasonal dynamics of the mean of gravimetric soil water content (%) and coefficient of variation of soil water content across the whole soil profile in different stands in 2019. Horizontal bands depict the predicted 95% confidence interval. The blue dotted line divides the entire growing season into three periods. The meaning of $Y_{PLC}$, $Y_{PHC}$, $MP_{LC}$, and $MP_{HC}$ can be referred to Fig. 1.
Figure 3

Isotopic values (‰) dynamics in different stands in 2019. Horizontal bands depict the predicted 95% confidence interval. Shallow soil layer is the 0–30 cm layer. Middle soil layer is the 30–100 cm layer. Deep soil layer is the 100–200 cm and 100–600 cm layer in the young stands and mature stands, respectively. The blue dotted line divides the entire growing season into three periods. The meaning of $Y_{P\text{LC}}$, $Y_{P\text{HC}}$, $M_{P\text{LC}}$, and $M_{P\text{HC}}$ can be referred to Fig. 1.
Figure 4

The vertical distribution of root water uptake (RWU), fine root length density (FRLD), and soil water content (SWC) in different stands. FRLD was only sampled at the end of the growing season, RWU and SWC were sampled monthly from April to September. The line is a smooth curve, which is predicted using the loess function in the software R. The shading around the smooth curve represents the standard error. The meaning of YP_{LC}, YP_{HC}, MP_{LC}, and MP_{HC} can be referred to Fig. 1.
Figure 5

The matching degree dynamics in different stands in 2019. $M_{FR}$ refers to a measure of matching degree between fine root distribution and root water uptake pattern, $M_{SR}$ refers to a measure of matching degree between soil water content distribution and root water uptake pattern. The meaning of $Y_{PLC}$, $Y_{PHC}$, $MP_{LC}$, and $MP_{HC}$ can be referred to Fig. 1.
Figure 6

The matching degree between the fine root length density distribution (FRLD) and root water uptake pattern (RWU) changes with different factors. SWC_{profile} (%), SWC_{shallow} (%), SWC_{middle} (%), SWC_{deep} (%) represent the average soil water content of the whole profile, shallow, middle, and deep soil layers in each month, respectively. CV_{SWC} represents the coefficient of variation of soil water content across the profile. P (mm), T (°C), ET_{0} (mm) represent the monthly precipitation, monthly average air temperature, and monthly reference evapotranspiration, respectively. All abscissas (factors) were log-transformed. Pearson's correlation coefficient (R) was used to explore the relationship between various factors and the matching degree. The meaning of YP_{LC}, YP_{HC}, MP_{LC}, and MP_{HC} can be referred to Fig. 1.
Figure 7

The matching degree between the soil water content distribution (SWC) and root water uptake pattern (RWU) changes with different factors. SWC\textsubscript{profile} (%), SWC\textsubscript{shallow} (%), SWC\textsubscript{middle} (%), SWC\textsubscript{deep} (%) represent the average soil water content of the whole profile, shallow, middle, and deep soil layers in each month, respectively. CV\textsubscript{SWC} represents the coefficient of variation of soil water content across the profile. P (mm), T (°C), ET\textsubscript{0} (mm) represent the monthly precipitation, monthly average air temperature, and monthly reference evapotranspiration, respectively. All abscissas (factors) were log-transformed. Pearson's correlation coefficient ($R$) was used to explore the relationship between various factors and the matching degree. The meaning of YP\textsubscript{LC}, YP\textsubscript{HC}, MP\textsubscript{LC}, and MP\textsubscript{HC} can be referred to Fig. 1.
Figure 8

The relationship between the $M_{FR}$ and $M_{SR}$. $M_{FR}$ refers to a measure of matching degree between fine root distribution and root water uptake pattern, $M_{SR}$ refers to a measure of matching degree between soil water content distribution and root water uptake pattern. Pearson's correlation coefficient ($R$) was used to explore the relationship between $M_{FR}$ and $M_{SR}$. The meaning of $YP_{LC}$, $YP_{HC}$, $MP_{LC}$, and $MP_{HC}$ can be referred to Fig. 1.