Root water uptake patterns are controlled by tree species interactions and soil water variability

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Abstract

Root water uptake depends on soil moisture which is primarily fed by t~~T~~hroughfall in forests. ~~is the largest source of water~~Several biotic and abiotic elements shape the spatial distribution of throughfall~~ entering the soil in forests, and its spatial distribution depends on several biotic and abiotic factors.~~. It is well documented that ~~the distribution of ~~throughfall patterns result~~s~~ in reoccurring higher and lower water inputs at certain locations. However, ~~the role of horizontal root water uptake patterns in understanding the effects of throughfall patterns on subsurface water dynamics remains unresolved~~how the spatial distribution of throughfall affects root water uptake patterns remains unresolved. Therefore, ~~–~~we investigate root water uptake patterns by considering spatial patterns of throughfall and soil water patterns in addition to soil and neighboring tree characteristics. In a beech-dominated mixed deciduous forest in a temperate climate, we conducted ~~weekly ~~intensive throughfall sampling at locations paired with soil moisture sensors during the 2019 growing season. We employed a linear mixed-effects model to understand controlling factors for root water uptake patterns. Our results show that soil water patterns and

interactions among neighbouring trees are the most significant factors regulating root water uptake patterns. Temporally stable throughfall patterns did not influence root water uptake patterns. Similarly, soil properties were unimportant for spatial patterns of root water uptake. We found that wetter locations (rarely associated with throughfall hotspots) promoted greater root water uptake. Root water uptake in monitored soil layers also increased with neighbourhood species richness. Ultimately our findings suggest that complementarity mechanisms within the forest stand, in addition to soil water variability and availability, govern root water uptake patterns.

Key words: root water uptake, throughfall, soil water, spatial patterns, beech

1) Introduction

Root water uptake depends on soil moisture, which is replenished by precipitation. At the same time, the vegetation ~~–~~canopy intercepts and redirects precipitation into throughfall and stemflow, collectively referred to as below-canopy precipitation. Thus, even before soil water can be taken up by roots, it has already been influenced by the canopy.

Throughfall is typically the largest component of below canopy precipitation (Levia and Frost, 2006; Sadeghi et al., 2020). For instance, in temperate forests about 70% of above canopy precipitation ends up as throughfall (Levia and Frost, 2003; Sadeghi et al., 2020). ~~Hence, throughfall serves as the primary source for replenishing soil moisture in vegetated areas.~~

Below-canopy precipitation is modified by several biotic and abiotic factors (Levia and Frost, 2006; Levia et al., 2011), including vegetation type, canopy architecture (Crockford and Richardson, 2000; Pypker et al., 2011; Levia et al., 2017), and forest structure (Rodrigues et al., 2022), meteorological elements such as wind speed (Staelens et al., 2008; Van Stan et al., 2011; Fan et al., 2015), precipitation intensity and event size (Dunkerley, 2014; Magliano et al., 2019; Zhang et al., 2016; Staelens et al., 2008). As a result, throughfall inherently varies across space and time. However, previous studies showed that the spatial distribution of throughfall persists over time (Keim et al., 2005; Staelens et al., 2006; Guswa and Spence, 2012; Carlyle-Moses et al., 2014; Metzger et al., 2017; Van Stan et al., 2020).

~~Throughfall~~ Throughfall patterns -have been hypothesized to affect the spatial variation in water uptake (Bouten et al., 1992; Coenders-Gerrits et al., 2013~~; Schwärzel et al., 2009~~) and soil moisture distribution ~~introducetranslate the spatial variability of water inputs into soil moisture (Raat et al., 2002; Blume et al., 2009; Zimmermann et al., 2009; Zehe et al., 2010; Bachmair et al., 2012; Rosenbaum et al., 2012; Zhang et al., 2016).~~(Raat et al., 2002; Blume et al., 2009; Zimmermann et al., 2009; Zehe et al., 2010; Bachmair et al., 2012; Rosenbaum et al., 2012; Zhang et al., 2016). Yet, empirical evidence is scarce. A decade ago Coenders-Gerrits et al., (2013) proposed that throughfall patterns are translated into soil wetting dynamics with a model based on combined hillslope topographic and throughfall data collected in a beech-dominated catchment. However, in this model, the effect of throughfall patterns on soil moisture patterns rapidly ceased, and became more similar to the bedrock topography.~~.~~ Regarding the latter result, the model and reality differ, as the correlation between measured bedrock topography and soil moisture is low (Tromp-van Meerveld and McDonnell, 2006), -which Coenders-Gerrits et al., (2013) attributed to root water uptake. -Later, Metzger et al. (2017) showed through field observations that although throughfall spatial variation ~~patterns~~ strongly increases shortly after rainfall~~,~~ it ~~also~~ drops quickly again in the drained state, so the impact ~~-~~rapidly disappears. -Later, Fischer-Bedtke et al., (2023) confirmed in the same field site that recurring throughfall patterns left a notable imprint on soil moisture response to rainfall yet~~,~~ the effect on absolute values of soil water content in drained state was rather weak. More recently, Zhu et al. (2021) observed that stable throughfall patterns were weakly related to the spatial distribution of soil moisture since this relationship was restricted only to relatively wet soil locations and throughfall hotspots. They also showed that throughfall patterns had weaker influence on the temporal dynamics of soil water content compared to soil bulk density and litter layer properties.

Taken together, several studies have searched for patterns of throughfall in soil moisture spatial variation. As comparatively weak relationships were found, some p~~P~~revious studies have suggested that root water uptake ~~(~~(Bouten et al., 1992; Schwärzel et al., 2009) could be the cause. Specifically, based on a one-dimensional soil-water model, Bouten et al. (1992) proposed that throughfall patterns alter and localize root water uptake as well as promote fast drainage. As a result, spatial variation in root water uptake could diminish the effect of throughfall patterns into spatio-temporal variation of soil water. However, other researchers suggested that other factors, such as ~~–~~soil properties (Metzger et al., 2017), preferential flow

(Jost et al., 2004; Blume et al., 2009; Molina et al., 2019; Fischer-Bedtke et al., 2023) and , and litter layer processes (Raat et al., 2002) may be at the heart of the weak and short-term effects of throughfall patterns on -soil moisture variability.

Regardless, Fischer-Bedtke et al., (2023) found that recurring throughfall patterns left a notable imprint on soil moisture response to rainfall, although the effect on absolute values of soil water content after drainage was rather weak. There, other factors such as soil macroporosity, distance from the tree and other processes, namely fast flow,, water uptake, more stronglyposed stronger influence on d soil moisture patterns.

 Moreover, bBased on a one-dimensional soil-water model, Bouten et al. (1992) proposed that throughfall patterns alter and localize root water uptake as well as promote fast drainage. As a result, spatial variation in root water uptake could diminish translating throughfall patterns into spatio-temporal variation of soil water.

However, to the best of our knowledge, the feedback mechanism of throughfall patterns on root water uptake variation has not yet been investigated empirically. More common are studies related to However, to the best of our knowledge, the feedback mechanism of throughfall patterns on root water uptake variation has not yet been investigated in the fieldempirically. Therefore, it is unclear how water uptake patterns play a role in translating throughfall patterns into spatio-temporal variation of soil water and vice versa.

sSoil watermoisture distribution. Soil water availability, which could potentially be enhanced bey throughfall, variability maycan shapeaffects root water -root water uptake patterns even more than root abundance networks (Kühnhammer et al., 2020; Guderle et al., 2018). On the flip side, root water uptake can amplify or homogenize soil water moisture variability (Hupet and Vanclooster, 2005; Teuling and Troch, 2005; Ivanov et al., 2010; Baroni et al., 2013; Martínez García et al., 2014). Moreover, variations in soil water content reflect on root water uptake (Hupet et al., 2002; Schume et al., 2004; Schwärzel et al., 2009; Guderle and Hildebrandt, 2015; Jackisch et al., 2020).

Temporal and diurnal changes in local soil water content can be employed to quantify root water uptake by dissecting soil water flow and water uptake under meteorological conditions that ensure sustained transpiration demand (Guderle and Hildebrandt, 2015; Jackisch et al., 2020; Hupet et al., 2002). While other methods exist, such as using isotopic Other methods, especially using tracers, exist to evaluate the spatial distribution of root water uptake. Specifically, stable water isotopes can be used to estimate water sources for water uptake by comparing the isotopic composition of plant xylem water to that of potential water sources using different methods including graphical inference, end-member mixing models, multi-source linear mixing models, and physically based analytical models (Rothfuss and Javaux, 2017, Zarebanadkouki et al., 2013). In addition, tracking isotopically enriched water can assist in the determination of water uptake dynamics (e.g., Zarebanadkouki et al., 2013). In contrast to these methods, daily fluctuations in soil water allow for estimating the spatial distribution of ecosystem evapotranspiration using standard measurements of soil water content (Guderle and Hildebrandt, 2016) without the need for additional infrastructure.

In additionNext to water input to spatial variation of throughfall and soil moisture, soil properties are among the abiotic factors that maycan alter root water uptake patterns (Nadezhdina et al., 2007; Kirchen et al., 2017) and soil moisture. Also they control soil water redistribution (Grayson et al., 1997; Cosh et al., 2008; Jarecke et al., 2021) and water availability for root structures (Vereecken et al., 2007; Cai et al., 2018). For a given evaporative demand, water uptake at a particular location is a function of water transport resistance between root and soil in addition to the soil-water potential (Cardon and Letey, 1992; Shani and Dudley, 1996; Lhomme, 1998). Both characteristics depend on local soil properties and soil water status, and the latter in turn is affected by the local water uptake rate. Soil moisture variability may shape root water uptake patterns even more than root networks (Kühnhammer et al., 2020; Guderle et al., 2018). On the flip side, root water uptake can amplify or homogenize soil moisture variability (Hupet and Vanclooster, 2005; Teuling and Troch, 2005; Ivanov et al., 2010; Baroni et al., 2013; Martínez García et al., 2014). Soil Taken together, in addition to root water uptake, Sproperties control soil water redistribution (Grayson et al., 1997; Cosh et al., 2008; Jarecke et al., 2021) and water availability for root structures (Vereecken et al., 2007; Cai et al., 2018). Moreover, variations in soil water content reflect root water uptake (Hupet et al., 2002; Schume et al., 2004; Schwärzel et al., 2009; Guderle and Hildebrandt, 2015; Jackisch et al., 2020).

Temporal and diurnal changes in local soil water content can be employed to quantify root water uptake by dissecting soil water flow and water uptake under meteorological conditions that ensure transpiration demand Temporal and diurnal changes in local soil water content can be employed to quantify root water uptake by dissecting soil water flow and water uptake under meteorological conditions that ensure sustained transpiration demand (Guderle and Hildebrandt, 2015; Jackisch et al., 2020; Hupet et al., 2002). While other methods exist, such as using isotopic tracers (Rothfuss and Javaux, 2017, Zarebanadkouki et al., 2013), daily fluctuations in soil water allow for estimating the spatial distribution of ecosystem evapotranspiration using standard measurements of soil water content (Guderle and Hildebrandt, 2016) without the need for additional infrastructure.

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RMoreoverFinally, plant individual and ecosystem processes affect uptake: Rroot networks can also regulate soil moisture distribution by transporting water from connect wetter places toand drier locations, which has been observed in a variety of ecosystems (e.g., Emerman and Dawson, 1996; Katul and Siqueira, 2010; Yu and D’Odorico, 2015; Priyadarshini et al., 2016; Hafner et al., 2017). In addition, tree size, age, neighboring tree species, and ecosystem structure affect the spatio-temporal variation in root water uptake (Volkmann et al., 2016; Spanner et al., 2022; Kostner et al., 2002; Dawson, 1996; Brinkmann et al., 2019; Gaines et al., 2016; Silvertown et al., 2015; Guo et al., 2018; Brum et al., 2019; Krämer and Hölscher, 2010). Neighboring tree species with different hydraulic strategies may extract water from different soil regions (Silvertown et al., 2015; Guo et al., 2018; Brum et al., 2019), and therefore more diverse forest stands can be more resilient under drought stress (Pretzsch et al., 2013). However, soil water scarcity during droughts can initiate or enhance competition mechanisms for water among different tree species (González de Andrés et al., 2018; Vitali et al., 2018; Magh et al., 2020). Furthermore, studies conducted in temperate forest ecosystems have demonstrated that the relationship between tree species richness and water uptake varies (Krämer and Hölscher, 2010; Kunert et al., 2012; Meißner et al., 2012; Forrester, 2014; Lübbe et al., 2016).

Taken together, throughfall and soil water variability, soil properties, and root water uptake patterns form complex and intertwined interactions in the terrestrial hydrological cycle. It has not yet been shown empirically how root water uptake patterns are affected by throughfall and spatial distribution of soil water content. In line with previous modeling results (Bouten et al., 1992; Coenders-Gerrits et al., 2013) we hypothesize that throughfall hotspots enhance water availability at certain locations that elevate root water uptake. Further we investigate the role of soil water variation in combination with soil properties and neighboring tree characteristics on root water uptake patterns. We pose the following questions to test the main hypothesis and guide the investigation:

i) How do throughfall patterns influence root water uptake patterns?
ii) How does soil moisture and its variation, along with soil properties, control variation in root water uptake?
iii) What is the role of biotic factors, namely size, distance, number, and species richness of neighbouring trees on root water uptake patterns?

Here, we address these questions by employing a linear mixed effects model based on weekly throughfall sampling at locations paired with intensive soil moisture measurements in a beech-dominated unmanaged forest. We estimate root water uptake using a water balance method applied at soil moisture measurement point. This method dissects soil water flow and water uptake by exploring the differences in soil water content change per time between day and night (Guderle and Hildebrandt, 2015; Jackisch et al., 2020). While other methods exist, such as using isotopic tracers (Rothfuss and Javaux, 2017, Zarebanadkouki et al., 2013), daily fluctuations in soil water allow for estimating the spatial distribution of ecosystem evapotranspiration using standard measurements of soil water content (Guderle and Hildebrandt, 2016) without the need for additional infrastructure. In addition, we incorporate data on field capacity, bulk density, and neighboring tree characteristics namely size and species-.

2) Materials and Methods

2.1) Research Site and Field Sampling

2.1.1) Research Site

The research site is located in the forested upper hill region of the Hainich low mountain range in Thuringia, Germany, as a part of the Hainich Critical Zone Exploratory (CZE) (Küsel et al., 2016). The altitude in the research site ranges from 362 m to 368 m a.s.l. Mean annual air temperature varies between 7.5 and 9.5 °C, and the mean annual precipitation ranges from less than 600 to 1000 mm in the CZE (Küsel et al., 2016).

In the study area, thin-bedded alternations of limestones and marlstones of carbonate rock (Middle Triassic) form the bedrock overlain by a shallow Pleistocene loess layer with cambisols and luvisols as dominant soil types (IUSS Working Group, 2006; Metzger et al., 2021). The median soil depth above the weathered bedrock is 37 cm, with soil depths ranging from 15 cm to a maximum depth of 87 cm (Metzger et al., 2017).

In 2019, the tree community in the research site consisted of 574 individuals of various ages (diameter at breast height ≥ 5cm). The dominant species is European beech (*Fagus sylvatica* L.), which makes up 70% of the tree community, followed by sycamore maple (*Acer pseudoplatanus* L.) with 21 %, and European ash (*Fraxinus excelsior* L.) with 4%. These dominant species are accompanied by Large-leaved linden (*Tilia platyphyllos* Scop.), European hornbeam (*Carpinus betulus* L.), Norway maple (*Acer platanoides* L.), Scots elm (*Ulmus glabra* L.), and Wild service tree (*Sorbus torminalis* (L.) Crantz). The stand has a total basal area of 40 m^2 ha^{-1} and has been unmanaged since 1997 (Kohlhepp et al., 2017).

2.1.2) Soil moisture monitoring and soil properties

The forest site (1 ha) was equipped with a soil moisture monitoring network (SoilNet; Bogena et al., 2010) consisting of SMT100 frequency domain sensors (Treuebner GmbH, Neustadt, Germany). Metzger et al. (2017) first described the soil moisture monitoring setup. Briefly, the observation platform (Figure 1) was divided into 100 subplots (10 m × 10 m), and 49 subplots were equipped with soil moisture sensors at two random measuring points each, for a total of 98 locations. At each measuring point, sensors were placed at two different depths, 7.5 cm (top sensors) and 27.5 cm (bottom sensors). The soil moisture network is maintained through a regular bi-weekly routine to avoid potential failures such as depleted sensors batteries, hardware problems, etc.

Undisturbed soil samples were collected during the sensor installation in 2014 and 2015 to estimate bulk density and water content at field capacity. In addition, we collected additional disturbed soil samples (n = 40) near sensor locations in 2019. Bulk density was determined from oven-dried (24h, 105°C) soil mass weight and water content at field capacity by applying 60 hPa pressure to the saturated undisturbed sample for 72 h.

Soil properties vary slightly from top to subsoil at the research site. While silty loam is the dominant soil texture in both layers, the clay content is higher in the subsoil (Metzger et al., 2021). The median volumetric water content at- field capacity is 44% in the topsoil and 42% in the subsoil. Moreover, the water content at -field capacity varies from 27% to 60% and from 31% to 62% in the topsoil and subsoil, respectively. The average bulk density (d_{bulk}) of the topsoil is 1.16 g cm^{-3}, with a range of 0.73 to 1.5 g cm^{-3}. In the subsoil, the average bulk density (d_{bulk}) is slightly higher at 1.37 g cm^{-3} but has a similar range (0.7 - 1.6 g cm^{-3}) (See supplement for details).

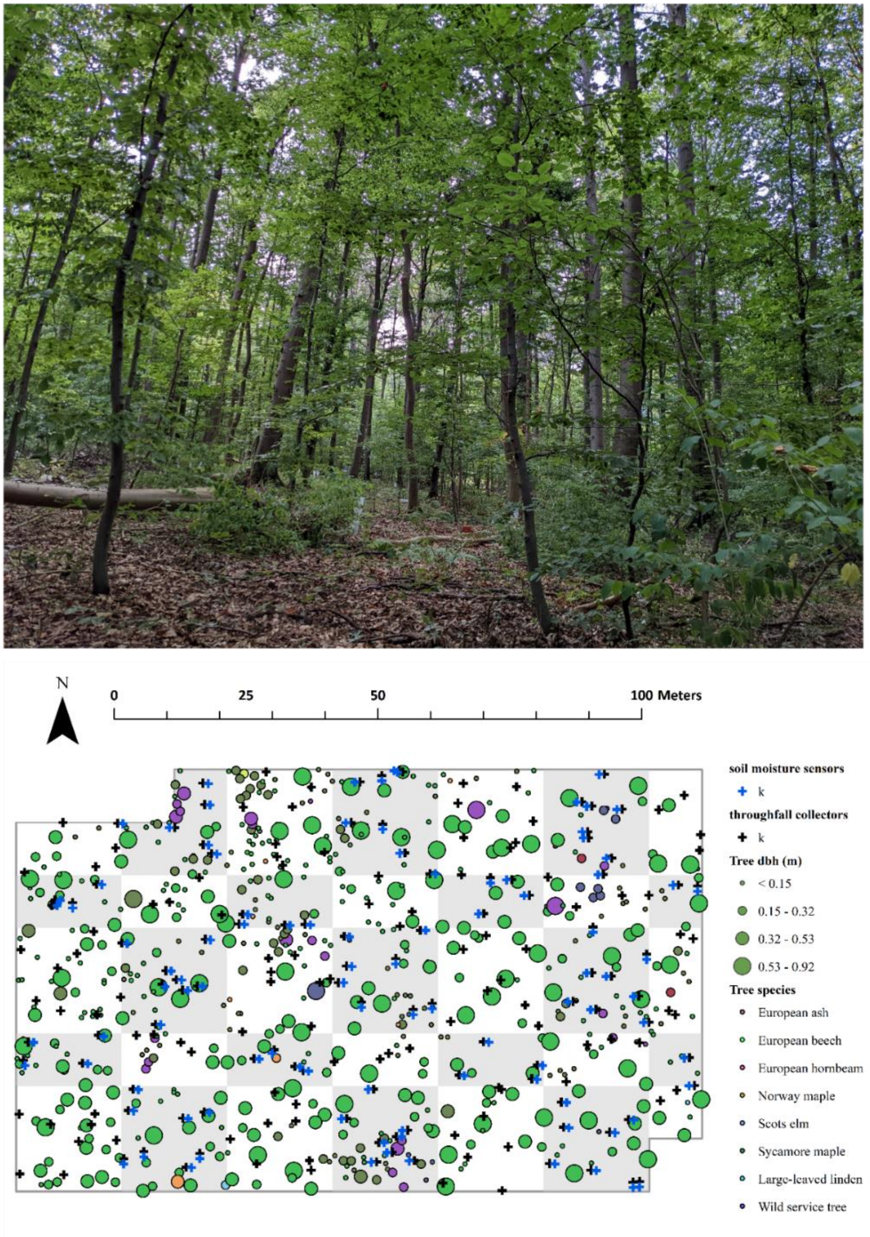

Figure 1 (above) The photo of the site. (below) the field monitoring setup of stratified randomly distributed throughfall collectors and soil moisture sensors together with the trees which are sized according to the diameter at breast height (dbh) and coloured according to the species. Throughfall collectors are paired with soil moisture sensors at 98 locations (n=182) in the grey shaded subplots. White coloured subplots are equipped with only throughfall collectors.

2.1.3) Gross precipitation and throughfall sampling

Five gross precipitation funnels were placed 1.5 m above ground level in an adjacent open grassland (ca. 250 m distance to the research site). As described in Metzger et al. (2017) and Demir et al. (2022), the precipitation funnels were made of a circular plastic funnel (12 cm in diameter) and sampling bottle (2 L in volume), and ping pong balls were placed in the funnel orifice to prevent evaporation losses.

During the early growing season of 2019, we placed throughfall collectors in soil moisture monitoring subplots at 98 locations. We paired these throughfall collectors with the soil moisture sensors by placing them within 1 m of each other. The paired collectors were placed down-slope to avoid interference with soil moisture measurements. For the rest of the research site, in 51 other subplots, we adopted a separate independent stratified random design from Metzger et al. (2017). Briefly, we placed two throughfall collectors in each subplot that was not equipped with soil moisture sensors. All throughfall collectors were placed roughly 37 cm above the ground.

We conducted weekly manual measurement of throughfall and gross precipitation during the 2019 growing season (April to August). Sampling was conducted on rain free days only. Thus, the sampling interval ranged between six and eight days.

We used the paired throughfall collectors (n = 98) to identify the drivers of root water uptake patterns, as we derived root water uptake values based on soil water content measurements (see below). However, we used all randomly placed throughfall collectors (n = 200) to describe the spatio-temporal variation of throughfall within the research site.

2.2) Estimation of potential evapotranspiration

We calculated the daily potential evapotranspiration by applying the concept of thermodynamic limits of convection (Kleidon and Renner, 2013; Kleidon et al., 2014):

$$E_{pot} = \frac{1}{\lambda} \frac{s}{s+\gamma} \frac{R_{sn}}{2} \quad (1)$$

Where R_{sn} is absorbed solar radiation (W m^{-2}), λ is the latent heat of vaporization (2.5×10^6 Jkg^{-1}), γ is the psychrometric constant (65 PaK^{-1}), and s is the slope of the saturation vapor pressure curve (PaK^{-1}).

Here, we acquired solar radiation, air temperature, and precipitation data for the throughfall sampling period from a nearby weather station ("Reckenbuel") which is located approximately 1.4 km northeast of the research site and provides data in 10 minutes intervals. The site-specific albedo for the summer period was adopted from Otto et al. (2014).

We used the precipitation data measured at the weather station to define rain events and dry periods, as described below.

2.3) Data analysis

2.3.1) Quality control of soil water content data

We systematically reviewed the six-minute soil water content data for quality control in two steps: 1) identification of problems (such as jumps to extremely low and high values, duplicated time stamps of different values, long discontinuities in the measurements, and lack of temporal variation in the time series despite rain events), 2) classification and removal of detected outliers and irregularities. We visually identified and removed unrealistic measurements such as extremely low (< 5 vol-%) and high values far beyond the field capacity (> 75 vol-%) and long plateaus of repeated values despite rain events. We also excluded any time series that exhibited long-term discontinuities that prevented us from calculating root water uptake. During the visual inspection, we eliminated values with duplicated time stamps that violated the actual temporal trend. Next, we scanned the data using the Hampel filter function of the 'pracma' R package (Borchers, 2021) with customized moving window length and Pearson's rule threshold value (Pearson, 1999) to flag possible outliers.

Despite regular maintenance, many sensors failed to provide data that met the quality criteria during the growing season (March-August) in 2019. Only 56 sensor locations (out of 98) provided data from both top and bottom sensors that met the qualification criteria described above with varying date intervals throughout the growing season. Of these, only 34 sensor locations were used to estimate root water uptake as they simultaneously provided data from both top and bottom sensors within the dry periods.

2.3.2) Soil water calculation

We estimated soil water (S) at measurement locations for the monitored soil layer based on volumetric soil water content measured by top and bottom sensors.

$$S_{i,d} = \sum z_t \theta^t_{i,d} + z_b \theta^b_{i,d} \quad (2)$$

We similarly integrated the soil water at field capacity ($S_{FC,i}$,)

$$S_{FC,i} = \sum z_t \theta^t_{FC,i} + z_b \theta^b_{FC,i} \quad (3)$$

where z_t is the depth of the soil column monitored by the top sensor and z_b is the depth of soil represented by the bottom sensor, and $\theta_{i,d}$ is -volumetric soil water content at location *i* on date *d*, and $\theta_{FC,i}$ the soil water content at the field capacity.

We calculated bulk density at the sensors' locations for the monitored soil layer.

$$\overline{d_{bulk,i}} = \frac{\sum z_t d^t_{bulk,i} + z_b d^b_{bulk,i}}{\sum z_t + z_b} \quad (4)$$

where $d^t_{bulk,i}$ and $d^b_{bulk,i}$ are the bulk density of the topsoil and subsoil, respectively, at location *i*.

2.3.3) Descriptive Statistics

We calculated the coefficient of quartile variation (CQV) and the interquartile range to describe spatial variation of throughfall, volumetric soil water content, and root water uptake. Also, we estimated octile skewness (OS_8) of throughfall based on the first and seventh octile-.

$$CQV = \frac{Q_3 - Q_1}{Q_3 + Q_1} \quad (5)$$

$$OS_8 = \frac{(Q_7 - median) - (median - Q_1)}{Q_7 - Q_1} \quad (6)$$

We characterized spatial patterns of daily root water uptake (E_t) by calculating the spatial deviation from the mean ($\delta E_{t\ i,d}$, Equation 7) (Vachaud et al., 1985).

$$\delta E_{t\ i,d} = \frac{E_{t,\ i,d} - \overline{E_{t,d}}}{\overline{E_{t,d}}} \quad (7)$$

where $E_{t,\ i,d}$ is daily root water uptake estimated at *i* sensor location on date *d* and $\overline{E_{t,d}}$ is spatial average of daily root water uptake on date *d*.

Similarly, we calculated the spatial deviation of soil water and throughfall to identify their spatial patterns.

2.4) Root water uptake estimation

We estimated root water uptake using the multi-step, multi-layer regression method (MSML), which is a water-balance method and derives evapotranspiration from diurnal differences in soil water content (Guderle and Hildebrandt, 2015; Guderle et al., 2018). This approach does not require prior information on root structure but relies on high temporal and spatial resolution data on multiple soil layers. Previous studies using additional measurements such as sap-flow and lysimeters demonstrated that the MSML method successfully estimates transpiration in both forest and grassland ecosystems (Guderle et al., 2018; Jackisch et al., 2020).

As described in Guderle and Hildebrandt (2015), the MSML derives root water uptake from distinct differences in the day and night portions of soil moisture time series. The main assumption is that, in the absence of rainfall-driven rapid vertical soil water flow, evapotranspiration occurs only during the day, while soil water flow occurs both during the day and at night. As a result, soil moisture time series reflect a distinct day/night signal under dry weather conditions.

In applying this method to our study, we first excluded potential periods of fast vertical flow periods from the time series due to previous rainfall events and identified periods for estimating daily root water uptake. We considered an 8 h buffer period to include canopy dripping and 48 h for the cessation of rainfall influence on soil water. Thus, a total of 56 h was the time interval used to define the start of the water uptake estimation period. The period when the root water uptake is estimated is hereafter referred to as the dry period.

Next, we split each soil moisture time series into a day (transpiration active period) and a night branch, as explained by Guderle and Hildebrandt (2015). We defined the transpiration period (starts 2 h after sunrise and ends 2 h before sunset) based on local sunrise and sunset time. Sunrise and sunset times were obtained from the R package 'suncal' (Thieurmel and Elmarhraoui, 2022). We fit linear models to each split branch of the time series and derived the slopes. The difference between the slope of the day branch (m_{tot}) and the average slope of the antecedent and preceding night ($\overline{m_{flow,i}}$) gives the rate of water uptake. Thus, we estimated daily evapotranspiration at each soil water content location *i* (Equation 8, 9) by accounting for soil layer thickness and slope difference.

$$E^{t,b}_{t,msml,i} = (m^{t,b}_{tot,i} - \overline{m^{t,b}_{flow,i}})\, d^{t,b}_{z,i}{}_{z,i} \quad (8)$$

$$E_{t,i} = \sum(E^{t}_{t,msml,i} + E^{b}_{t,msml,i}) \quad (9)$$

2.5) Linear Mixed Effects Model

We employed a linear mixed effects model to investigate the driving factors for root water uptake patterns. A linear mixed effects model is a multivariate statistical tool that describes the relationship between a dependent variable and explanatory variables (fixed effects) while controlling for dependencies in the data that may arise due to repeated sampling with certain designs (random effects). Fixed effects are informative, repeatable levels of explanatory and quantified variables that can influence the mean of the dependent variable, and they can be tested. In addition, in a linear mixed-effects model, how the relationship between the dependent variable and one predictor depends on the level of another predictor can be represented via interaction term.

Random factors are uninformative levels of predictor variables but can explain parts of the residual of the fixed effects model by calculating different intercepts for different category levels. They are included in mixed effects models to account for qualitative information from repeated sampling with respect to individuals, time stamps, or treatments. Here, sensor location and dry period, i.e. date, are taken as random effects.

For the model, we used only paired throughfall and soil moisture measurement locations where both top and bottom sensors provided data during the dry periods. All considered explanatory drivers, which are included as fixed factors in the model, are listed in Table 1. These factors include abiotic and biotic variables that possibly influence relative local root water uptake: They are daily spatial average soil water storage, the spatial deviation of soil water from the mean, soil water at field capacity and bulk density of the monitored soil layer-.

To account for spatial variability in throughfall, we calculated the spatial deviation from the mean by using Equation 7. Here we considered this variable at a two-different time scales: the sampling week(s) prior to root water uptake estimation, and over the entire throughfall sampling period.

Further, as biotic factors, we included number of trees, and number of species within a 5 m radius of each soil moisture location, and inverse-distance-weighted basal area (BA) within 5 m radius of each soil moisture location, calculated as follows:

$$BA_i = \frac{\sum_{R=1}^{R} W_R A_{tree}}{A} \quad (10)$$

with $$W_R = \frac{(x_i - x_R)^2}{\sum_R (x_i - x_R)^2} \quad (11)$$

where i is the soil moisture sensor located at x_i, R is the tree index located at x_R, and A_{tree} is the individual basal area of the corresponding tree, A is the area around the soil moisture sensor i with 5 m in radius. Even though our research plot is a beech-dominated forest, in some spots, two to four species were present within a 5 m radius of the soil moisture sensors.

We also included interaction terms (Table 1) as fixed factors in the model to capture complex and non-linear relationships among the biotic and abiotic factors.

We conducted all analyses with the R statistical software (R Core Team, 2022) and used the *lmer* function in the 'lme4' package (Bates et al., 2015) for the model development. We visually checked the model assumptions using the 'check_model' function of the 'performance' package (Lüdecke et al., 2021).

In addition, we calculated both conditional and marginal R^2 of the model with the 'MuMIn' package (Bartoń, 2020). While the conditional R^2 includes the variance of the entire model, the marginal R^2 subsumes only the fixed effects (Bartoń, 2020). Before fitting the linear mixed effects model, we tested for co-linearity of the considered variables and scaled the data with a Z-transformation by using the 'scale' function in base R (R Core Team, 2022), which allowed us to evaluate the individual effect of fixed effects by comparing slopes and significance levels.

We developed the optimal model by applying a systematic model selection procedure based on Akaike's Information Criterion (AIC) comparison in combination with the examination of the factors. Model selection began with the beyond-optimal model, which included all possible fixed and random effects. We stepwise evaluated each fixed effect based on its respective significance (*p* value comparison) by fitting the model the maximum likelihood (ML) to be able to compare AIC values (Zuur et al., 2009). In each step, starting with interaction terms, we identified the least significant effect and formulated a model without it. We compared the AIC values of the model before and after removing the effect, discarding it in case the AIC was unaffected or decreased. We followed the procedure with the next equally detected effect, and repeated it until only significant fixed effects remained, and the model with the lowest AIC (the optimal model) was obtained.

As a final step, the best model was refitted with restricted maximum likelihood (REML) (Zuur et al., 2009).

Table 1 List of fixed and random factors considered for estimating the root water uptake patterns through linear mixed effects model. Interaction is shown with ‘x’.

Fixed Factors	
Single Factors	**Interaction Factors**
Spatial average of soil water storage in the monitored soil layer ($\bar{S}$)	$\bar{S} \times S_{FC}$
Spatial deviation of soil water storage from the mean (δS)	$\delta S \times S_{FC}$
Field capacity of the monitored soil layer (S_{FC})	$\delta S \times BA$
Bulk density capacity of the monitored soil layer (d_{bulk})	$\bar{S} \times BA$
Spatial deviation of throughfall of events measured in sampling week previous to the corresponding dry period ($\delta P_{TF_{last\ ev.}}$)	$\delta S \times n_{tree}$
The median of spatial deviation of throughfall measured within the whole sampling period ($\widetilde{\delta P_{TF}}$)	$\bar{S} \times n_{tree}$
Number of trees (n_{tree})	$\delta P_{TF_{last\ ev.}} \times S_{FC}$
Basal area (BA)	$\delta P_{TF_{temp.\ stable.}} \times S_{FC}$
Number of species ($n_{sp,tree}$)	$\delta P_{TF_{last\ ev.}} \times d_{bulk}$
	$\delta P_{TF_{temp.\ stable.}} \times d_{bulk}$
	$n_{sp,tree} \times WA_{int}$
Random factors	
Soil moisture sensor location	
Dry period	

3) Results

3.1) Spatio-temporal distribution of throughfall and soil water content

In 12 out of the 16 sampling weeks, the weekly gross precipitation was more than half of the total potential evapotranspiration. Table 2 shows the distribution of throughfall sampled in 2019 (April-August) at 200 collectors and the 98 collectors that were paired with soil moisture sensors. Weekly throughfall increased with an increase in rain. The coefficient of quartile variation (CQV) of throughfall was generally lower for larger cumulative weekly rains. On average, the collectors paired with soil-moisture sensors received similar amounts of throughfall to all collectors (Table 2). The CQV of data from the paired collectors ranged from 0.27 to 0.6, which is similar to the CQV of throughfall sampled at all collectors. The octile skew (OS_8) of paired and all collectors was also similar.

As the growing season progressed in 2019, the average soil water content decreased in both the topsoil and subsoil. In April and early May, the average volumetric soil water content in the topsoil was above 30%, and dropped to below 10% by the end of August. In the subsoil, the volumetric soil water content similarly declined from above 40 % to below 20 % over the sampling period (Figure 2). On average, soil water changed from 52.5mm to 17.5 mm in the topsoil and from 80 mm to 40mm in the subsoil.

We derived root water uptake for four periods (a total of 19 days) under different soil wetness conditions that captured the seasonal variation of soil water content, including late spring when the soil water content was higher and drier periods during the summer following re-wetted soil conditions with late summer rains. As listed in Table 3 and shown in Figure 2, two periods were in late May and early June, and each lasted two days. The third period began in late June and lasted 11 days; the last was four days in late July. From the start of the first dry period to the end of the last, the average soil water content declined from 33 to 15 % in the topsoil and from 43 to 27% in the subsoil. Table 3 shows that within the dry periods, the coefficient of quartile variation (CQV) of soil water content was between 0.09 -0.14 and 0.08 to 0.16 in the topsoil and subsoil, respectively. During the dry periods, the spatial heterogeneity of soil water content in the subsoil increased systematically. In contrast, the spatial variation of soil water content in the topsoil was not correlated with soil dryness.

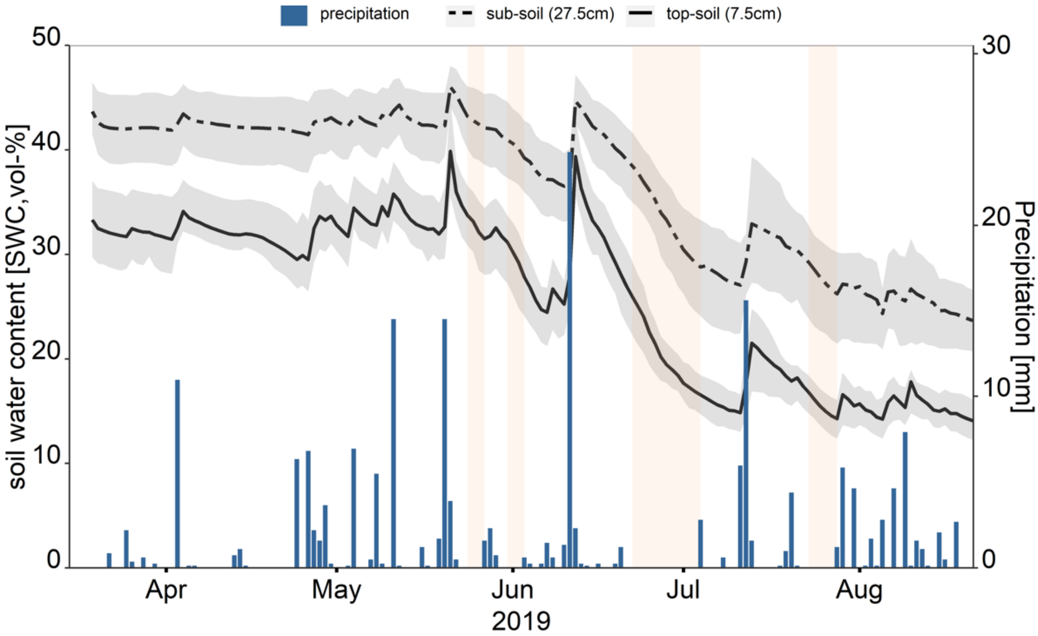

Figure 2 Soil moisture temporal variation in top and subsoil together with the daily precipitation measured at the nearby Reckenbühl station (approximately 1.4 km to the Northeast). The solid and dashed lines are spatial mean of soil water content estimated based on top (7.5 cm) and bottom (27.5 cm) sensors, and grey shaded areas show first and third quartiles. The reddish shaded areas show defined dry periods within the throughfall sampling when root water uptake could be estimated.

Table 2 Cumulative potential evapotranspiration in mm ($E_{pot,cum}$), gross precipitation (P_g), the ratio of total precipitation to the potential evapotranspiration, spatial mean of throughfall based on all collectors ($\overline{\boldsymbol{P_{TF}}}$), spatial mean of throughfall based paired collectors ($\overline{\boldsymbol{P_{TF}}}$) in mm, interquartile range (IQR), coefficient of quartile variation (CQV) and octile skewness (OS_8) of both all and paired throughfall collectors during the sampling week. The values are ordered according to the cumulated gross precipitation size.

Date	$E_{pot,cum}$	P_g	P_g/E_{pot}	$\overline{P_{TF}}$	$\frac{IQR}{\overline{P_{TF}}}$	$\frac{CQV}{\overline{P_{TF}}}$	$\frac{OS_8}{\overline{P_{TF}}}$	$\overline{P_{TF}}_{paired}$	$\frac{IQR}{\overline{P_{TF}}_{paired}}$	$\frac{CQV}{\overline{P_{TF}}_{paired}}$	$\frac{OS_8}{\overline{P_{TF}}_{paired}}$
04-06-2019	13.55	0.76	0.06	0.35	0.18	0.25	0.46	0.34	0.16	0.24	0.49
26-06-2019	20.87	1.73	0.08	0.97	0.44	0.24	0.16	0.98	0.53	0.27	0.27
17-04-2019	5.62	2.42	0.43	1.72	0.27	0.08	0.23	1.72	0.33	0.09	0.09
18-06-2019	9.46	4.00	0.42	2.58	0.62	0.12	-0.03	2.57	0.53	0.10	-0.08
29-05-2019	10.15	6.27	0.62	3.77	1.24	0.17	-0.52	3.63	1.50	0.21	-0.42
24-07-2019	13.52	7.80	0.58	4.61	1.06	0.12	-0.34	4.48	0.88	0.10	-0.63
21-08-2019	8.94	8.54	0.96	5.19	1.06	0.10	-0.47	5.17	0.97	0.10	-0.44
30-07-2019	12.68	10.73	0.85	7.81	2.25	0.15	-1.51	7.58	2.28	0.15	-1.17
07-05-2019	6.65	12.56	1.89	9.21	1.33	0.07	-0.75	9.21	1.99	0.11	-1.05
14-08-2019	8.51	13.79	1.62	11.19	2.65	0.12	-1.40	10.99	2.98	0.13	-1.13
08-08-2019	13.91	23.87	1.72	16.60	2.65	0.08	-1.10	16.52	2.65	0.08	-1.17
30-04-2019	5.93	24.47	4.13	18.44	3.09	0.08	-1.63	18.30	2.65	0.07	-1.23
17-07-2019	8.28	29.27	3.54	24.22	3.54	0.07	-2.08	24.39	3.54	0.07	-2.59
15-05-2019	7.42	29.53	3.98	22.10	3.54	0.08	-2.11	22.21	3.54	0.08	-2.11
22-05-2019	6.74	41.82	6.20	30.94	3.54	0.06	-3.04	30.54	3.54	0.06	-3.46
13-06-2019	14.47	71.84	4.96	57.77	8.51	0.07	-5.82	57.99	7.29	0.06	-6.52

Table 3 The spatial average of daily volumetric soil water content ($\overline{\theta_{top\text{-}soil}}$, vol-%) in topsoil (0-17.5 cm), and ($\overline{\theta_{subsoil}}$, vol-%) in subsoil (17.5 – 37.5 cm) during the defined dry periods. The inter quartile range (IQR), and coefficient of quartile variation (CQV) of daily volumetric soil water content in both layers during the dry periods.

Date	$\overline{\theta_{top\text{-}soil}}$ (vol-%)	**IQR** $\theta_{top\text{-}soil}$ (vol-%)	**CQV** $\theta_{top\text{-}soil}$ (vol-%)	$\overline{\theta_{sub-soil}}$ (vol-%)	**IQR** $\theta_{subsoil}$ (vol-%)	**CQV** $\theta_{subsoil}$ (vol-%)	**Dry Period**
25 -05-2019	33.17	5.72	0.09	42.82	6.72	0.08	1
26-05-2019	32.12	6.62	0.10	42.46	6.67	0.08	1
01-06-2019	30.23	6.87	0.12	40.61	6.9	0.09	2
02-06-2019	29.22	7.23	0.13	40.11	6.85	0.09	2
23-06-2019	25.01	6.69	0.14	37.80	6.38	0.08	3
24-06-2019	24.04	6.45	0.14	36.94	6.22	0.08	3
25-06-2019	22.52	5.43	0.12	36.13	6.54	0.09	3
26-06-2019	21.48	5.07	0.12	35.24	6.71	0.10	3
27-06-2019	20.20	4.25	0.11	33.98	7.75	0.12	3
28-06-2019	19.45	3.85	0.10	33.31	8.08	0.12	3
29-06-2019	18.98	3.83	0.10	32.36	8.05	0.12	3
30-06-2019	18.44	3.52	0.09	31.37	8.15	0.13	3
01-07-2019	17.67	3.62	0.10	30.45	8.18	0.13	3
02-07-2019	17.29	4.18	0.12	29.84	8.87	0.15	3
03-07-2019	16.89	3.72	0.11	29.26	8.98	0.15	3
24-07-2019	16.15	3.48	0.11	28.56	8.7	0.16	4
25-07-2019	15.51	3.47	0.11	27.85	8.67	0.16	4
26-07-2019	14.98	3.57	0.12	27.21	8.49	0.16	4
27-07-2019	14.57	3.65	0.13	26.65	8.63	0.16	4

3.2) Soil water storage, potential evapotranspiration, and root water uptake

The integrated field capacity of the monitored soil depth was 160 mm on average at the research site. Table 4 shows that soil water -was much lower than the field capacity during the dry periods, and the mean soil water storage dropped below 42 mm in late July. In addition, Table 4 demonstrates that the average root water uptake ($\overline{E_t}$) ranged from 0.94 mm d^{-1} to 3 mm d^{-1} while potential evapotranspiration (E_{pot}) ranged from 1.75 mm d^{-1} to 3.12 mm d^{-1}. The discrepancy between average root water uptake and the potential evapotranspiration increased as soil water decreased, especially during the longest dry period (Table 4). Root water uptake showed greater spatial variation than water input and soil wetness. The coefficient of quartile variation (CQV) of root water uptake ranged from 0.15 to 0.28, which was higher than the CQV of throughfall and volumetric soil water content in both soil layers.

Table 4 The daily average air temperature (T_{air} ,°C), potential evapotranspiration (E_{pot}, mm), mean soil water storage ($\bar{S}$, mm) in monitored soil layer (0 - 37.5 cm), and spatial mean of daily root water uptake ($\bar{E_t}$, mm) based on all soil moisture sensors, and the ratio of the root water uptake to the potential evapotranspiration together with and standard deviation (SD) and coefficient of quartile variation (CQV) of the daily root water uptake during the defined dry periods

Date	T_{air} (°C)	E_{pot} (mm)	$\bar{S}$ (mm)	$\bar{E_t}$ (mm)	$\bar{E_t}/E_{pot}$ (%)	SD $\bar{E_t}$	CQV $\bar{E_t}$	Dry Period
25-05-2019	12.74	1.80	71.94	1.09	60.56	0.38	0.28	1
26-05-2019	14.43	1.90	70.57	1.30	68.42	0.48	0.25	1
01-06-2019	18.42	2.59	67.16	2.26	87.26	0.98	0.27	2
02-06-2019	21.38	2.77	65.79	2.50	90.25	1.12	0.18	2
23-06-2019	19.45	2.79	59.81	2.83	101.43	0.90	0.19	3
24-06-2019	20.22	2.82	58.16	2.62	92.91	0.76	0.17	3
25-06-2019	22.52	2.89	55.96	2.67	92.39	0.78	0.16	3
26-06-2019	25.73	2.96	54.13	3.00	101.35	0.88	0.15	3
27-06-2019	18.83	2.75	51.91	2.28	82.91	0.55	0.16	3
28-06-2019	16.07	2.58	50.55	1.53	59.30	0.40	0.20	3
29-06-2019	19.59	2.85	49.55	2.11	74.04	0.60	0.20	3
30-06-2019	25.54	3.12	48.26	2.57	82.37	0.86	0.18	3
01-07-2019	20.63	2.30	46.69	1.59	69.13	0.53	0.18	3
02-07-2019	14.88	1.75	45.81	1.08	61.71	0.42	0.24	3
03-07-2019	13.77	1.91	44.95	0.94	49.21	0.30	0.23	3
24-07-2019	24.39	2.76	43.61	1.88	68.12	0.64	0.19	4
25-07-2019	25.33	2.82	42.31	1.77	62.77	0.60	0.24	4
2019-07-26	23.27	2.64	41.18	1.40	53.03	0.55	0.18	4
2019-07-27	21.29	2.68	40.23	1.21	45.15	0.47	0.19	4

3.3) Soil water, throughfall, and root water uptake patterns

At soil moisture measurement points where daily root water uptake was determined (n = 34), we calculated the spatial deviation from the median of throughfall, soil water storage, and root water uptake to illustrate the spatial patterns. Figure 3 shows that some locations received repeatedly less (or more) throughfall than average ($\delta P_{TF} < 0$), some locations were repeatedly wetter or drier ($\delta S < 0$), and some places regularly had lower or higher root water uptake (δE_t) throughout the sampling period. However, these locations were not related to each other. In fact, Figure 3 demonstrates that neither throughfall nor soil water patterns are directly correlated with the root water uptake patterns. For example, the locations with higher water uptake were not coupled with elevated throughfall input (locations ~~colored~~coloured dark) or higher soil water storage. In addition, soil water storage patterns were not correlated with throughfall patterns.

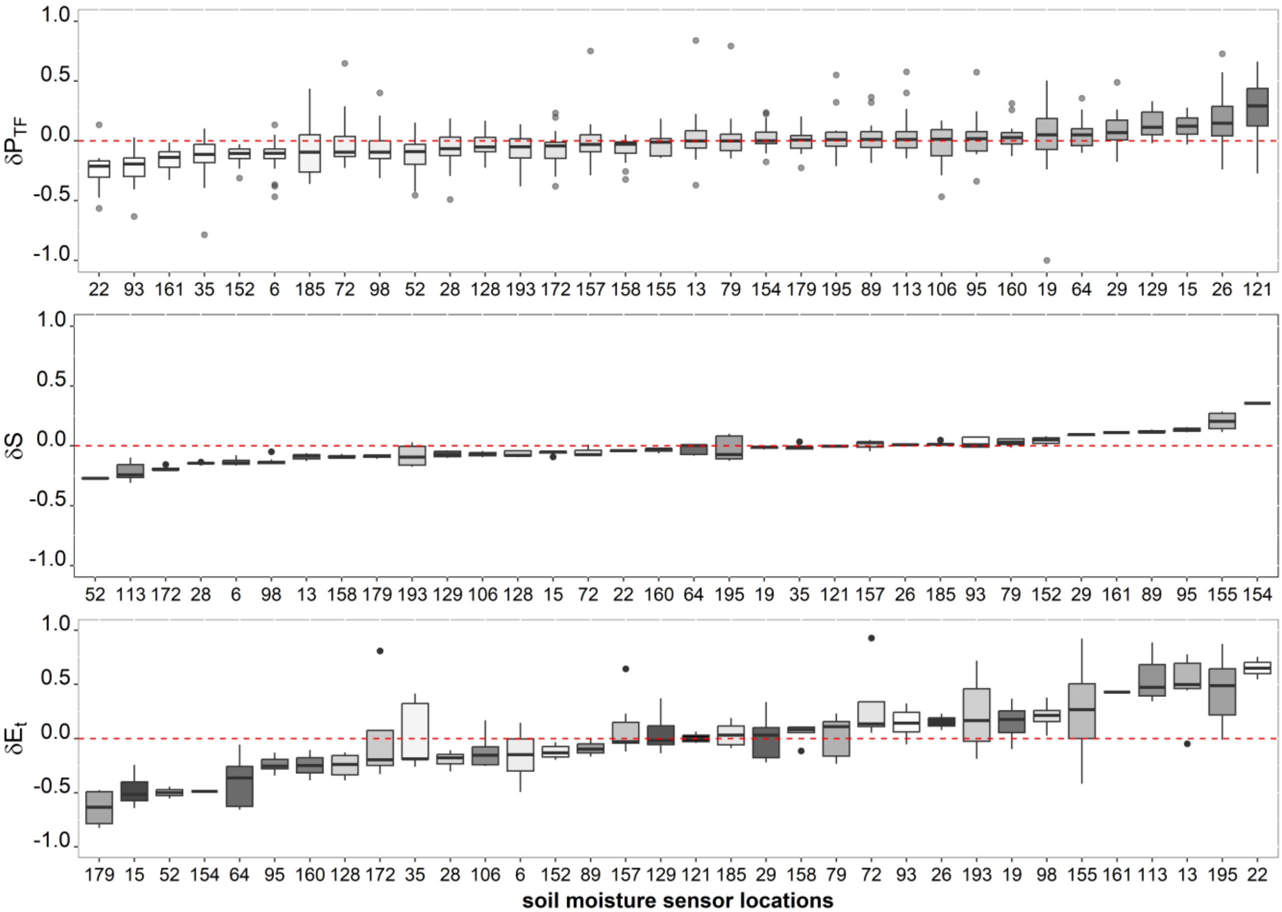

Figure 3 Temporal stability of throughfall patterns which is estimated by the spatial deviation from the mean (δP_{TF}) throughout the sampling period in 2019 (April-August), soil water (δS) and root water uptake (δE_t) based on the spatial deviation from the mean during the defined dry periods. Soil moisture sensor locations colored according to throughfall input. Soil moisture sensor locations are colored from lighter to darker in the throughout figure according to throughfall input.

3.54) Fixed factors regulating root water uptake patterns

We used a linear mixed effects model to disentangle the effects of throughfall, soil water, soil properties, and the neighbouring tree characteristics on root water uptake patterns. The fixed and random effects contributed almost equally to the model. The R^2 of the model was 0.77, and the contribution of the fixed effect to the R^2 was 0.39 (See the supplement for more details on the optimal model).

Figure 4 shows only the significant fixed effects for root water uptake patterns. Spatial deviation of soil water from the mean (i.e., soil water patterns) was the only single and the most significant factor positively related to the spatial deviation of root water uptake. Thus, water uptake was elevated at locations where the most water was retained in the soil at the given time, i.e., greater soil water storage.

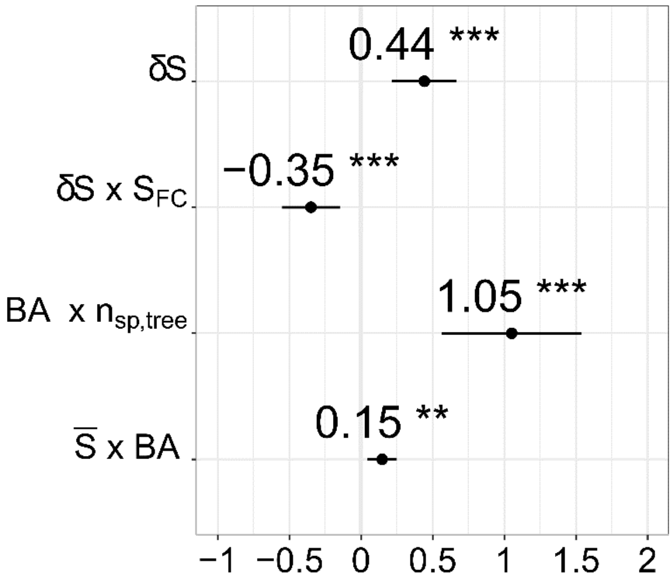

Figure 4 The significant fixed factors of the best model to estimate root water uptake patterns (δE_t). Values on the x-axis indicate the slope of the relations. All variables were scaled by Z-transformation. Interaction is shown with 'x'. Here δS is the spatial deviation of soil water, S_{FC} is the field capacity, $n_{sp,tree}$ is the number of species, BA is the basal area, and $\bar{S}$ is soil water storage. Significance codes are *** ≅0, ** ≅ 0.001. (the details on the model can be found in the supplement)

Field capacity by itself was not a significant factor affecting local root water uptake. However, it strongly influenced how local soil water controlled root water uptake as a part of the significant interaction term. Figure 5a illustrates how to root water uptake was more dependent on local soil water when field capacity was low (i.e., higher macroporosity). In contrast, soil bulk density and therefore total porosity was not part of the final model.

Although the spatial average of soil water storage, e.g., the state of wetness, was not an important factor for local root water uptake by itself, it moderated the impact of basal area (BA) on the spatial distribution of water uptake. We found that as the plot dries, uptake shifts from places with higher to places with lower basal area (Figure 5b). Furthermore, the statistical model revealed that water uptake increased with the higher basal area at locations where multiple species co-existed (Figure 5c). However, the number of species and the basal area were individually not significant fixed effects. Lastly, throughfall patterns were not significant predictors of local root water uptake. Only the median of the spatial deviation of throughfall, which represents temporally stable patterns within the sampling period ($\widetilde{\delta P_{TF}}$), marginally improved the final model.

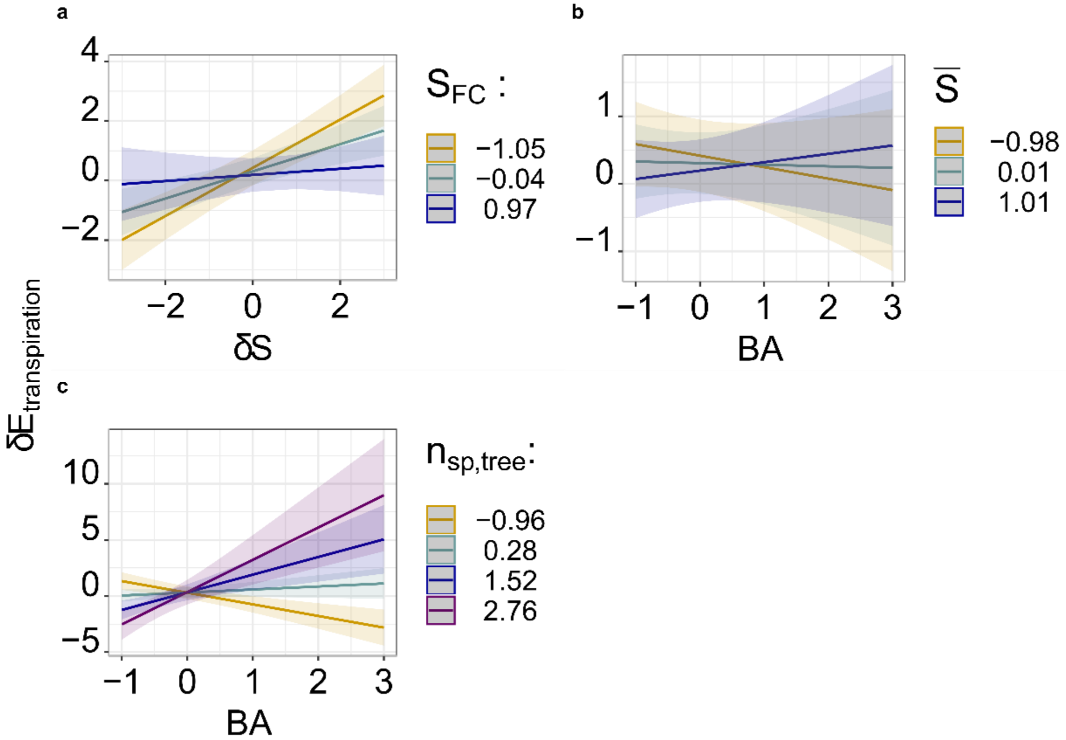

Figure 5 Visualisation of the significant relations shown in Figure 4, representing the significant drivers of root water uptake patterns during the defined dry periods. Relation to (a) interactive relation of the spatial deviation of soil water storage and field capacity (S_{FC}), (b) the interactive relation of basal area (BA) and the spatial average of soil water storage ($\bar{S}$), (c) the interactive relation of number of species ($n_{sp,tree}$) and basal area (BA.).

4) Discussion

We investigated the role of throughfall, soil water patterns, and soil and tree characteristics on the spatial variation of root water uptake. In the following sections we discuss three main findings, which are: (1) Contrary to our hypothesis, throughfall patterns do not play a role not in root water uptake patterns despite the recurrence of distinctly localized greater and lesser throughfall inputs. (2) How and where water is stored in the soil, which is strongly determined by soil hydraulic properties, dominates water uptake patterns. (3) The size and species of neighbouring trees regulate relative local water uptake such that locations surrounded by more diverse neighbourhoods are subject to greater water uptake.

4.1) Spatial variation in throughfall does not affect root water uptake patterns

We adequately captured the spatial distribution and temporal stability of throughfall at locations where local root water uptake was derived. Consistent with previous observations in temperate forests (e.g., Whelan and Anderson, 1996; Staelens et al., 2006; Metzger et al., 2017), the amount of weekly rainfall significantly altered the spatial distribution of throughfall such that more rainfall, and thus more throughfall, resulted in less spatial variability. Previous studies repeatedly showed that throughfall patterns exhibit temporal stability in forest ecosystems (e.g., Keim et al., 2005; Staelens et al., 2006; Wullaert et al., 2009; Rodrigues et al., 2022). At our research site, using event-based sampling, Metzger et al., (2017) and Fischer-Bedtke et al., (2023)demonstrated that throughfall patterns persist over time, which was also true for our weekly sampling in 2019. With canopy cover being the key driver of throughfall (Fischer-Bedtke et al., 2023), it is not surprising that weekly cumulative events resulted in a localized high and low throughfall input.

Contrary to expectations (Bouten et al., 1992; Guswa and Spence, 2012; Coenders-Gerrits et al., 2013; Fischer-Bedtke et al., 2023), our results showed that throughfall hotspots do not increase or facilitate greater root water uptake. In addition, the linear mixed effects model results confirmed that throughfall patterns do not drive the variation in root water uptake. We attributed the absence of this to two reasons: (1) decoupled soil water and throughfall patterns, (2) non-water limited conditions.

Regarding (1), we confirmed that the temporally stable throughfall patterns do not correspond to the post-event soil water and root water uptake patterns. We paired the measurements of throughfall and soil water content measurements – and thus the estimates of root water uptake- within a distance of 1 m. The spatial correlation length of soil water content and throughfall is on the order of 6-10 m in natural temperate forests (Keim et al., 2005; Gerrits et al., 2010; Zehe et al., 2010). In the same study site with the spatially extended throughfall sampling, Fischer-Bedtke et al., (2023) found that the throughfall correlation length increased with decreasing event size, varying from 6.2 m to 9.5 m depending on the size of the rain events. Thus, the paired sampling design in our study likely provided co-located throughfall and soil moisture measurements. However, variation in soil water storage was not related to throughfall patterns despite temporally persistent local high and low throughfall inputs.

Some studies, mostly conducted in the arid regions and coniferous forests, reported that soil wetting patterns were not or only partly linked to throughfall variation, despite recurrent throughfall patterns (Raat et al., 2002; Shachnovich et al., 2008; Zhu et al., 2021). Forest floor thickness, horizontal water flow, and soil properties were suggested as reasons for the decoupled patterns. Other modelling and field studies conducted in temperate deciduous forests found that throughfall patterns influenced soil moisture response to rain event rather than post-event soil water storage variability (Coenders-Gerrits et al., 2013; Metzger et al., 2017; Fischer et al., 2023). These studies attributed possible reasons to local processes such as preferential flow due to soil water repellency, the soil pore structure, or elevated root water uptake. Our results support that it is not root water uptake but preferential flow paths that are likely to decouple the throughfall and soil water patterns. In fact, Fischer-Bedtke et al., (2023) using independent throughfall and soil water content sampling designs, demonstrated that the signature of throughfall patterns dissipated in the post-event soil water variation. However, they detected the stronger influence of throughfall patterns in the soil moisture response to rainfall in the 2015 and 2016 growing seasons. The temporal variation in soil water content in the 2019 growing season was similar to the seasonal decline in soil water content in 2015 (Metzger et al., 2017). Dry soil conditions can lead to rapid drainage due to reduced water holding capability (Jost et al., 2004; Blume et al., 2009; Wiekenkamp et al., 2016; Demand et al., 2019; Molina et al., 2019) regardless of throughfall amount and its variation. Therefore, our findings support that the localized throughfall input potentially enhances preferential flow because of low soil retention (Fischer-Bedtke et al., 2023) rather than local root water uptake. As a result, the fast flow processes likely dominate how water is stored and transported at our site, erasing the throughfall distribution signature in soil water and root water uptake patterns. Moreover, any short-term response of uptake to throughfall could not be captured as water uptake was calculated only after 56 hours had elapsed since the last rain event, yet we showed that temporally stable hotspots are not associated with elevated water uptake. Hence, our results are consistent with previous propositions stating that the spatial variation of throughfall affects drainage and subsurface flow (Keim et al., 2006; Blume et al., 2009; Guswa and Spence, 2012), while root activities such as water uptake and hydraulic redistribution do not alter canopy-attributed heterogeneity in drainage pathways (Guswa, 2012).

The second reason (2) is related to water-limitation conditions. In central Europe, 2019 was the second consecutive extremely dry summer (Boergens et al., 2020), which damaged beech forests (Obladen et al., 2021). On average, however, the potential evapotranspiration demand was met at the study site despite the low soil water storage. The ratio of root water uptake to potential evapotranspiration was mostly above 65%, which is within the expected range even in the absence of shallow groundwater storage (Nie et al., 2021). Hence, local biotic and soil tied abiotic factors determined the spatial variation of root water uptake during growing season rather than throughfall -water input- patterns. However, the discrepancy between daily potential evapotranspiration and root water uptake only increased as the soil in the sampled layers dried out, due to a potential shift in the water uptake depth (see below).

4. 2) Relative and average soil wetness shapes root water uptake patterns

We found that spatial variation in soil water storage strongly regulates local water uptake such that wetter locations enhance root water uptake. This finding is consistent with expectations as transpiration rate relies on soil water availability and distribution (Couvreur et al., 2014; Klein et al., 2014; Hildebrandt et al., 2016). Here, we provide further support that root water uptake is likely to reduce the spatial variability in soil water storage as has been previously suggested (Hopmans and Bristow, 2002; Ivanov et al., 2010; Neumann and Cardon, 2012).

Trees take up more water in locations where water is not subject to throughfall-driven rapid drainage (see above), as a result root water uptake patterns are determined by where water is retained longer in the soil. Our results support previous studies suggesting that tree transpiration demand is met by water with longer residence time in the soil matrix - passive storage - while groundwater recharge is fed by rapid flow - active storage (e.g, Evaristo et al., 2019; Sprenger et al., 2019). In our statistical analyses, we investigated the soil properties of- bulk density and field capacity, which are strongly dependent on other soil properties that control aggregation and soil structure. Although bulk density is strongly related to texture, porosity, soil organic carbon content , , all of which also affect water retention (Zacharias and Wessolek, 2007; Looy et al., 2017), surprisingly soil bulk density was not retained as a predictive variable in the optimal model. In contrast, the interaction term including field capacity and local soil water storage was significant in the model with a negative relationship with relative water uptake, showing that the combination of higher field capacity (fewer macropores) and low soil water hinders water uptake because water more is more strongly bound in the soil. Differences in local soil properties regulate the matric potential at a certain soil wetness. Thus, wetter locations do not necessarily correspond to those of easier root water uptake due to differences in the soil water retention characteristics (Vereecken et al., 2007; Cai et al., 2018) for which field capacity serves as a proxy. However soil properties alone were less important (smaller effects size of the interaction term including field capacity) than other factors despite their control on the spatial distribution of soil moisture (Vereecken et al., 2022).

In addition, the spatial mean of soil water - a measure of overall wetness of the stand - influenced root water uptake patterns, yet the effect depended on the basal area of neighboring trees. We found that as the study site dries out, local water uptake increased in locations with smaller basal areas. Conversely, wetter site conditions facilitate greater water uptake at locations with higher basal areas, i.e., dense clusters of large trees. We interpret this as a sign that larger trees are likely to shift their water uptake to deeper soil layers to meet transpiration demands, beyond the monitored soil depth (37 cm), as follows: Higher basal area is likely to increase transpiration demand and enhance water uptake as long as water is available. Moreover, locations with higher basal area exhaust the water storage more rapidly as these locations host larger root structure and root biomass (Le Goff and Ottorini, 2001). At the same time, larger sized trees can shift uptake to deeper layers (Gaines et al., 2016).

Beech trees have extensive root systems at shallower depths similar to other temperate tree species, such as European ash and sycamore maple (Kreuzwieser and Gessler, 2010; Brinkmann et al., 2019) Despite their shallower root system (Leuschner, 2020) in response to declining soil water content in the topsoil, temperate tree species can tap water from the deeper soil layers (Brinkmann et al., 2019; Agee et al., 2021; Seeger and Weiler, 2021). Recently, Agee et al. (2021) used a three-dimensional water uptake model based on observations in temperate mixed-deciduous forest to show that water uptake is shifted to the deeper soil layers as soil moisture depletes, which is consistent with the field observations. Moreover, Krämer and Hölscher (2010) observed in beech and mixed deciduous stands that roots can extract water at depths down to 70 cm soil depth. Similar to our site, theirs had a shallow soil layer underlain by weathered limestone, but the soil depth varied between 50 and 120 cm. Brinkmann et al., (2019) also observed similar depth range for beech-trees in a mixed forest by tracing stable water isotopes of soil and xylem water.

Further tree age and size can affect both individual and stand level transpiration because of the different physiological characteristics and biometrics of trees associated with them (Kostner et al., 2002; Tsuruta et al., 2023). Within the same species, the larger -presumably older- trees have an advantage in accessing the deeper water storages because of their larger root biomass (Le Goff and Ottorini, 2001) and root plasticity may be able to shift the depth of water uptake while younger trees rely on shallower soil water storages (Dawson, 1996). Our results can be interpreted as tree size, which can be attributed to tree age, affecting root water uptake patterns through differential root biomass development. Furthermore, in the Hainich the coexisting species most likely represent highly coherent rooting depth distribution among trees (Gebauer et al., 2012; Meinen et al., 2009) yet adopt different water uptake strategies (see below). Hence consistent with previous studies focusing on temperate tree species, the linear mixed effect model results indicate that trees of different sizes response to declining soil water content by shifting water uptake depth.

4.3) Tree species richness regulates root water uptake patterns

In addition to the basal area, we included the number of species and number of tree individuals in the linear mixed effects analysis to further explore the biotic drivers of root water uptake patterns. While the number of trees was unimportant, the number of species and the basal area showed a significant interaction effect on the local water uptake. The result indicates that an increase in species richness leads to greater root water uptake, depending on the size and/or density of the neighboring trees: Higher basal area, combined with more species, elevates water uptake. In other words, the interactions among neighboring tree species strongly determine root water uptake patterns, and for the same basal area, more water can be taken up in a diverse neighborhood than in a less diverse locations.

In temperate forests, transpiration has been observed to change with tree species richness at the stand level (Krämer and Hölscher, 2010; Gebauer et al., 2012; Kunert et al., 2012; Meißner et al., 2012; Forrester, 2014). Although some studies indicate a positive relationship between tree diversity and water uptake rate (Forrester et al., 2010; Krämer and Hölscher, 2010; Kunert et al., 2012), tree species diversity is not always positively related to water uptake. While Krämer and Hölscher (2010) observed a positive correlation between water uptake and species richness of the plots in the upper soil layers during soil drying in 2006 at the same study site, Meißner et al. (2012) found no relationship between tree diversity and root water uptake in 2009. They attributed this finding to wetter soil conditions. In contrast, Lübbe et al. (2016) observed a weak effect of diversity on transpiration in wetter soil conditions but not in drier conditions compared to previous studies (e.g., Pretzsch et al., 2013; del Río et al., 2014). Shortage of water can inflate competition mechanisms for water among tree species (González de Andrés et al., 2018; Vitali et al., 2018; Magh et al., 2020). Our results indicate that competition between neighboring tree species increases water uptake capacity at more diverse spots (Wambsganss et al., 2021).

In addition, different co-existing tree species can facilitate resource uptake or reduce competition, depending on the temporal and spatial availability of the sources, which is often defined as complementarity (Forrester and Bauhus, 2016). As reviewed and listed by Silvertown et al. (2015), several studies suggest that co-existing tree species reduce competition for subsurface water sources by adopting different vertical root water uptake strategies, referred to as hydrological niche partitioning. In addition, trees can transport water from wet to dry parts of the soil layers through their roots (Neumann and Cardon, 2012). The mechanism is called hydraulic redistribution or hydraulic lift, which can provide water availability to the shallow roots in drier layers (Burgess et al., 1998; Jonard et al., 2011; Hafner et al., 2017; Lee et al., 2018; Rodríguez-Robles et al., 2020; Hafner et al., 2021). In an experiment with six temperate tree species, including the European beech, Hafner et al. (2021) found that the neighboring tree species diversity may not be important for exploiting water uptake through hydraulic redistribution. Both hydraulic niche partitioning and redistribution have been observed vertically, whereas horizontal patterns are largely unexplored the context of niche partitioning (Hildebrandt, 2020). Our results do not provide direct evidence for either hydraulic redistribution or horizontal niche partitioning. However, they indicate that horizontal root water uptake patterns are regulated by species richness and interactions among neighbouring trees. Thus, we emphasize here the complex interplay between tree species diversity, complementary mechanisms, and water uptake patterns, which is consistent not only with the above-mentioned plot-scale studies, but also with larger-scale studies. For instance Knighton et al., (2019) using the Budyko framework across more than one hundred catchments found that transpiration losses in catchments with deep rooted and mixed species forests differed from those in monoculture catchments. In other words, both plot and catchment scale studies support our results showing that interactions among different coexisting species play a significant role in the spatio-temporal variation of root water uptake.

5) Conclusion

We investigated the factors that influence the spatial patterns of root water uptake by considering heterogeneity in throughfall and soil water. To that end, we acquired a comprehensive data set based on throughfall measurements paired with soil moisture sensors in a mixed deciduous forest. Soil and neighboring tree characteristics were also included in the linear mixed effects model. We found that variation in root water uptake did not correspond to throughfall consequently rejecting our hypothesis that variation in throughfall is imprinted in water uptake patterns. Wetter soil locations, also poorly associated with higher throughfall, increased local root water uptake. In contrast, how average soil water conditions modified root water uptake depended on the neighborhood basal area. As the site dried out, large trees likely took up water in deeper layers to meet transpiration demands. Furthermore, an increase in species diversity promoted root water uptake, similarly depending on the size of neighboring trees, suggesting active complementarity mechanisms in the forest stand. In conclusion, our results manifest that soil water distribution and neighboring tree characteristics regulate root water uptake patterns more than soil properties and throughfall variation.

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Data availability

The dataset is currently being prepared for publication in an official repository. The DOI will be published with the data at the latest when the data are published.

Author contributions

GD and AH designed the throughfall measurement setup, AH and JCM designed soil moisture measurement. GD conducted the field sampling with assistance from JF and the students listed in the Acknowledgments. GD analyzed the data, developed the linear mixed effects model, and analyzed the results with AH and AG. GD prepared the first version of the manuscript, and all authors contributed to discussions and the final version of the manuscript.

Competing interests

Anke Hildebrandt is part of the editorial board of HESS. The peer-review process was guided by an independent editor, and the authors have also no other competing interests to declare.

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