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Transpiration patterns and water use strategies of beech and oak trees along a hillslope

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Abstract

The role of landscape topography in mediating subsurface water availability and ultimately tree transpiration is still poorly understood. To assess how hillslope position affects tree water use, we coupled sap velocity with xylem isotope measurements in a temperate beech-oak forest along a hillslope transect in Luxembourg. We generally observed greater sap velocities at the upslope locations in trees from average-sized trees, suggesting the presence of more suited growing conditions. We found a lower difference in sap velocity among hillslope positions for larger trees, likely due to the exploitation of deeper and more persistent water sources and the larger canopy light interception. Beech trees exploited a shallower and seasonally less persistent water source than oak trees, due to the shallower root system than oak trees. The different water exploitation strategy could also explain the stronger stomatal sensitivity of beech to vapour pressure deficit compared to oak trees. Xylem isotopic composition was seasonally variable at all locations, mainly reflecting the contribution of variable soil water sources and suggesting that groundwater did not contribute, or only marginally contributed, to tree transpiration. Overall, our results suggest that trees along the hillslope mainly rely on water stored in the unsaturated zone and that seasonally shallow groundwater table may not necessarily subsidize water uptake for species that do not tolerate anoxic conditions. Contrary to previous studies, at our site, we did not find higher sap velocity downslope as the subsurface hillslope structure promotes vertical water flux over lateral redistribution in the vadose zone.

KEYWORDS

Critical Zone, hillslope, sap velocity, stable water isotopes, transpiration, tree water sources

1 | INTRODUCTION

Water availability in space and time is one of the key elements shaping forest ecosystems and their adaptive response to environmental stress. Landscape position is a dominant factor that controls the spatio-temporal variability of water available for tree transpiration (Looker et al., 2018). Several studies observed that a variation in water availability along a topographic gradient can result in different tree

species distribution, growth rate, and transpiration fluxes (Elliott et al., 2015; Fan, 2015; Hawthorne & Miniati, 2018; Tromp-van Meerveld & McDonnell, 2006). Topography critically controls plant transpiration via the influence of slope and aspect on the amount of incoming solar radiation (Renner et al., 2016) and on water availability through hillslope hydrological processes (Fan et al., 2017). The age distribution and composition of natural forests are typically adapted to the varying water availability in different parts of the ecosystem in

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order to meet species-specific growth requirements (Band et al., 1993; Lin et al., 2019). Trees covering the hilltop and ridgeline, which are often characterized by thin soils, are frequently less productive in biomass (Hoylman et al., 2018; Kume et al., 2016) but can adapt in certain cases to utilize water from weathered bedrock and rock moisture (Dawson et al., 2020; Klos et al., 2018; Rempe & Dietrich, 2018). On the contrary, trees located in topographically convergent locations may take advantage of shallower groundwater tables (Barbeta & Peñuelas, 2017; Brooks et al., 2015; Eamus et al., 2006; Pettit & Froend, 2018). Shallow groundwater replenishes soil water via upward capillary fluxes or temporary groundwater rise, modulating the water content in the unsaturated zone (Brooks et al., 2015). Groundwater can also directly sustain plant transpiration when the water table is within the root zone (Brooks et al., 2015; David et al., 2013; Miller et al., 2010). Trees at footslope locations can also benefit from water that is laterally redistributed from upslope areas (Band et al., 1993; Hwang et al., 2020; Lin et al., 2019). Nevertheless, some studies have observed high drought sensitivity, a small basal increment, and a reduced leaf area index in trees growing at downslope locations (Elliott et al., 2015; Hwang et al., 2020). This behaviour has been associated with the combined effect of higher water consumption by upslope vegetation compared to downslope vegetation and consequent lower downslope water subsidy available for trees in convergent areas (Hawthorne & Miniati, 2018; Hwang et al., 2020). The lack of consistent findings on how hillslope position controls forest water use may originate from the interplay of the site-specific structure of the Critical Zone, which is the near-ce environment extending from the tree canopy through the soil up to the weathered bedrock (Brooks et al., 2015; Rempe & Dietrich, 2018). The subsurface properties of the Critical Zone (e.g., porosity, permeability, texture, regolith depth, layering and weathered bedrock water storage capacity) control water availability through hydrological processes occurring in hillslopes (Brooks et al., 2015; Hahm et al., 2019; Klaus & Jackson, 2018; Penna et al., 2009).

Trees can utilize different below-ground water sources to sustain transpiration (Barbeta & Peñuelas, 2017). The accessibility of different water sources by trees is not only determined by water redistribution, subsurface structure, and the degree of subsurface heterogeneity, but also by root distribution and activity (Fan et al., 2017). Along a topographic gradient, rooting depth and biomass may vary depending on moisture availability in the subsurface, in order to meet the nutrient and water needs of trees (Tsuruta et al., 2020). Plants have developed different below-ground strategies to access nutrients and water and to respond to changes in their spatio-temporal availability (Bardgett et al., 2014; Fry et al., 2018). Tree water consumption is related to several species-specific features including architectural root traits (i.e., rooting depth and root length density) (Fry et al., 2018), xylem architecture (diffuse- vs. ring-porous species) (Wang et al., 1992) and stomatal regulation (isohydric vs. anisohydric species) (McDowell et al., 2008a; Uhl et al., 2013). Since roots differ in their functional and physical roles (Fry et al., 2018), the mere presence of roots at a given depth is not a reliable indicator of their contribution to water use (Ehleringer & Dawson, 1992). Additionally, it has been shown that

the correspondence between physically present and functionally active roots is species- and time-dependent (Volkman et al., 2016).

Until today, a range of ecohydrological studies successfully employed stable isotopes (i.e., hydrogen ($^1\text{H}/^2\text{H}$) and oxygen ($^{16}\text{O}/^{18}\text{O}$)) in the water molecule in the soil-plant continuum to investigate tree water use (Penna et al., 2018). Xylem water isotopic composition is presumed to reflect the integrated isotopic composition of water sources accessed by the tree (Dawson et al., 2002). It was shown that trees can adapt their water source from shallow to deep soil water following water availability (Brinkmann et al., 2018; Lanning et al., 2020). This species-specific plasticity might be key for their survival and competitiveness under increasing water scarcity (Volkman et al., 2016). The spatial and temporal water source partitioning between different species is still poorly tested and contrasting results have been found (Allen et al., 2019; Bello et al., 2019; Grossiord et al., 2014; Meißner et al., 2013; Volkman et al., 2016). While Meinzer et al. (2001) highlighted the potential of niche complementarity as a competition avoidance strategy, Grossiord (2019) and Gillerot et al. (2020) suggested that tree diversity does not systematically increase the performance of forest communities. Indeed, it was only in drought-prone environments that forest resistance to drought was enhanced by higher diversity (Grossiord et al., 2014). Despite the body of previous work, we lack studies addressing plant water use along hillslope transects. Specifically, combined assessments of transpiration rates and water uptake depths along hillslope transects might help to better understand water use strategies and plasticity of different tree species. Such a combined assessment supports a more detailed comprehension of the seasonal interactions and feedbacks between vegetation and hydrological processes occurring at the hillslope scale.

To address this gap, we carried out an ecohydrological study along a hillslope transect populated by oak (*Quercus petraea* (Matt.) Lieb. x *robur*) and European beech trees (*Fagus sylvatica* L.) in Luxembourg. Beech and oak trees are coexisting species in Central Europe (Barbaroux & Bréda, 2002; Grossiord et al., 2014); however, they may become competitors during drought conditions, resulting in negative consequences on forest vitality and composition (Petritan et al., 2017). Although taxonomically related, the morphological and ecological differences between the two species can result in temporally and spatially different patterns of water utilization (Zapater et al., 2011). We monitored soil moisture, groundwater level, sap velocity and hydro-meteorological variables for one growing season (April–October 2019). Additionally, we determined the isotopic composition of precipitation, soil water, groundwater and xylem water in order to assess the influence of topography on water use. The combination of these measurements allows for discrimination between water sources used by tree species for assessing the physiological response of trees to water availability along a hillslope.

Our study was driven by the general conjecture that landscape position controls tree water use through subsurface water redistribution, including spatially-variable groundwater table depth along the hillslope. Furthermore, we conjectured that the characteristics of a species result in a different response between species at the same hillslope position. In particular, we addressed the following specific research

questions: (i) How does landscape position affect the spatial and temporal patterns of water use? (ii) How do two co-occurring species (beech and oak) characterized by different physiological and hydraulic traits respond to a variable water supply over the growing season?

2 | MATERIALS AND METHODS

2.1 | Study area, ecohydrological monitoring and sampling areas

The experiment was carried out between March and October 2019 at a transect along a south-facing forested hillslope ranging from 485 m to 515 m a.s.l. in the Weierbach catchment (45 ha) in Luxembourg (Figure 1). The hillslope transect is 348 m long spanning from the stream bank up to a plateau area. The moderate, oceanic climate in the region is largely influenced by air masses from the Northern Atlantic Ocean (Hissler et al., 2021, Pfister et al., 2017). Long-term annual precipitation (2007–2018) is approximately 783 mm at the Roodt weather station (3.5 km from the study site). The mean annual air temperature is 8.3°C and 13.5°C during the growing season (1 April to 31 October) from 2007 to 2018.

The forest stand on the selected hillslope transect was characterized in a survey of 18 consecutive 20 × 20-m plots along the hillslope transect (Figure 1) recording the number of trees, species, and diameter at breast height (DBH). The basal area for each tree was calculated from the DBH. Based on the digital elevation model (DEM), we derived the topographic position index (TPI, Hoyleman et al., 2018; Weiss, 2001) to classify landscape position with respect to a defined neighbourhood. The TPI was computed as follows:

$$TPI = z_i - \bar{z}_{i,100} \quad (1)$$

where z is the elevation for the i th pixel and $\bar{z}_{i,100}$ is the average elevation in a 100 m radius around the i th pixel. We defined the plateau area for $TPI > 0.5$, the midslope for $0.5 > TPI > -0.5$, and the footslope for $TPI < -0.5$. The upper five plots fell into the category plateau, the subsequent nine plots into the midslope, and the lowest four plots were associated with the footslope. A fully stocked mixed forest with European beech trees (78% of the forest stand, 60% in basal area) and pedunculate and sessile oak hybrid trees (22% of the forest stand, 40% in basal area) populates the hillslope transect. The two oak species often form hybrids, which are phenologically difficult to differentiate. Hence, we did not differentiate between the species and refer

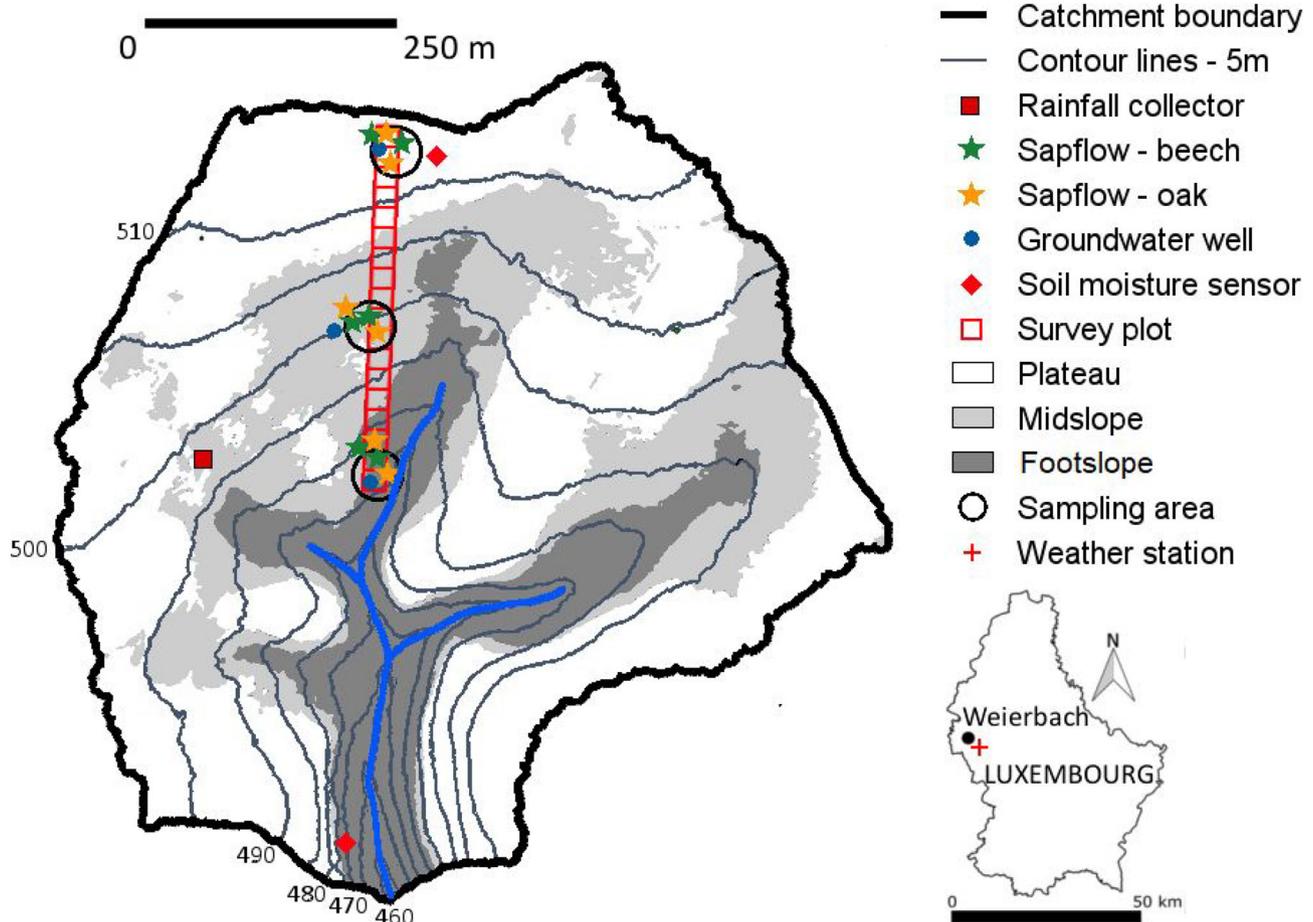


FIGURE 1 Site overview with the forest inventory plots (red squares). At each sampling area, a groundwater well (blue dot) was installed and two trees for each species (beech, oak) were equipped with sap flow sensors (green star for beech, yellow star for oak) with two different diameter classes

to them as oak. Shrubs are absent and the understory mainly consists of blueberries (*Vaccinium myrtillus*). Trees were divided into three diameter classes (Table 1). Given the relatively small diameter differences between individual trees in the plateau area (the upper part of the hillslope, see Figure 1), we define the forest as even-aged. The forest becomes more heterogeneous downslope (Table 1). The plateau area is characterized by a lower basal area and lower forest density than the midslope and footslope (Figure 2). The forest structure in the Weierbach catchment is the result of past and current management practices. Oak trees are evenly distributed across the whole area, while beech tree allometry strongly varies between the three areas with increasing density from the plateau to the footslope (Figure S1). For each landscape position (plateau, midslope, footslope), we established one sampling area (Figure 1).

Soils are shallow (<1 m) and the lithology consists mainly of a Pleistocene periglacial cover bed overlying Devonian slate from the Ardennes massif (Juilleret et al., 2011). The analysis of eight profiles showed that soil characteristics (e.g., structure, porosity, bulk density, particle density and texture) were similar across the catchment (Glaser et al., 2016). On the plateau, the subsolum is characterized by Regolithic Saprolite with gleyic properties, while the hillslope is characterized by a Regolithic Saprock substratum with dense vertical cracks (Juilleret et al., 2016). The solum is a stony loam soil with a mean thickness of 50 cm and an average porosity of 30%. In the subsolum, the size of schist/slate fragments strongly increases while the drainage porosity decreases. On average, the slate bedrock starts at a depth of 140 cm and is highly weathered (Gourdol et al., 2021) and permeable

TABLE 1 Number of trees (plant/ha) per tree diameter at breast height (DBH, cm) classes for beech and oak trees at the three locations along the hillslope

DBH	Plateau		Midslope		Footslope		Total
	Beech	Oak	Beech	Oak	Beech	Oak	
0–25	5	0	153	0	238	6	402
25–50	50	20	72	33	113	63	351
50–75	35	20	28	39	31	19	172

Note: The total indicates the total number of trees per diameter class per hectare.

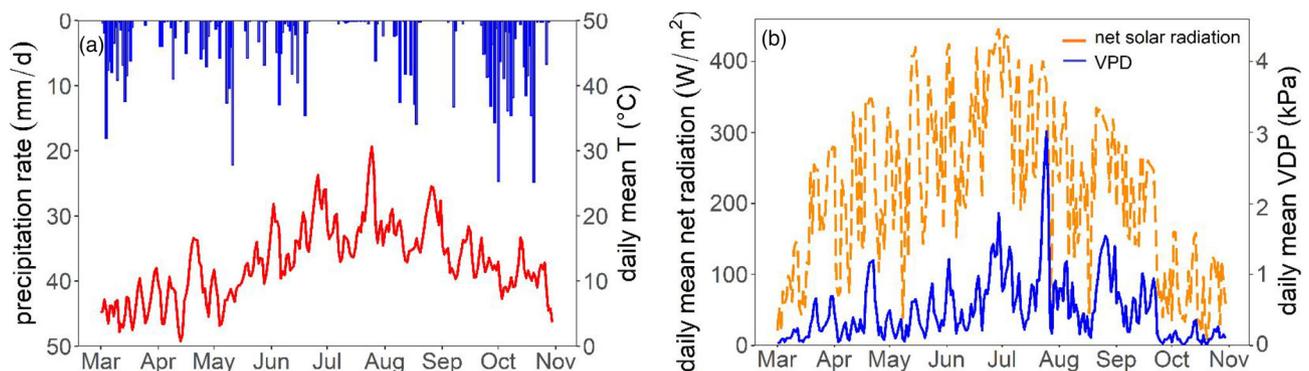


FIGURE 2 (a) Daily total precipitation amount (mm/d) and daily mean air temperature (°C) and (b) daily mean net radiation (W/m²) and daily mean vapour pressure deficit (VPD) (kPa) observed at the Roodt weather station

(Bonanno et al., 2021; Scaini et al., 2018). The subsurface structure leads to a dominance of vertical hydrological fluxes, while lateral flow occurs in the deeper hillslope (Glaser et al., 2019, 2016) and contributes to streamflow (Rodriguez et al., 2021; Rodriguez & Klaus, 2019).

Temperature (T), relative air humidity (RH), solar radiation and precipitation (15-min logging intervals) data were available from the weather station. Using T and RH, we calculated the daily mean vapour pressure deficit (VPD) using Equation 2:

$$VPD = 0.61375 \times e^{(17.502 \times T / (240.97 + T))} \times \left(1 - \frac{RH}{100}\right) \quad (2)$$

Volumetric soil moisture was measured at the plateau and at a footslope at a different hillslope close to the catchment outlet with water content reflectometers (CS650, Campbell Scientific, UK). Each profile consisted of four probes installed horizontally at 10, 20, 40, and 60 cm depth recording at 30-min intervals (Figure 1). At each location, one groundwater well was installed (10, 9, 3.5 m deep, and screened for 5, 4, 2.5 m from the bottom at the plateau, midslope and footslope, respectively) and was equipped with water pressure transducers (Orpheus Mini, OTT, Germany) recording data at 15 min logging intervals.

2.2 | Measurement of sap velocity

At each of the three sampling areas (Figure 1), we selected one tree from the most frequent diameter class (25–50 cm, referred to as average diameter class) and one tree from the diameter class 50–75 cm (referred to as large diameter class) of both species for sap velocity measurements (Table 1). The selected trees were equipped with heat-pulse sap flow sensors (SFM1, ICT International Pty Ltd., Australia) (Table 2). We positioned the sap flow sensors at the north-east side of the trunk, 1.3 m above the ground and shielded them from direct sun exposure. The sensors consist of a central heating needle and two needles, each with two thermistors (located at 12.5 and 27.5 mm from the bark on a 35-mm-long needle) recording the temperature upstream and downstream of the heater. Needles were installed one above the other with a vertical distance of 0.5 cm. The heat pulse

TABLE 2 Tree, location, tree DBH, sapwood area and time period with available sap velocity data

Tree	Location	DBH (cm)	Sapwood area (cm ²)	Available sap flow data
beech 1	plateau	32.8	544.8	07/04/2019 to 31/10/2019
beech 2	plateau	58.9	1676.7	07/04/2019 to 23/05/2019 to 09/07/2019 to 31/10/2019
beech 3	midslope	31.5	504.9	07/04/2019 to 31/10/2019
beech 4	midslope	71.3	2420.6	07/04/2019 to 31/10/2019
beech 5	footslope	30.9	485.2	07/04/2019 to 31/10/2019
beech 6	footslope	57.9	1625.2	07/04/2019 to 23/05/2019 to 09/07/2019 to 31/10/2019
oak 1	plateau	45.8	335.2	07/04/2019 to 31/10/2019
oak 2	plateau	73.5	853.1	07/04/2019 to 31/10/2019
oak 3	midslope	39.8	299.4	07/04/2019 to 23/05/2019 to 09/07/2019 to 31/10/2019
oak 4	midslope	66.8	824.7	07/04/2019 to 23/05/2019 to 09/07/2019 to 31/10/2019
oak 5	footslope	36.6	315.7	07/04/2019 to 31/10/2019
oak 6	footslope	63.6	832.9	07/04/2019 to 23/05/2019 to 09/07/2019 to 31/10/2019

velocity (V_h in cm h^{-1}) was calculated with Equation 3 (Burgess et al., 2001) at the inner and the outer thermistor:

$$V_h = \frac{k}{x} \ln\left(\frac{T_1}{T_2}\right) 3600 \quad (3)$$

where k is the thermal diffusivity ($\text{cm}^2 \text{s}^{-1}$) set to 0.0025 (Marshall, 1958), x is the distance between the heater and either temperature probe (0.5 cm), and T_1 ($^{\circ}\text{C}$) and T_2 ($^{\circ}\text{C}$) are the increases in temperature in the downstream and upstream thermistor, respectively.

Data were recorded from 7 April 2019 until 31 October 2019 at 30-min intervals covering the 2019 growing season. Sap velocity (V_{sap} in cm h^{-1}) for every monitored tree was calculated based on heat pulse velocity according to Equation 4 (Barrett et al., 1995) (Figure 4).

$$V_{\text{sap}} = V_h B \frac{\rho_b (c_w + m_c \cdot c_s)}{\rho_s \cdot c_s} \quad (4)$$

where V_h is the calculated heat pulse velocity (cm h^{-1}), B is the wound correction factor set to 0.13 cm (Marshall, 1958), ρ_b the basic density of wood set to 0.5 g cm^{-3} (Burgess & Downey, 2014), c_w the specific heat capacity of the wood matrix ($1200 \text{ J kh}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Becker & Edwards, 1999), c_s the specific heat capacity of sap (water, $4182 \text{ J kh}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Lide, 1992), ρ_s the density of sap water (1 g cm^{-3}), and m_c the water content of sapwood (set to 0.5 g cm^{-3} ; Burgess & Downey, 2014).

Following Renner et al. (2016), sap velocities measured by the inner and outer thermistor were averaged to obtain the daily mean sap velocity, which is used as a proxy of tree transpiration (Smith & Allen, 1996). For our analyses, we were interested in the response of sap velocity to environmental conditions (i.e., soil moisture and VPD) as an indicator for stomatal control, therefore we scaled daily mean sap velocities between 0 and 1 for further analysis, where 0 and 1 were the minimum and maximum daily mean velocities recorded by each tree over the entire growing season.

2.3 | Wood core, soil and water sampling for isotopic analysis

We carried out 14 bi-weekly sampling campaigns over one entire growing season from 8 April 2019 (before leaf flush) until 21 October 2019 (when leaves were turning yellow). For each campaign, we randomly selected two beech and two oak trees from the dominant diameter class (25- to 50-cm DBH) at each of the sampling areas (Table 1). The maximum distance between trees equipped with sap flow sensors and trees that were sampled for xylem water was 25 m. We collected trunk cores encompassing only the sapwood with a Pressler borer, removed the bark, and transferred the remaining xylem wood into 30-ml glass vials sealed with caps and Parafilm[®]. Samples were stored in a freezer (-22°C) until water extraction (see Section 2.4). During five sampling campaigns (8 April, 23 April, 3 June, 17 June and 1 July), we also sampled soil cores to assess the soil water isotopic composition. At each sampling area, we extracted three soil cores from the top 60 cm divided into five depth classes (0–5, 5–10, 10–20, 20–40 and 40–60 cm) with a soil auger. A 60-cm depth was the lower limit of sampling due to the interface between the soil and rock clasts of the basal layer (Juilleret et al., 2011). Each soil sample was stored in zip bags with as little air as possible until analysis (see Section 2.4). We sampled groundwater at the sampling areas and rainfall bi-weekly with a rainfall collector (Palmex Ltd.) placed in a clearing (Figure 1).

2.4 | Water extraction from plant and soil material and isotopic analyses

We extracted xylem water from wood cores through a cryogenic vacuum distillation line (Orlowski et al., 2016) by submerging the sample in a 100°C oil bath for 3 h under a vacuum of 0.03 hPa. Evaporated water was collected in U-shaped tubes, which were submerged in liquid nitrogen (-197°C). The pressure was continuously recorded to assure that the lines remained leak-tight throughout the entire

extraction. The average extraction efficiency of the cryogenic vacuum distillation line is 99.7%, which was assessed by oven drying 210 extracted samples at 105°C for 24 h and weighing them afterwards. The isotopic composition of the extracted water ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) was analysed using a Picarro cavity ring down spectrometer (CRDS) (L2140-i, Picarro, USA) coupled with a Micro-Combustion Module™ (MCM) in order to remove organic compounds (ethanol, methanol and/or other biogenic volatile compounds). To detect possible organic contamination, xylem samples were screened with ChemCorrect™ (Picarro Inc., Santa Clara, CA, USA) software, which attempts to identify contamination through fitting to a known library of spectral features. In order to minimize the potential memory effect (Penna et al., 2012), each sample was analysed 10 times and only the last five measurements were used to calculate the average isotope signal. Our quality control lab standard water was 0.02‰ for $\delta^{18}\text{O}$ and 0.3‰ for $\delta^2\text{H}$. Precipitation and groundwater samples were analysed on a LGR Liquid Water Isotope Analyzer (TIWA-45-EP, Los Gatos Research, Inc., Mountain View, CA, USA).

We analysed soil samples for their water stable isotopic composition with direct liquid-water-vapour equilibration (Wassenaar et al., 2008). We prepared the sampling bags with a blot of silicone on the outside to later serve as a septum. After each sampling campaign, sampling bags were heat sealed upon arrival at the lab, pierced, and inflated with dry air with a needle, and left to equilibrate for 24 h to allow water liquid-vapour equilibration. In parallel, three bags were filled with 40 ml of water with known isotopic composition (ranging between -10.3 – 2.9 in $\delta^{18}\text{O}$ and -154.0 – 9.9 in $\delta^2\text{H}$) and dry air and left 24 h to equilibrate. Headspace vapour was sampled directly with a needle connected to the Picarro analyser coupled with MCM for the samples and the three bags with known values. We used two known values as standards for calibration and one known value for validation. For this analysis, our quality control lab standard showed an average deviation from the real value of 0.07‰ for $\delta^{18}\text{O}$ and 1.7‰ for $\delta^2\text{H}$.

The local meteoric water line (LMWL) at the study site, based on biweekly precipitation samples collected from 2011 to 2018, is $\delta^2\text{H} = 7.4 \delta^{18}\text{O} + 6.5$. This rather low slope is characteristic for the region as shown for the IAEA precipitation isotope station in Trier (Klaus et al., 2015; Stumpp et al., 2014), which is approximately 64 km from the study site. We calculated the *lc*-excess for xylem water following Landwehr and Coplen (2004):

$$lc - excess = \delta^2\text{H} - a \cdot \delta^{18}\text{O} - b \quad (5)$$

where *a* and *b* are the slope and intercept of the LMWL, respectively.

2.5 | Data analysis

We analysed differences in sap velocities and $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in xylem, groundwater, and soil water between species and sampling areas using the software R (v.3.2.1; R Core Team, 2015). Comparisons of sap velocities between sampling areas, species, and diameter classes

were analysed with the Pairwise Wilcoxon test. The Pairwise Wilcoxon test was also used to analyse differences in the isotopic composition of groundwater sampled at the three sampling areas. Comparisons of the xylem isotopic composition between different species, sampling areas, and sampling dates were analysed via the non-parametric Mann-Whitney test.

3 | RESULTS

3.1 | Environmental conditions over the 2019 growing season

The cumulative precipitation from 1 March 2019 to 31 October 2019 was 608.6 mm and the mean air temperature was 11.9°C (Figure 2a). The daily mean VPD and solar radiation increased during the growing season, reaching a peak in July (Figure 2b). Soil moisture progressively decreased between May and September at all depths, but from September, it increased due to a decrease in evapotranspiration and recurrent precipitation. The topsoil moisture content (10 cm) mostly reflected the precipitation pattern; the soil moisture signal in the deeper soil was generally damped compared to the topsoil (Figure 3b,c). Deeper soil (60 cm) at the plateau displayed a consistently higher volumetric water content compared to shallower soil (Figure 3b). At the footslope, soil moisture was higher in the topsoil and decreased over time reaching the same values of deeper layers from July onwards (Figure 3c). The groundwater level at the plateau and midslope position showed a similar temporal trend. The groundwater level was highest in spring and decreased throughout the growing season, reaching 4.7 m and 5.7 m below the surface at the plateau and midslope positions, respectively (Figure 3d). The groundwater table at the footslope location was quite steady over the study period with an average of 2.6 m below surface (Figure 3d).

3.2 | Sap velocity: Species, site and size-specific differences

The daily mean sap velocity exhibited species, site, and size-specific variations. Due to instrument failure, not all sensors supplied a complete record over the growing season (Table 2). Beech trees showed earlier leaf emergence (approx. 18–26 April) than oak trees (approx. 1–7 May), consistent with increasing sap velocity during these periods (Figure 4). We observed a strong seasonal pattern in sap velocity at the three sampling areas for both monitored diameter classes (Figure 4). Sap velocity increased in spring, reaching the maximum at the end of June when atmospheric water demand and soil moisture were high. Concurrently with decreasing soil moisture and high evaporative demand, sap velocity decreased gradually and showed minimum values in mid-August. Short-term increases of sap velocity occurred during the summer following precipitation events (e.g., middle of August, cf. Figure 2a). From the end of August, we

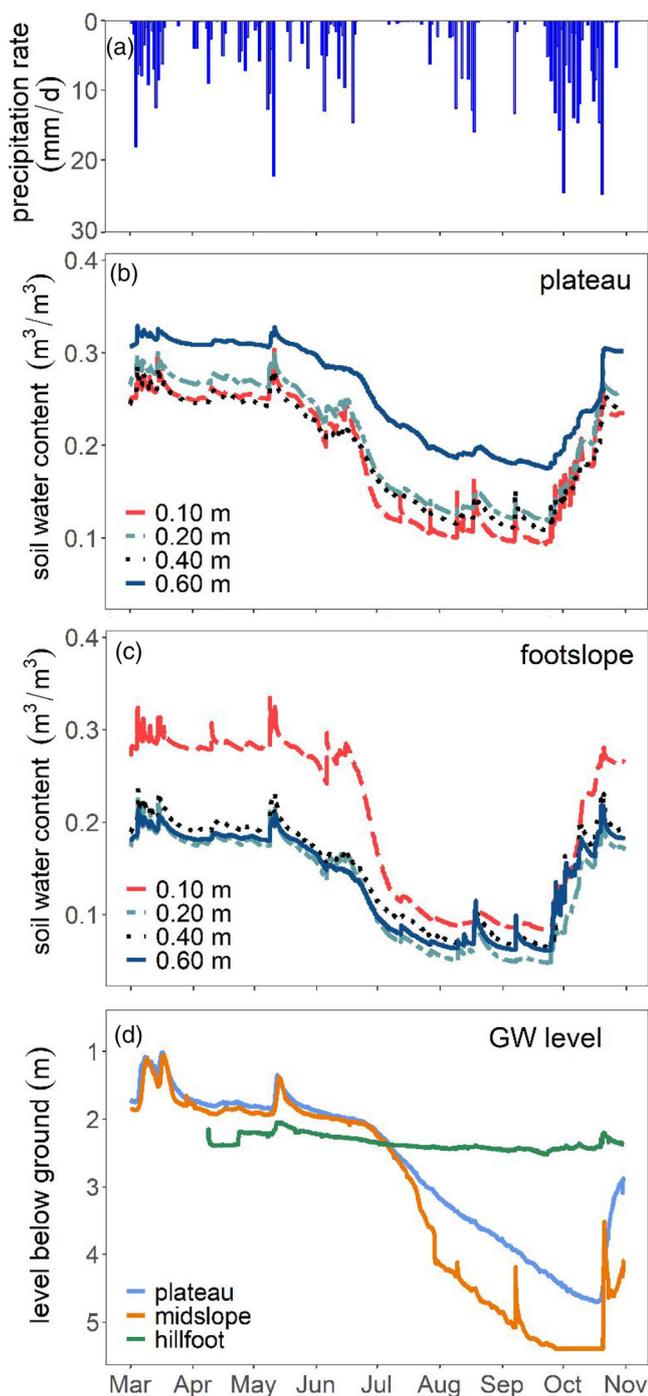


FIGURE 3 (a) Precipitation at the Roodt weather station, volumetric soil water content (SWC) recorded at 30 min intervals measured at the (b) plateau sampling area and at the (c) footslope location and (d) groundwater level below ground surface (m) measured at the three sampling areas

observed a progressive decline in sap velocity, as soil moisture remained low and VPD decreased (Figures 2 and 3).

The daily mean sap velocities of beech trees from the average diameter class (25–50 cm DBH) were consistently higher at the midslope than at the other locations ($p < 0.05$, Pairwise Wilcoxon test) (Figure 4a). Beech trees at the footslope location experienced a

delayed increase in sap velocity but reached the same velocities as plateau trees in summer. Sap velocity for beech trees from the large diameter class (50- to 75-cm DBH) (Figure 4c) was not different between the sampling areas. Mean daily sap velocities in beech trees were statistically not different among the average and the large diameter class ($p > 0.05$, Pairwise Wilcoxon test) (Figures 4a and 4c). Oak trees experienced significantly higher sap velocities at the plateau for both diameter classes than the other locations ($p < 0.05$, Pairwise Wilcoxon test) (Figures 4b and 4d). For the average diameter class, sap velocity was statistically similar for oak trees at the footslope and midslope, while for oak trees of the large diameter class, the plateau tree displayed the highest, followed by the one midslope and footslope (Figure 4d). For oak trees, sap velocity was approximately 2.5 times higher for the large diameter class than for trees from the average diameter class. We did not find a statistical difference between the two species in sap velocity for the large diameter class ($p > 0.05$, Pairwise Wilcoxon test) when comparing dates where all sensor data was available (Figure 4c,d). Sap velocities were significantly higher for the average diameter class of beech trees than oak trees ($p < 0.05$, Pairwise Wilcoxon test) (Figure 4a,b).

3.3 | Relationship between sap velocity, vapour pressure deficit and soil moisture

The relationship between normalized sap velocities from trees from the average diameter class and daily average VPD and the relationship between normalized sap velocity and daily average soil moisture across the four measured depths (from the plateau cluster) showed anticlockwise hysteresis for both species (Figures 5 and 6). However, the shape of the loop was different for the beech and oak trees (Figures 5 and 6) suggesting a species-specific response to the two environmental controls. In the early growing season, sap velocity progressively increased in all monitored plants concurrently with an increase in VPD (Figure 5). For beech trees, maximum sap velocity occurred when VPD values ranged between 1.2 and 1.4 kPa (Figure 5). However, at the end of July, when average VPD values were above 1.85 kPa, sap velocities in beech trees dropped by about 35%–50% (Figure 5). Contrary to beech, oak trees maintained maximum sap velocities (Figure 5). When VPD ranged between 1.2 and 1.4 kPa again in August, beech trees did not meet the pre-stress sap velocities (Figures 5 and 6).

We also observed a marked temporal pattern in the relationship between sap velocity and soil moisture and different behaviours between the two species (Figure 6). Sap velocity increased for both species at the beginning of the growing season when soil moisture was high. Sap velocity in beech trees experienced a marked decline compared to oak trees once soil water content approached $0.2 \text{ m}^3 \text{ m}^{-3}$. Oak trees maintained stable and high sap velocities and dropped only when the soil moisture content was lower than $0.15 \text{ m}^3 \text{ m}^{-3}$. We did not observe differences in the relation between VPD or soil moisture and normalized sap velocity

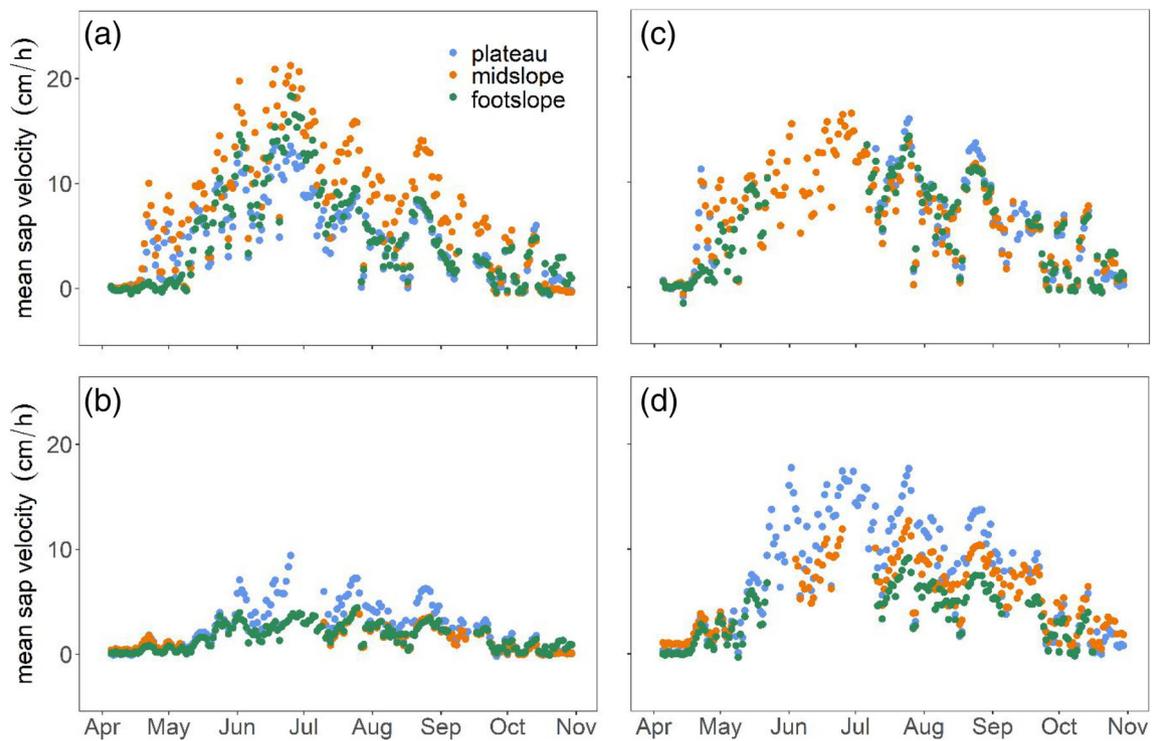


FIGURE 4 Sap velocity (cm h^{-1}) of beech and oak at three sampling areas; (a) beech from the average diameter class, (b) oak from the average diameter class, (c) beech from the large diameter class and (d) oak from the large diameter class

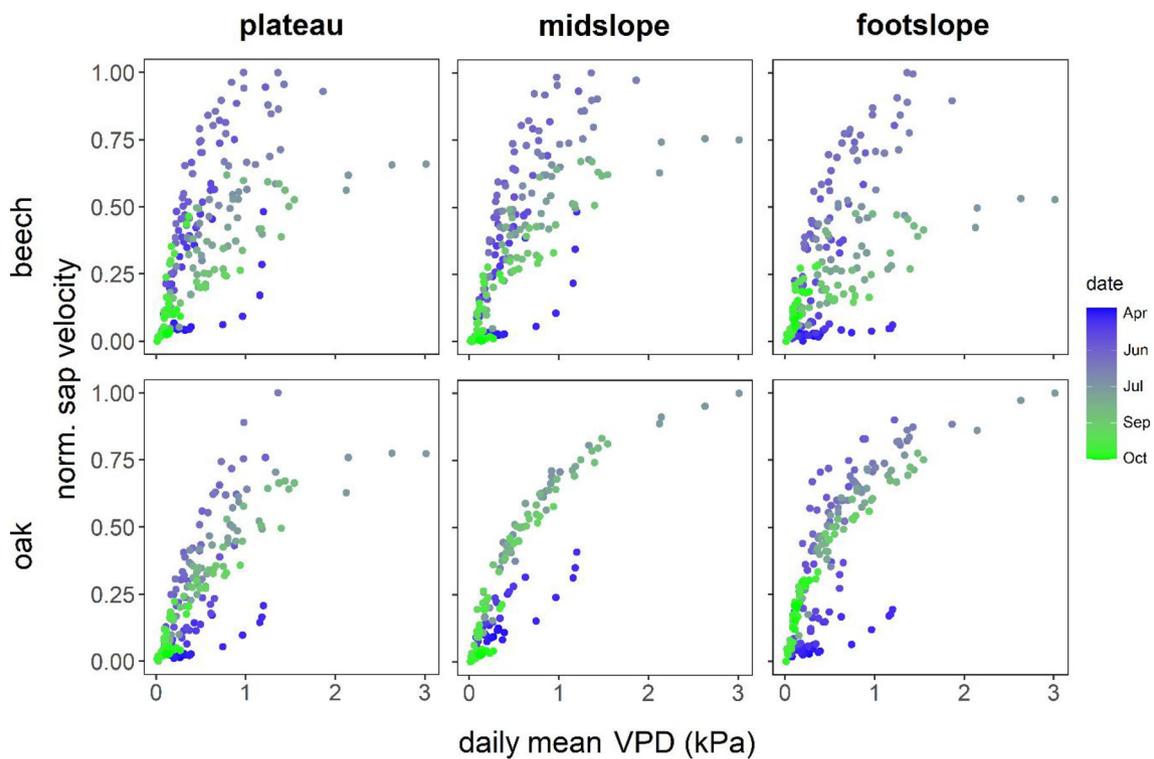


FIGURE 5 Relationship between normalized mean sap velocity and daily average vapour pressure deficit (VPD) (kPa) from beech and oak trees from the average diameter class at the three sampling areas at different hillslope positions with data from 5 April 2019 to 31 October 2019

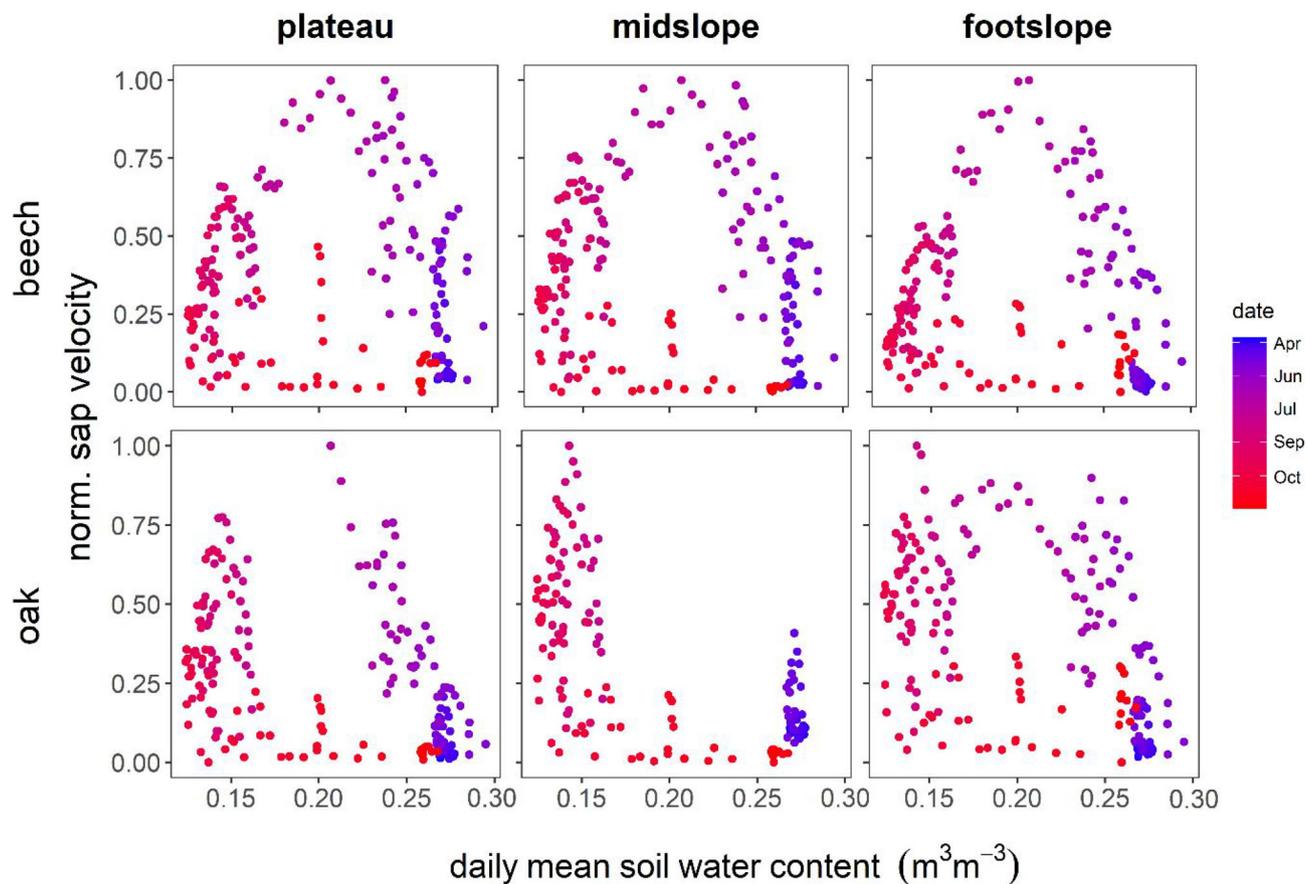


FIGURE 6 Relationship between normalized mean sap velocity of beech and oak trees from the average diameter class at the three sampling areas at different hillslope positions and daily mean soil water content ($\text{m}^3 \text{m}^{-3}$) at the plateau site from 5 April 2019 to 31 October 2019

between the different sampling areas (Figures 5 and 6). Sap flow data for trees from the large diameter class showed the same patterns (data not presented).

3.4 | Isotopic composition of water, soil and xylem samples

The isotopic composition of the bi-weekly precipitation samples collected between 1 March and 31 Oct 2019 ranged from -14.6‰ to -2.3‰ and from -97.6‰ to -17.2‰ in $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively. The groundwater isotopic composition was quite stable over time but was statistically significantly different between the three sampling areas ($p < 0.05$, Kruskal–Wallis test) displaying progressively lighter isotopic values moving from the plateau (mean -8.3‰ $\delta^{18}\text{O}$, -53.5‰ $\delta^2\text{H}$) to the midslope (mean -8.4‰ $\delta^{18}\text{O}$, -54.0‰ $\delta^2\text{H}$) and the footslope location (mean -8.5‰ $\delta^{18}\text{O}$, -55.1‰ $\delta^2\text{H}$). Soil water showed less negative isotopic values in shallow soil layers and more negative values in deeper soil layers (Figure S2). No significant differences in soil water isotopic composition occurred between different sampling areas ($p > 0.05$, Wilcoxon rank sum test). Deeper soil layers displayed a generally constant isotopic composition over time compared to the shallower layers, which tended to become isotopically

heavier over time. In the dual isotope plot (Figure 7), soil isotopic values plotted along the LMWL.

Xylem water from both species plotted below the LMWL in the dual-isotope space (Figure 7). This was a consistent occurrence across all sampling campaigns and sampling areas (Figure 7). In particular, the xylem samples from beech trees plotted farther away from the LMWL than those from oak trees (Figure 7). The isotopic composition of xylem water was highly variable throughout the growing season (Figure 8). Xylem water from the first sampling campaign (8 April 2019) before the leaf flush was significantly higher in δ -values for both isotopes (Wilcoxon rank sum test, $p < 0.05$) compared to later dates (Figure 8) and was situated in the upper right area of the dual-isotope plot (Figures 7 and S3). Concurrently with leaf flush, the δ -values became markedly lighter (Figure 8a,b) and xylem water fell in the lower left part of the dual-isotope space (Figures 7 and S3). Xylem water from both species became progressively heavier in both isotopes over the growing season, although two sampling campaigns that were carried out one day after rainfall led to a deviation from this general trend (cf. late July and September sampling, Figure 8). For both isotopes, the interquartile range and variability over the sampling season were higher for beech trees than for oak trees (Figures 8 and 9). Xylem water from beech trees displayed a more pronounced variability at the sampling date and seasonal scale than xylem water from oak

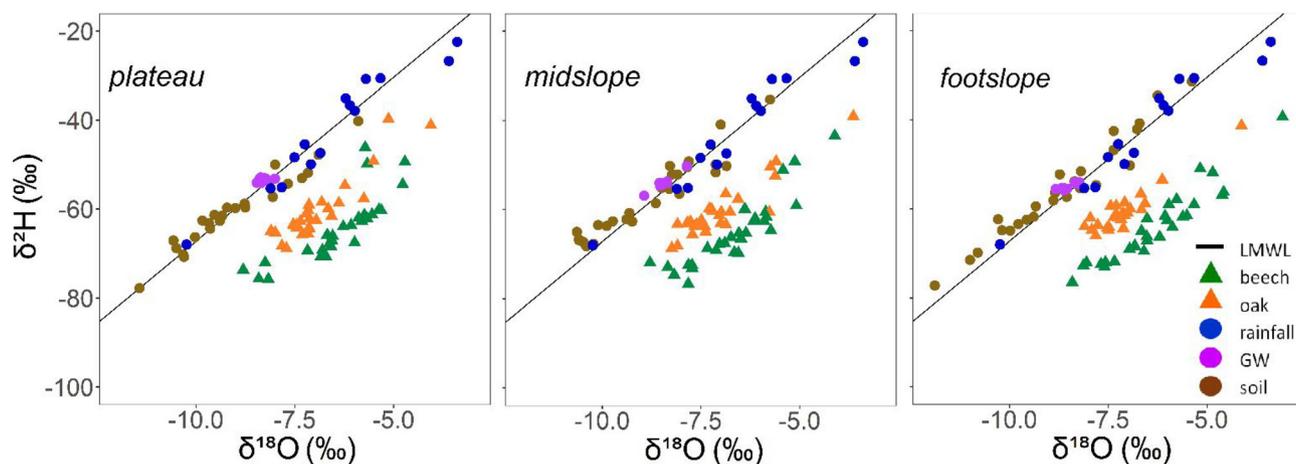


FIGURE 7 Dual-isotope ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) plot of xylem water from the two species studied and their potential sources (soil water at five depth, groundwater) for every sampling campaign conducted in 2019. Soil was sampled on 8 and 23 April, 3 and 17 June and 1 July. The black line indicates the LMWL ($\delta^2\text{H} = 7.4 \delta^{18}\text{O} + 6.5$)

trees, which exhibited more consistent isotopic composition over time (Figure 8). From the end of May to the end of the 2019 growing season, xylem water from beech trees showed heavier $\delta^{18}\text{O}$ values than in oak trees ($p < 0.05$) but lighter in $\delta^2\text{H}$ ($p > 0.05$). We found a statistical difference in xylem l -excess between the two species (Figure 9c) (Wilcoxon rank sum test, $p > 0.05$) over the whole study period. We did not observe significant differences ($p > 0.05$, Wilcoxon rank sum test) in beech tree xylem $\delta^{18}\text{O}$, $\delta^2\text{H}$, and l -excess along the hillslope when xylem data were grouped together (Figure 9). Additionally, no topographic effect was evident in l -excess over time (Figure 10). However, from June to September, beech trees at the plateau location exhibited more negative l -excess than the other locations. For oak trees, we did not observe significant differences in xylem $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ($p > 0.05$, Wilcoxon rank sum test) between the three locations but l -excess was significantly different between the plateau and the footslope ($p < 0.05$, Wilcoxon rank sum test) (Figure 9).

4 | DISCUSSION

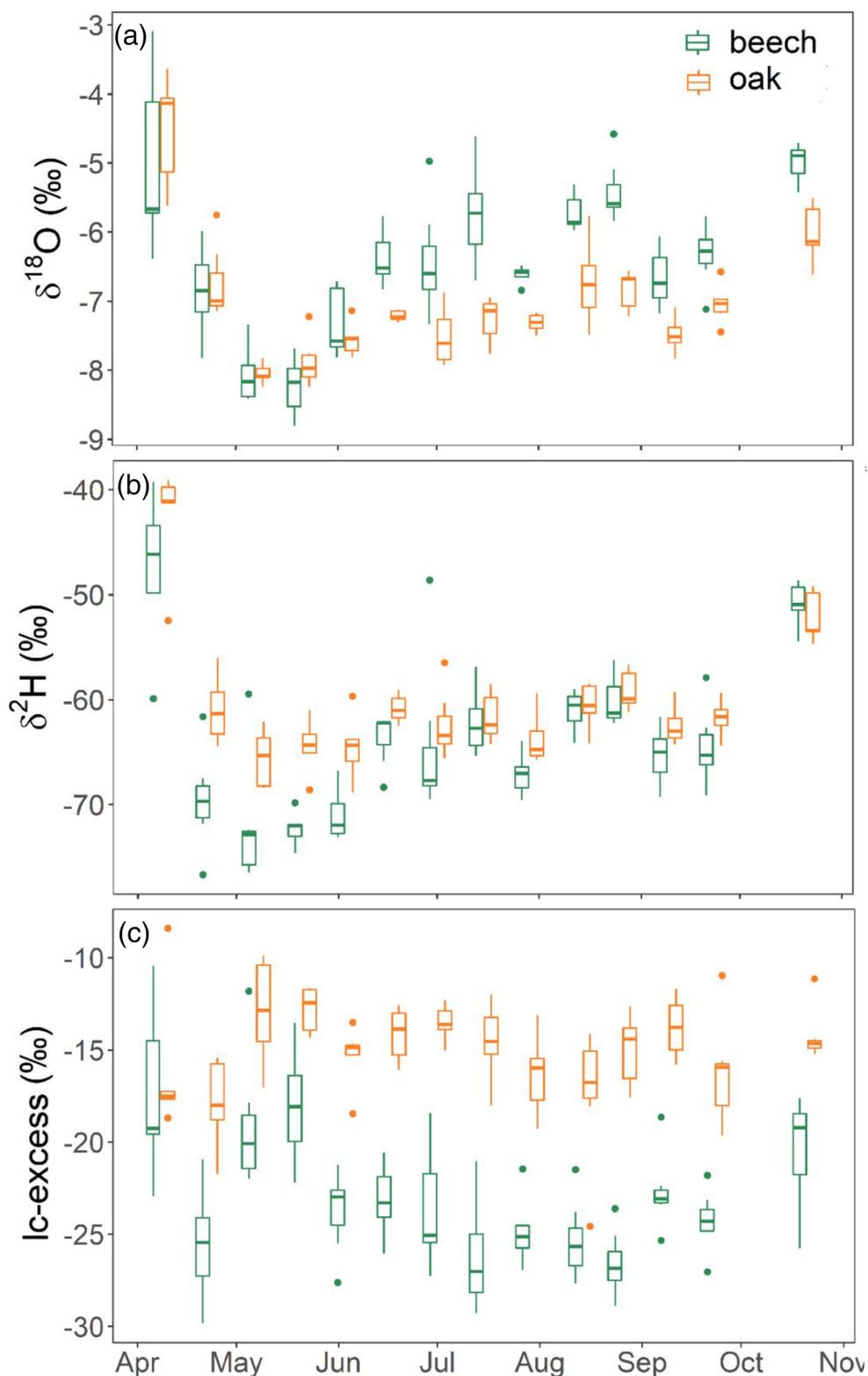
4.1 | Spatial and temporal pattern in tree water use along the hillslope

We generally observed higher sap velocities in trees from the average diameter class growing at plateau and midslope locations compared to those at the footslope suggesting that growing conditions at upslope areas were more suitable. Here, trees may benefit from a lower degree of competition for water and greater access to light due to the lower forest density compared to the footslope location (Pretzsch & Forrester, 2017) (Figure S1). We observed minor differences in sap velocity between locations for large diameter trees, because they likely have access to a deeper and more stable water reservoir (cf. Gaines et al., 2016; Goldsmith et al., 2012) and occupy dominant positions which ensure greater light interception than the average

trees in the stand. From the beginning of the growing season until late June when leaves were completely unfolded, sap velocities increased along the hillslope due to the increasing VPD and sufficient soil water supply (Figures 3 and 4). From June onwards, xylem water isotopes progressively became heavier (Figure 8) and the l -excess became more negative indicating that trees relied on water sources that had been increasingly affected by isotopic enrichment, such as shallow soil water. From July onwards, soil moisture decreased, the groundwater table at plateau and midslope locations receded, and sap velocities decreased. The response of sap velocity to environmental controls (VPD and soil moisture) was species-specific but similar in all locations (Figures 5 and 6) indicating that the sampled trees mainly absorbed water from similar sources, irrespective of hillslope position. However, at the footslope, sap velocities were equal to or lower than at the midslope and plateau locations (Figure 4) despite a seasonally high and stable groundwater table (Figure 3d). This may indicate that increased groundwater accessibility did not foster higher transpiration rates.

Xylem isotopic composition varied seasonally but differed between the sampling areas in only a few sampling campaigns (Figure 7). This result suggests that at our study site trees might not directly rely on groundwater or used it to such a limited extent that no clear differentiation in isotopic composition between trees vegetating in higher positions in the landscape was detectable. In studies where trees were found to exploit groundwater, xylem water isotopic composition hardly varied over time because groundwater isotopic composition was rather stable compared to rain and soil water (Carrière et al., 2020; David et al., 2013). The observed high and seasonally stable groundwater table at the footslope may even restrict root development and confine roots to shallow soil and saprolite layers, since saturated environments can limit root expansion and plant productivity for species that do not tolerate permanent hypoxic or anoxic conditions (Fan et al., 2017; Hasenmueller et al., 2017; Rossatto et al., 2014; Roy et al., 2000) such as beech and oak trees

FIGURE 8 (a) $\delta^{18}\text{O}$, (b) $\delta^2\text{H}$ and (c) lc-excess of xylem water for each sampling campaign across the growing season. The data from each species were averaged over the three sampling areas. The centre line in the boxplot indicates the median, and the lower and upper extremes indicate the first and third quartile, respectively. The whiskers indicate points within 1.5 times the interquartile range above or below the median



(Schmull & Thomas, 2000). Additionally, the lack of daily groundwater table fluctuations, even when sap velocity was high (Figure 3d), may indicate that trees did not rely, or only marginally relied, on groundwater (cf. Naumburg et al., 2005). Diurnal water table fluctuations have been mostly observed in riparian areas and used to directly assess groundwater consumption by plants (Martinetti et al., 2021; Moro et al., 2004; Soylu et al., 2012), but these studies involved wetland

species that cope with anoxic conditions in the root zone. However, at our study site the potential tree water uptake from groundwater at the footslope might have been balanced by groundwater inflow from upslope areas (Rinderer et al., 2017). The progressively declining water table at upslope locations over the growing season may have left behind an aerated soil profile at field capacity, which became available for deeper root exploitation (Naumburg et al., 2005). Trees

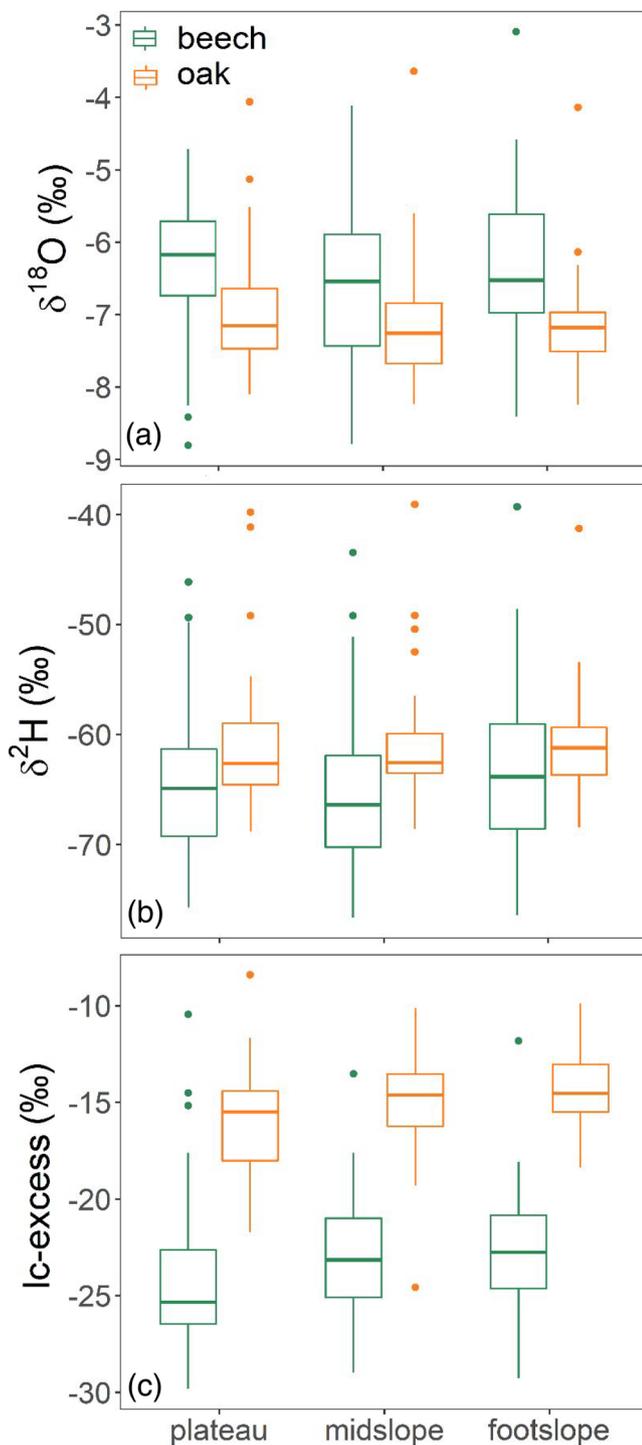


FIGURE 9 (a) $\delta^{18}\text{O}$, (b) $\delta^2\text{H}$ and (c) Ic-excess of xylem water for each sampling campaign at the three sampling plots for all sampling campaigns conducted in 2019. The centre line in the boxplot indicates the median, and the lower and upper extremes indicate the first and third quartile, respectively. The whiskers indicate points within 1.5 times the interquartile range above or below the median

located in the upper portion of hillslopes are usually found to develop a dimorphic root system that allows them to access the weathered rock moisture during dry periods (Fan et al., 2017). Hahm et al. (2020)

were able to demonstrate that the receding groundwater table progressively offers a large water reservoir held in the weathered bedrock, which is accessed by deeper roots, and that rock moisture can offer a significant contribution to transpiration in a variety of lithological settings (Rempe & Dietrich, 2018). However, the isotopic characterization of this potential water source is often neglected in isotope studies due to difficulties in accessing and measuring below-ground compartments (Rempe & Dietrich, 2018).

Xylem water in our study displayed a hydrogen isotope ratio more depleted than any of the water sources considered, as shown in other studies (Barbeta et al., 2019; Oerter et al., 2019; Oerter & Bowen, 2017). Some possible explanations for this offset have been proposed in the literature, including isotopic separation between bound and mobile soil water (Brooks et al., 2010), water compartmentalization between flowing and stored water in the stem (von Freyberg et al., 2020; Zhao et al., 2016), and isotopic fractionation at the soil-root interface (Barbeta et al., 2020; Poca et al., 2019). Other studies have provided some indications that the isotopic offset could arise from $\delta^{18}\text{O}$ fractionation processes (Marshall et al., 2020; Vargas et al., 2017), challenging the argument of negligible ^{18}O fractionation during root water uptake (Rothfuss & Javaux, 2017). We do not have evidence that goes beyond the behaviours recently discussed (Beyer & Penna, 2021; von Freyberg et al., 2020), but we cannot exclude that unsampled saprolite and weathered bedrock waters could act as additional sources potentially explaining this offset.

Furthermore, the lack of higher sap velocity at the footslope location, which is contrary to observations in several other studies due to the lateral redistribution of soil moisture (Hawthorne & Miniati, 2018), deeper soil, and higher water holding capacity (Kumagai et al., 2008; Mitchell et al., 2012; Tromp-van Meerveld & McDonnell, 2006) provides some insight into the hydrological functioning of the Critical Zone at the Weierbach. Due to the high hydraulic conductivities in the Weierbach catchment (Glaser et al., 2016) and the lack of shallow impeding layers, the hillslope structure does not promote the lateral downslope redistribution of soil water via interflow (Klaus & Jackson, 2018). This results in reduced subsidies to soil moisture at footslope locations, contrary to what was observed in other studies (Hawthorne & Miniati, 2018; Lin et al., 2019). Due to the highly fractured bedrock (Juilleret et al., 2011; Martínez-Carreras et al., 2016), upslope patches are hydrologically connected only through the saturated zone with downslope areas allowing groundwater at the footslope location to maintain a constant and shallow water table over the investigated period (Rinderer et al., 2017). This behaviour shows the critical importance of landscape characteristics determining water redistribution, water availability for vegetation, and ultimately growing conditions.

4.2 | Species-specific response to variable water supply

Our study showed that beech and oak trees clearly have different water uses, representing a resource-driven niche partitioning. The

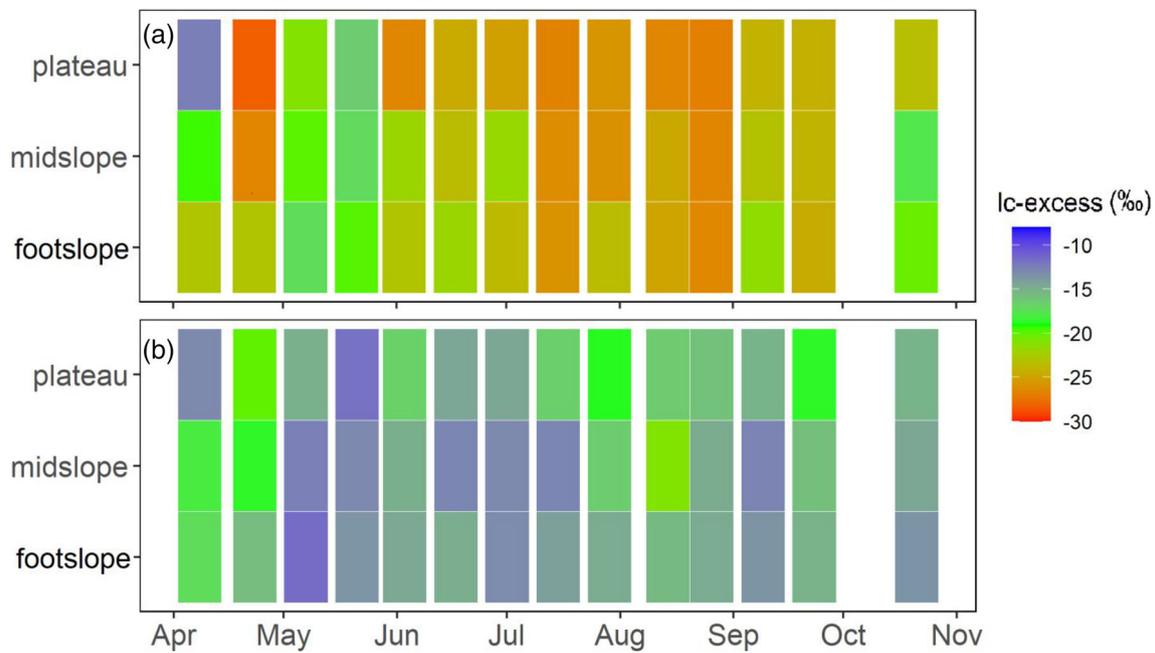


FIGURE 10 $\delta^{13}\text{C}$ -excess of xylem water from (a) beech and (b) oak trees at the three sampling areas over the growing season

systematically more negative and seasonally more variable xylem $\delta^{13}\text{C}$ -excess (Figure 8c) of beech trees compared to oak trees suggests the use of a water source more exposed to isotopic enrichment, likely near-surface soil water. Such a difference can be associated with species-specific root architecture. This explanation is consistent with in situ root measurements at other sites (Coners & Leuschner, 2005; Leuschner et al., 2001). For instance, in a beech-oak forest stand, Leuschner et al. (2001) found that beech was a superior below-ground competitor of the topsoil where the maximum fine root densities occurred to colonize the nutrient-rich organic layer. In contrast, oak was considered a deep-rooted species able to access deeper subsurface water (Lanning et al., 2020). Through a meta-analysis across several sites, Fan et al. (2017) found that the average rooting depth of the genus *Quercus* was 5.23 and only 0.8 m for *Fagus*.

The different timing of leaf emergence observed for the two species, as also shown by sap velocities (Figure 4), indicates that water use partitioning does not only occur spatially in the subsurface driven by root distribution, but also temporally (Meinzer et al., 2001). This phenological variation has been linked to wood hydraulic conductivity (Wang et al., 1992). Over the dormant season, ring-porous species like oak with large vessels may experience a higher loss in hydraulic conductivity than diffuse-porous species like beech (Cruiziat et al., 2002). To overcome winter embolism and restore the water flow pathway, oak trees invest in the formation of early wood before leaf expansion (Bréda & Granier, 1996), while stem growth in beech trees starts after leaf flush (Barbaroux & Bréda, 2002). At the time when leaves flush out, the xylem water in our study displayed an extremely heavy isotopic composition. This is consistent with previous studies and results from evaporation through the bark during periods of limited sap flow

(Barbeta et al., 2019; Martín-Gómez et al., 2017; Oerter et al., 2019; Phillips & Ehleringer, 1995).

Accessibility to different water sources could also explain the different hysteretic response of sap velocities to the environmental drivers (VPD and soil moisture). The increasing VPD and high soil moisture content in the first part of the growing season supported an increase in sap velocity in both species (Figures 5 and 6). However, the high VPD values and reduced water supply from late July onwards induced stomatal closure in beech trees in order to minimize water loss. Conversely, oak trees showed a lower sensitivity to these environmental forces with sap velocity reaching its maximum when VPD approached 3 kPa, despite reduced soil moisture content. The different degree of stomatal sensitivity to the environmental forcing coupled with different xylem isotopic composition suggests the use of a deeper and more stable water source for oak trees and a shallower and ephemeral water source in beech trees, supporting the findings of Bakker et al. (2008) and Grossiord et al. (2017).

In order to meet water requirements and regulate water status, trees have developed different adaptations, like stomatal response (isohydric vs anisohydric species), xylem architecture (diffusive vs. ring-porous), and rooting depth (Matheny et al., 2017; McDowell et al., 2008b). The interplay of these characteristics defines tree transpiration response to a variable water supply. The deep rooting strategy of oak trees enables them to overcome the hydraulic failure risk given their anisohydric stomatal regulation (Matheny et al., 2017) and ring-porous xylem (Cruiziat et al., 2002) by exploiting deeper water sources. Anisohydric species have a weaker stomatal sensitivity than isohydric species such as beech trees, which reduce water consumption via stomata closure to avoid water stress damage (Magh et al., 2020).

5 | CONCLUSIONS

In this work, we examined the role of landscape topography (hillslope position) on the spatial and temporal patterns of water use in a mixed forest of beech and oak trees through sap velocity and stable water isotope measurements. We showed different patterns of sap velocity in different hillslope positions, with trees generally displaying higher sap velocity in upper locations than in downslope areas where the groundwater table was shallower and temporally less variable. These results, coupled with seasonally variable xylem isotopic composition, suggest that the trees studied relied on vadose zone water storage irrespective of the hillslope position and the corresponding groundwater table depth. Contrary to many previous studies that showed the influence of the shallow groundwater table on transpiration rates, the shallower and more stable groundwater table at the footslope did not foster higher sap velocities at our study site compared to upper locations. Additionally, our study site does not experience shallow downslope water redistribution through interflow which results in no substantial differences in vadose zone water supply between hillslope positions and ultimately no higher sap velocity in downslope areas. Thus, we reject our first conjecture that hillslope position controls tree water use through subsurface water redistribution. In our case, high and stable groundwater table at the footslope location might even reduce root expansion in species that do not tolerate saturated environments.

Furthermore, our results confirm that beech and oak trees have different ecohydrological niches driven by their species-specific water exploitation strategies and hydraulic traits, which are crucial to determining a tree ability to recover from water shortage periods. Beech trees, although more drought-sensitive than oak trees, are a superior above-ground competitor. This characteristic, combined with a marked shade tolerance, allowed them to regenerate extensively at our study site, while oak seedlings and saplings were absent. This confirms our second conjecture that species-specific characteristics result in a different response in different species at the same hillslope position.

Overall, our findings highlight that the link between forest community and the Critical Zone structure is highly dynamic due to species-specific interaction with water availability and subsurface flow patterns. Future management practices should operate to create optimal conditions for forest resilience, accounting for subsurface structure to promote more drought-tolerant species in order to ensure ecosystem functioning in face of future climate change.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could appear to influence the work reported in this paper. Julian Klaus is Associated Editor of *Ecohydrology* at the time of the review process.

AUTHORS' CONTRIBUTION

Ginevra Fabiani: Conceptualization, investigation, formal analysis, visualization, writing—original draft. **Remy Schoppach:** Conceptualization, resources, writing—review and editing. **Daniele Penna:** Conceptualization, supervision, writing—review and editing. **Julian Klaus:** Conceptualization, funding acquisition, supervision, validation, writing—review and editing, project administration.

DATA AVAILABILITY STATEMENT

The data used in this study are the property of the Luxembourg Institute of Science and Technology (LIST) and can be obtained upon request to the corresponding author, after approval by LIST.

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REFERENCES

- Allen, S. T., Kirchner, J. W., Braun, S., Siegwolf, R. T. W., & Goldsmith, G. R. (2019). Seasonal origins of soil water used by trees. *Hydrology and Earth System Sciences*, 23, 1199–1210. <https://doi.org/10.5194/hess-23-1199-2019>
- Bakker, M. R., Turpault, M. P., Huet, S., & Nys, C. (2008). Root distribution of *Fagus sylvatica* in a chronosequence in western France. *Journal of Forest Research*, 13, 176–184. <https://doi.org/10.1007/s10310-008-0068-6>
- Band, L. E., Patterson, P., Nemani, R., & Running, S. W. (1993). Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. *Agricultural and Forest Meteorology*, 63, 93–126. [https://doi.org/10.1016/0168-1923\(93\)90024-C](https://doi.org/10.1016/0168-1923(93)90024-C)
- Barbaroux, C., & Bréda, N. (2002). Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology*, 22, 1201–1210. <https://doi.org/10.1093/treephys/22.17.1201>
- Barbeta, A., & Peñuelas, J. (2017). Relative contribution of groundwater to plant transpiration estimated with stable isotopes. *Scientific Reports*, 7, 1–10. <https://doi.org/10.1038/s41598-017-09643-x>
- Barbeta, A., Jones, S. P., Clavé, L., Wingate, L., Gimeno, T. E., Fréjaville, B., Wohl, S., & Ogee, J. (2019). Unexplained hydrogen isotope offsets complicate the identification and quantification of tree water sources in a riparian forest. *Hydrology and Earth System Sciences*, 23, 2129–2146. <https://doi.org/10.5194/hess-23-2129-2019>
- Barbeta, A., Gimeno, T. E., Clavé, L., Fréjaville, B., Jones, S. P., Delvigne, C., Wingate, L., & Ogee, J. (2020). An explanation for the isotopic offset between soil and stem water in a temperate tree species. *The New Phytologist*, 227, 766–779. <https://doi.org/10.1111/nph.16564>
- Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29, 692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
- Barrett, D. J., Hatton, T. J., Ash, J. E., & Ball, M. C. (1995). Evaluation of the heat pulse velocity technique for measurement of sap flow in

- rainforest and eucalypt forest species of south-eastern Australia. *Plant, Cell & Environment*, 18, 463–469. <https://doi.org/10.1111/j.1365-3040.1995.tb00381.x>
- Becker, P., & Edwards, W. R. N. (1999). Corrected heat capacity of wood for sap flow calculations. *Tree Physiology*, 19, 767–768. <https://doi.org/10.1093/treephys/19.11.767>
- Bello, J., Hasselquist, N. J., Vallet, P., Kahmen, A., Perot, T., & Korboulewsky, N. (2019). Complementary water uptake depth of *Quercus petraea* and *Pinus sylvestris* in mixed stands during an extreme drought. *Plant and Soil*, 437, 93–115. <https://doi.org/10.1007/s11104-019-03951-z>
- Beyer, M., & Penna, D. (2021). On the spatio-temporal under-representation of isotopic data in ecohydrological studies. *Frontiers in Water*, 3, 1–9. <https://doi.org/10.3389/frwa.2021.643013>
- Bonanno, E., Blöschl, G., & Klaus, J. (2021). Flow directions of stream-groundwater exchange in a headwater catchment during the hydrologic year. *Hydrological Processes*, 35(8), e14310. <https://doi.org/10.1002/hyp.14310>
- Bréda, N., & Granier, A. (1996). Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Annales des Sciences Forestières*, 53, 521–536. <https://doi.org/10.1051/forest:19960232>
- Brinkmann, N., Eugster, W., Buchmann, N., & Kahmen, A. (2018). Species-specific differences in water uptake depth of mature temperate trees vary with water availability in the soil. *Plant Biology*, 21, 71–81. <https://doi.org/10.1111/plb.12907>
- Brooks, P. D., Chorover, J., Fan, Y., Godsey, S. E., Maxwell, R. M., McNamara, J. P., & Tague, C. (2015). Hydrological partitioning in the critical zone: Recent advances and opportunities for developing transferable understanding of water cycle dynamics. *Water Resources Research*, 51, 6973–6987. <https://doi.org/10.1002/2015WR017039>. Received
- Brooks, R. J., Barnard, H. R., Coulombe, R., & McDonnell, J. J. (2010). Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience*, 3, 100–104. <https://doi.org/10.1038/ngeo722>
- Burgess, S., & Downey, A. (2014). SFM1 sap flow meter manual armidale.
- Burgess, S. S. O., Adams, M. A., Turner, N. C., Beverly, C. R., Ong, C. K., Khan, A. A. H., & Bleyby, T. M. (2001). An improved heat pulse method to measure low and reverse rates of sap flow in woody plants: A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and Estimation of conduit taper for th. *Tree Physiology*, 21, 589–598.
- Carrière, S. D., Martin-StPaul, N. K., Cakpo, C. B., Patris, N., Gillon, M., Chalikakis, K., Doussan, C., Olioso, A., Babic, M., Jouineau, A., Simioni, G., & Davi, H. (2020). The role of deep vadose zone water in tree transpiration during drought periods in karst settings—Insights from isotopic tracing and leaf water potential. *Science of the Total Environment*, 699. <https://doi.org/10.1016/j.scitotenv.2019.134332>
- Coners, H., & Leuschner, C. (2005). In situ measurement of fine root water absorption in three temperate tree species - Temporal variability and control by soil and atmospheric factors. *Basic and Applied Ecology*, 6, 395–405. <https://doi.org/10.1016/j.baae.2004.12.003>
- Cruziat, P., Cochard, H., & Améglio, T. (2002). Hydraulic architecture of trees: Main concepts and results. *Annals of Forest Science*, 59, 723–752. <https://doi.org/10.1051/forest:2002060>
- David, T. S., Pinto, C. A., Nadezhdina, N., Kurz-Besson, C., Henriques, M. O., Quilhó, T., Cermak, J., Chaves, M. M., Pereira, J. S., & David, J. S. (2013). Root functioning, tree water use and hydraulic redistribution in *Quercus suber* trees: A modeling approach based on root sap flow. *Forest Ecology and Management*, 307, 136–146. <https://doi.org/10.1016/j.foreco.2013.07.012>
- Dawson, T. E., Hahn, W. J., & Crutchfield-Peters, K. (2020). Digging deeper: what the critical zone perspective adds to the study of plant ecophysiology. *The New Phytologist*, 226, 666–671. <https://doi.org/10.1111/nph.16410>
- Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*, 33, 507–559. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095451>
- Eamus, D., Froend, R., Loomes, R., Hose, G., & Murray, B. (2006). A functional methodology for determining the groundwater regime needed to maintain the health of groundwater-dependent vegetation. *Australian Journal of Botany*, 54, 97–114. <https://doi.org/10.1071/BT05031>
- Ehleringer, J. R., & Dawson, T. E. (1992). Water uptake by plants: Perspectives from stable isotope composition.pdf.
- Elliott, K. J., Miniati, C. F., Pederson, N., & Laseter, S. H. (2015). Forest tree growth response to hydroclimate variability in the southern Appalachians. *Global Change Biology*, 21, 4627–4641. <https://doi.org/10.1111/gcb.13045>
- Fan, Y. (2015). Groundwater in the Earth's critical zone: Relevance to large-scale patterns and processes. *Water Resources Research*, 51, 3052–3069. <https://doi.org/10.1002/2015WR017037>
- Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 10572–10577. <https://doi.org/10.1073/pnas.1712381114>
- Fry, E. L., Evans, A. L., Sturrock, C. J., Bullock, J. M., & Bardgett, R. D. (2018). Root architecture governs plasticity in response to drought. *Plant and Soil*, 433, 189–200. <https://doi.org/10.1007/s11104-018-3824-1>
- Gaines, K. P., Stanley, J. W., Meinzer, F. C., McCulloh, K. A., Woodruff, D. R., Chen, W., Adams, T. S., Lin, H., & Eissenstat, D. M. (2016). Reliance on shallow soil water in a mixed-hardwood forest in central Pennsylvania. *Tree Physiology*, 36, 444–458. <https://doi.org/10.1093/treephys/tpv113>
- Gillerot, L., Forrester, D. I., Bottero, A., Rigling, A., & Lévesque, M. (2020). Tree neighbourhood diversity has negligible effects on drought resilience of European Beech, Silver Fir and Norway Spruce. *Ecosystems*, 24, 20–36. <https://doi.org/10.1007/s10021-020-00501-y>
- Glaser, B., Klaus, J., Frei, S., Frentress, J., Pfister, L., & Hopp, L. (2016). On the value of surface saturated area dynamics mapped with thermal infrared imagery for modeling the hillslope-riparian-stream continuum. *Water Resources Research*, 52, 8317–8342. <https://doi.org/10.1002/2015WR018414>
- Glaser, B., Jackisch, C., Hopp, L., & Klaus, J. (2019). How meaningful are plot-scale observations and simulations of preferential flow for catchment models? *Vadose Zone Journal*, 18, 1–18. <https://doi.org/10.2136/vzj2018.08.0146>
- Goldsmith, G. R., Muñoz-Villers, L. E., Holwerda, F., McDonnell, J. J., Asbjørnsen, H., & Dawson, T. E. (2012). Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest. *Ecohydrology*, 5, 779–790. <https://doi.org/10.1002/eco.268>
- Gourdol, L., Clement, R., Juilleret, J., Pfister, L., & Hissler, C. (2021). Exploring the regolith with electrical resistivity tomography in large-scale surveys: Electrode spacing-related issues and possibility. *Hydrology and Earth System Sciences*, 25, 1785–1812. <https://doi.org/10.5194/hess-25-1785-2021>
- Grossiord, C. (2019). Having the right neighbors: how tree species diversity modulates drought impacts on forests. *The New Phytologist*, 228, 42–49. <https://doi.org/10.1111/nph.15667>
- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Čečko, E., Forrester, D. I., Dawud, S. M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., Gessler, A., & Schlesinger, W. H. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National*

- Academy of Sciences of the United States of America, 111, 14812–14815. <https://doi.org/10.1073/pnas.1411970111>
- Grossiord, C., Sevanto, S., Dawson, T. E., Adams, H. D., Collins, A. D., Dickman, L. T., Newman, B. D., Stockton, E. A., & McDowell, N. G. (2017). Warming combined with more extreme precipitation regimes modifies the water sources used by trees. *The New Phytologist*, 213, 584–596. <https://doi.org/10.1111/nph.14192>
- Hahn, W. J., Rempe, D. M., Dralle, D. N., Dawson, T. E., Lovill, S. M., Bryk, A. B., Bish, D. L., Schieber, J., & Dietrich, W. E. (2019). Lithologically controlled subsurface critical zone thickness and water storage capacity determine regional plant community composition. *Water Resources Research*, 55, 3028–3055. <https://doi.org/10.1029/2018WR023760>
- Hahn, W. J., Rempe, D. M., Dralle, D. N., Dawson, T. E., & Dietrich, W. E. (2020). Oak transpiration drawn from the weathered bedrock vadose zone in the summer dry season. *Water Resources Research*, 56, 1–24. <https://doi.org/10.1029/2020WR027419>
- Hasenmueller, E. A., Gu, X., Weitzman, J. N., Adams, T. S., Stinchcomb, G. E., Eissenstat, D. M., Drohan, P. J., Brantley, S. L., & Kaye, J. P. (2017). Weathering of rock to regolith: The activity of deep roots in bedrock fractures. *Geoderma*, 300, 11–31. <https://doi.org/10.1016/j.geoderma.2017.03.020>
- Hawthorne, S., & Miniati, C. F. (2018). Topography may mitigate drought effects on vegetation along a hillslope gradient. *Ecohydrology*, 11, e1825. <https://doi.org/10.1002/eco.1825>
- Hissler, C., Martínez-Carreras, N., Barnich, F., Gourdol, L., Iffly, J. F., Juilleret, J., Klaus, J., & Pfister, L. (2021). The Weierbach experimental catchment in Luxembourg: A decade of critical zone monitoring in a temperate forest—From hydrological investigations to ecohydrological perspectives. *Hydrological Processes*, 35, 1–7. <https://doi.org/10.1002/hyp.14140>
- Hoyleman, Z. H., Jencso, K. G., Hu, J., Martin, J. T., Holden, Z. A., Seielstad, C. A., & Rowell, E. M. (2018). Hillslope topography mediates spatial patterns of ecosystem sensitivity to climate. *Journal of Geophysical Research - Biogeosciences*, 123, 353–371. <https://doi.org/10.1002/2017JG004108>
- Hwang, T., Band, L. E., Miniati, C. F., Vose, J. M., Knoepp, J. D., Song, C., & Bolstad, P. V. (2020). Climate change may increase the drought stress of mesophytic trees downslope with ongoing forest mesophication under a history of fire suppression. *Frontiers in Forests and Global Change*, 3. <https://doi.org/10.3389/ffgc.2020.00017>
- Juilleret, J., Iffly, J. F., Pfister, L., & Hissler, C. (2011). Remarkable Pleistocene periglacial slope deposits in Luxembourg (Oesling): Pedological implication and geosite potential. *Bull. la Société des Nat. Luxemb.*, 112, 125–130.
- Juilleret, J., Dondeyne, S., Vancampenhout, K., Deckers, J., & Hissler, C. (2016). Geoderma Mind the gap: A classification system for integrating the subsolum into soil surveys. *Geoderma*, 264, 332–339. <https://doi.org/10.1016/j.geoderma.2015.08.031>
- Klaus, J., & Jackson, C. R. (2018). Interflow is not binary: A continuous shallow perched layer does not imply continuous connectivity. *Water Resources Research*, 54, 5921–5932. <https://doi.org/10.1029/2018WR022920>
- Klaus, J., Chun, K. P., & Stumpp, C. (2015). Temporal trends in $\delta^{18}\text{O}$ composition of precipitation in Germany: Insights from time series modeling and trend analysis. *Hydrological Processes*, 29, 2668–2680. <https://doi.org/10.1002/hyp.10395>
- Klos, P. Z., Goulden, M. L., Riebe, C. S., Tague, C. L., O'Geen, A. T., Flinchum, B. A., Safeeq, M., Conklin, M. H., Hart, S. C., Berhe, A. A., Hartsough, P. C., Holbrook, W. S., & Bales, R. C. (2018). Subsurface plant-accessible water in mountain ecosystems with a Mediterranean climate. *Wiley Interdisciplinary Reviews Water*, 5, e1277. <https://doi.org/10.1002/wat2.1277>
- Kumagai, T., Tateishi, M., Shimizu, T., & Otsuki, K. (2008). Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed. *Agricultural and Forest Meteorology*, 148, 1444–1455. <https://doi.org/10.1016/j.agrformet.2008.04.010>
- Kume, T., Tsuruta, K., Komatsu, H., Shinohara, Y., Katayama, A., Ide, J., & Otsuki, K. (2016). Differences in sap flux-based stand transpiration between upper and lower slope positions in a Japanese cypress plantation watershed. *Ecohydrology*, 9, 1105–1116. <https://doi.org/10.1002/eco.1709>
- Landwehr, J. M., & Coplen, T. B. (2004). Line-conditioned excess: A new method for characterizing stable hydrogen and oxygen isotope ratios in hydrologic systems.
- Lanning, M., Wang, L., Benson, M., Zhang, Q., & Novick, K. A. (2020). Canopy isotopic investigation reveals different water uptake dynamics of maples and oaks. *Phytochemistry*, 175, 112389. <https://doi.org/10.1016/j.phytochem.2020.112389>
- Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., & Runge, M. (2001). Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management*, 149, 33–46. [https://doi.org/10.1016/S0378-1127\(00\)00543-0](https://doi.org/10.1016/S0378-1127(00)00543-0)
- Lide, D. R. (1992). *Handbook of chemistry and physics*. 73rd ed. (pp. 6–10). CRC Press Inc.
- Lin, L., Band, L. E., Vose, J. M., Hwang, T., Miniati, C. F., & Bolstad, P. V. (2019). Ecosystem processes at the watershed scale: Influence of flowpath patterns of canopy ecophysiology on emergent catchment water and carbon cycling. *Ecohydrology*, 12, 1–15. <https://doi.org/10.1002/eco.2093>
- Looker, N., Martin, J., & Hoyleman, Z., Jencso, K. (2018). Diurnal and seasonal coupling of conifer sap flow and vapour pressure deficit across topoclimatic gradients in a subalpine catchment 1–16. <https://doi.org/10.1002/eco.1994>
- Magh, R. K., Eiferle, C., Burzlaff, T., Dannenmann, M., Rennenberg, H., & Dubbert, M. (2020). Competition for water rather than facilitation in mixed beech-fir forests after drying-wetting cycle. *Journal of Hydrology*, 587, 124944. <https://doi.org/10.1016/j.jhydrol.2020.124944>
- Marshall, D. C. (1958). Measurement of sap flow in conifers by heat transport. *Plant Physiology*, 33, 385–396. <https://doi.org/10.1104/pp.33.6.385>
- Marshall, J. D., Cuntz, M., Beyer, M., Dubbert, M., & Kuehnhammer, K. (2020). Borehole equilibration: Testing a new method to monitor the isotopic composition of tree xylem water in situ. *Frontiers in Plant Science*, 11, 1–14. <https://doi.org/10.3389/fpls.2020.00358>
- Martinetti, S., Fatichi, S., Florianic, M., Burlando, P., & Molnar, P. (2021). Field evidence of riparian vegetation response to groundwater levels in a gravel-bed river. *Ecohydrology*, 14(2), e2264. <https://doi.org/10.1002/eco.2264>
- Martínez-Carreras, N., Hissler, C., Gourdol, L., Klaus, J., Juilleret, J., Iffly, J. F., & Pfister, L. (2016). Storage controls on the generation of double peak hydrographs in a forested headwater catchment. *Journal of Hydrology*, 543, 255–269. <https://doi.org/10.1016/j.jhydrol.2016.10.004>
- Martín-Gómez, P., Serrano, L., & Ferrio, J. P. (2017). Short-term dynamics of evaporative enrichment of xylem water in woody stems: Implications for ecohydrology. *Tree Physiology*, 37, 511–522. <https://doi.org/10.1093/treephys/tpw115>
- Matheny, A. M., Fiorella, R. P., Bohrer, G., Poulsen, C. J., Morin, T. H., Wunderlich, A., Vogel, C. S., & Curtis, P. S. (2017). Contrasting strategies of hydraulic control in two codominant temperate tree species. *Ecohydrology*, 10, 1–16. <https://doi.org/10.1002/eco.1815>
- McDowell, N., Pockman, W.T., Allen, C.D., Breshers, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., & Ypez, E. (2008a). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? 178. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>

- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yezzer, E. A. (2008b). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *The New Phytologist*, *178*, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Meinzer, F. C., Clearwater, M. J., & Goldstein, G. (2001). Water transport in trees: Current perspectives, new insights and some controversies. *Environmental and Experimental Botany*, *45*, 239–262. [https://doi.org/10.1016/S0098-8472\(01\)00074-0](https://doi.org/10.1016/S0098-8472(01)00074-0)
- Meißner, M., Köhler, M., & Hölscher, H. (2013). Diversity did not influence soil water use of tree clusters in a temperate mixed forest. *Web Ecology*, *13*, 31–42. <https://doi.org/10.5194/we-13-31-2013>
- Miller, G. R., Chen, X., Rubin, Y., Ma, S., & Baldocchi, D. D. (2010). Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resources Research*, *46*, 1–14. <https://doi.org/10.1029/2009WR008902>
- Mitchell, P. J., Benyon, R. G., & Lane, P. N. J. (2012). Responses of evapotranspiration at different topographic positions and catchment water balance following a pronounced drought in a mixed species eucalypt forest, Australia. *Journal of Hydrology*, *440–441*, 62–74. <https://doi.org/10.1016/j.jhydrol.2012.03.026>
- Moro, M. J., Domingo, F., & López, G. (2004). Seasonal transpiration pattern of *Phragmites australis* in a wetland of semi-arid Spain. *Hydrological Processes*, *18*(2), 213–227. <https://doi.org/10.1002/hyp.1371>
- Naumburg, E., Mata-Gonzalez, R., Hunter, R. G., McLendon, T., & Martin, D. W. (2005). Phreatophytic vegetation and groundwater fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on great basin vegetation. *Environmental Management*, *35*, 726–740. <https://doi.org/10.1007/s00267-004-0194-7>
- Oerter, E. J., & Bowen, G. (2017). In situ monitoring of H and O stable isotopes in soil water reveals ecohydrologic dynamics in managed soil systems. *Ecohydrology*, *10*, 1–13. <https://doi.org/10.1002/eco.1841>
- Oerter, E. J., Siebert, G., Bowling, D. R., & Bowen, G. (2019). Soil water vapour isotopes identify missing water source for streamside trees. *Ecohydrology*, *12*(4), e2083. <https://doi.org/10.1002/eco.2083>
- Orlowski, N., Breuer, L., & McDonnell, J. J. (2016). Critical issues with cryogenic extraction of soil water for stable isotope analysis. *Ecohydrology*, *9*, 3–10. <https://doi.org/10.1002/eco.1722>
- Penna, D., Borga, M., Norbiato, D., & Dalla Fontana, G. (2009). Hillslope scale soil moisture variability in a steep alpine terrain. *Journal of Hydrology*, *364*, 311–327. <https://doi.org/10.1016/j.jhydrol.2008.11.009>
- Penna, D., Stenni, B., Šanda, M., Wrede, S., Bogaard, T. A., Michelini, M., Fischer, B. M. C., Gobbi, A., Mantese, N., Zuecco, G., Borga, M., Bonazza, M., Sobotková, M., Čejková, B., & Wassenaar, L. I. (2012). Technical note: Evaluation of between-sample memory effects in the analysis of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water samples measured by laser spectrometers. *Hydrology and Earth System Sciences*, *16*, 3925–3933. <https://doi.org/10.5194/hess-16-3925-2012>
- Penna, D., Hopp, L., Scandellari, F., Allen, S. T., Benettin, P., Beyer, M., Geris, J., Klaus, J., Marshall, J. D., Schwendenmann, L., Volkman, T. H. M., von Freyberg, J., Amin, A., Ceperley, N., Engel, M., Frenress, J., Giambastiani, Y., McDonnell, J. J., Zuecco, G., ... Kirchner, J. W. (2018). Ideas and perspectives: Tracing terrestrial ecosystem water fluxes using hydrogen and oxygen stable isotopes—Challenges and opportunities from an interdisciplinary perspective. *Biogeosciences*, *15*, 6399–6415. <https://doi.org/10.5194/bg-15-6399-2018>
- Petritan, A. M., Bouriaud, O., Frank, D. C., & Petritan, I. C. (2017). Dendroecological reconstruction of disturbance history of an old-growth mixed sessile oak-beech forest. *Journal of Vegetation Science*, *28*, 117–127. <https://doi.org/10.1111/jvs.12460>
- Pettit, N. E., & Friend, R. H. (2018). How important is groundwater availability and stream perenniality to riparian and floodplain tree growth? *Hydrological Processes*, *32*, 1502–1514. <https://doi.org/10.1002/hyp.11510>
- Pfister, L., Martínez-Carreras, N., Hissler, C., Klaus, J., Carrer, G. E., Stewart, M. K., & McDonnell, J. (2017). Bedrock geology controls on catchment storage, mixing, and release: A comparative analysis of 16 nested catchments. *Hydrological Processes*, *31*, 1828–1845. <https://doi.org/10.1002/hyp.11134>
- Phillips, S. L., & Ehleringer, J. R. (1995). Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). *Trees*, *9*, 214–219. <https://doi.org/10.1007/BF00195275>
- Poca, M., Coomans, O., Urcelay, C., Zeballos, S. R., Bodé, S., & Boeckx, P. (2019). Isotope fractionation during root water uptake by *Acacia caven* is enhanced by arbuscular mycorrhizas. *Plant and Soil*, *441*, 485–497. <https://doi.org/10.1007/s11104-019-04139-1>
- Pretzsch, H., Forrester, D. I., & Bauhus, J. (2017). *Mixed-species forests*. <https://doi.org/10.1007/978-3-662-54553-9>
- Rempe, D. M., & Dietrich, W. E. (2018). Direct observations of rock moisture, a hidden component of the hydrologic cycle. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 2664–2669. <https://doi.org/10.1073/pnas.1800141115>
- Renner, M., Hassler, S. K., Blume, T., Weiler, M., Hildebrandt, A., Guderle, M., Schymanski, S. J., & Kleidon, A. (2016). Dominant controls of transpiration along a hillslope transect inferred from ecohydrological measurements and thermodynamic limits. *Hydrology and Earth System Sciences*, *20*, 2063–2083. <https://doi.org/10.5194/hess-20-2063-2016>
- Rinderer, M., McGlynn, B., & van Meerveld, I. (2017). Groundwater similarity across a watershed derived from time-warped and flow-corrected time series. *Water Resources Research*, *53*, 1–20. <https://doi.org/10.1002/2016WR019856>
- Rodriguez, N. B., & Klaus, J. (2019). Catchment travel times from composite storage selection functions representing the superposition of streamflow generation processes. *Water Resources Research*, *55*, 9292–9314. <https://doi.org/10.1029/2019WR024973>
- Rodriguez, N. B., Pfister, L., Zehe, E., & Klaus, J. (2021). A comparison of catchment travel times and storage deduced from deuterium and tritium tracers using StorAge Selection functions 401–428.
- Rossatto, D. R., Silva, L. C. R., Sternberg, L. S. L., & Franco, A. C. (2014). South African Journal of Botany Do woody and herbaceous species compete for soil water across topographic gradients? *Evidence for niche partitioning in a Neotropical savanna*, *91*, 14–18. <https://doi.org/10.1016/j.sajb.2013.11.011>
- Rothfuss, Y., & Javaux, M. (2017). Reviews and syntheses: Isotopic approaches to quantify root water uptake: A review and comparison of methods. *Biogeosciences*, *14*, 2199–2224. <https://doi.org/10.5194/bg-14-2199-2017>
- Roy, V., Ruel, J. C., & Plamondon, A. P. (2000). Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management*, *129*, 253–267. [https://doi.org/10.1016/S0378-1127\(99\)00170-X](https://doi.org/10.1016/S0378-1127(99)00170-X)
- Scaini, A., Hissler, C., Fenicia, F., Juilleret, J., Iffy, J. F., Pfister, L., & Beven, K. (2018). Hillslope response to sprinkling and natural rainfall using velocity and celerity estimates in a slate-bedrock catchment. *Journal of Hydrology*, *558*, 366–379. <https://doi.org/10.1016/j.jhydrol.2017.12.011>
- Schmull, M., & Thomas, F. M. (2000). Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Liebl., *Fagus sylvatica* L.) to waterlogging. *Plant and Soil*, *225*, 227–242. <https://doi.org/10.1023/A:1026516027096>
- Smith, D. M., & Allen, S. J. (1996). Measurement of sap flow in plant stems. *Journal of Experimental Botany*, *47*, 1833–1844. <https://doi.org/10.1093/jxb/47.12.1833>

- Soylu, M. E., Lenters, J. D., Istanbuluoglu, E., & Loheide, S. P. (2012). On evapotranspiration and shallow groundwater fluctuations: A Fourier-based improvement to the White method. *Water Resources Research*, 48, 1–17. <https://doi.org/10.1029/2011WR010964>
- Stumpp, C., Klaus, J., & Stichler, W. (2014). Analysis of long-term stable isotopic composition in German precipitation. *Journal of Hydrology*, 517, 351–361. <https://doi.org/10.1016/j.jhydrol.2014.05.034>
- Tromp-van Meerveld, H. J., & McDonnell, J. J. (2006). On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale. *Advances in Water Resources*, 29, 293–310. <https://doi.org/10.1016/j.advwatres.2005.02.016>
- Tsuruta, K., Yamamoto, H., Kosugi, Y., Makita, N., Katsuyama, M., Kosugi, K., & Tani, M. (2020). Slope position and water use by trees in a headwater catchment dominated by Japanese cypress: Implications for catchment-scale transpiration estimates. *Ecohydrology*, 13(8), e2245. <https://doi.org/10.1002/eco.2245>
- Uhl, E., Pretzsch, H., & Schu, G. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biology*, 15, 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- Vargas, A. I., Schaffer, B., Yuhong, L., & Sternberg, L. d. S. L. (2017). Testing plant use of mobile vs immobile soil water sources using stable isotope experiments. *The New Phytologist*, 215, 582–594. <https://doi.org/10.1111/nph.14616>
- Volkman, T. H. M., Haberer, K., Gessler, A., & Weiler, M. (2016). High-resolution isotope measurements resolve rapid ecohydrological dynamics at the soil-plant interface. *The New Phytologist*, 210, 839–849. <https://doi.org/10.1111/nph.13868>
- von Freyberg, J., Allen, S. T., Grossiord, C., & Dawson, T. E. (2020). Plant and root-zone water isotopes are difficult to measure, explain, and predict: Some practical recommendations for determining plant water sources. *Methods in Ecology and Evolution*, 11(11), 1352–1367. <https://doi.org/10.1111/2041-210x.13461>
- Wang, J., Ives, N. E., & Lechowicz, M. J. (1992). The Relation of foliar phenology to xylem embolism in trees. *Functional Ecology*, 6, 469. <https://doi.org/10.2307/2389285>
- Wassenaar, L. I., Hendry, M. J., Chostner, V. L., & Lis, G. P. (2008). High resolution pore water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ measurements by H_2O (liquid) – H_2O (vapor) equilibration laser spectroscopy. *Environmental Science & Technology*, 42, 9262–9267. <https://doi.org/10.1021/es802065s>
- Weiss, A. D. (2001). Topographic position and landforms analysis. Poster Present. ESRI user Conf. 200.
- Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., & Granier, A. (2011). Evidence of hydraulic lift in a young beech and oak mixed forest using ^{18}O soil water labelling. *Trees - Structure and Function*, 25, 885–894. <https://doi.org/10.1007/s00468-011-0563-9>
- Zhao, L., Wang, L., Cernusak, L. A., Liu, X., Xiao, H., Zhou, M., & Zhang, S. (2016). Significant difference in hydrogen isotope composition between xylem and tissue water in *Populus euphratica*. *Plant, Cell & Environment*, 39, 1848–1857. <https://doi.org/10.1111/pce.12753>

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