The influence of hillslope topography on beech water use: a comparative study in two different climates Contrasting water use strategies of beech trees along two hillslopes with different slope and climate

Ginevra Fabiani[1,2], Julian Klaus[3], and Daniele Penna[2,4]

[1]Catchment and Eco-Hydrology Group, Luxembourg Institute of Science and Technology, Belvaux, Luxembourg
[2]Department of Agriculture, Food, Environment and Forestry, University of Florence, Florence, Italy
[3]Department of Geography, University of Bonn, Bonn, Germany
[4]Oregon State University, Forest Engineering Resources and Management Department, Corvallis, USA

Correspondence: ginevra.fabiani@gmail.com

Abstract. Understanding the interactioninterrelation between topography and vegetation across different environments is important to assess how hydrological and climatic conditions affect tree physiological activity. This becomes especially important given the expected reduction in water availability and increase in water demand driven by climate change. These extremes could enhance the thermal and hydrologic gradients along slopes. Here, we aimed at testing if and how different climatic and hydrological conditions affect the physiological response to environmental variables of beech trees (*Fagus sylvatica* L.) along two different topographic sequences. For this purpose, we set up a comparative study on a gentle hillslope in the Weierbach catchment in Luxembourg (oceanic climate) and a steep hillslope in the Lecciona catchment in Italy (Mediterranean climate). We combined sap velocity measurements with isotopic measurements of soil, precipitation, stream water, groundwater, and xylem over 2019 and 2020 in the Luxembourgish site and 2021 in the Italian site. We found that in the Weierbach catchment, trees' response to environmental variables (i.e., vapour pressure deficit and relative extractable water in the soil) was similar among hillslope positions and between the two monitored years resulting from homogeneous growing conditions along the topographic sequence. We also did not find any statistical difference in the isotopic composition of xylem water among positions suggesting that beech trees relied on similar water sources across the landscape. In the Lecciona catchment, we observed lower sap velocities and shorter growing season in trees growing in the upper portions of the hillslope, likely related to water redistribution and different soil moisture along the hillslope catena. Xylem isotopic composition was significantly lighter at the footslope location throughout the growing season than in the upslope locations, suggesting location-specific water use. These results emphasize how differing hydrometeorological processes occurring at the hillslope scale can lead to contrasting tree performance responses.

1 Introduction

20 Global change ~~The ongoing climate crisis~~ is strongly affecting forest ecosystems by exacerbating ~~the~~environmental extremes, such as droughts and heatwaves (Allen et al., 2010; Choat et al., 2012). The increasing atmospheric evaporative demand (i.e., vapour pressure deficit; VPD) and reduced water availability (i.e., relative extractable water; REW) in soils expose trees to water deficit risk (Salomón et al., 2022a) impairing tree functioning (Giménez et al., 2013). ~~The severity of water limitation~~ Water availability is variable in space, time, and among domains of the hydrological cycle (i.e. atmosphere, belowground, surface

25 water) (Klaus et al., 2022; Tijdeman et al., 2022), and changes in water availability are ~~is~~ expected to affect the distribution of tree species ~~performance~~ based on their ecophysiological adaptations to varying water conditions (Hahm et al., 2018) ~~not only at the limits but also at the centre of their distribution range, where trees are assumed to benefit from the most suited growing conditions.~~. Multiple studies ~~that investigated~~on the effect of reduced water availability ~~water limitations~~ on forest vulnerability have neglected plot-scale landscape heterogeneity ~~at fine spatial resolutions~~, even though soil properties and topography are

30 important abiotic factors for forest health (Schwantes et al., 2018). The ~~interaction~~ interrelation of these factors results in thermal and water gradients across landscapes and ultimately shapes species composition and distribution (Méndez-Toribio et al., 2017). Belowground properties determine the water flow patterns along a hillslope (Klaus and Jackson, 2018; Xiao et al., 2021) resulting in different water availabilities in the subsurface, one of the main drivers of tree productivity (Hogg et al., 2008). Compared to uphill locations, topographically convergent areas are generally wetter due to the lateral redistribution of

35 water and increasing contributing area (Jencso et al., 2009; Western et al., 1999; Penna et al., 2009). The steepness of the slope leads to spatially variable microclimate, which is generally less evaporative-demanding at the footslope where wind speed and solar radiation are reduced (Hoylman et al., 2018). Deeper soils with higher storage capacity and organic matter typically occur at the footslope and are associated with greater stand primary productivity compared to hilltop locations (Elliott et al., 2015; Hawthorne and Miniat, 2018; Tromp-van Meerveld and McDonnell, 2006), where trees may experience more water

40 stress (Oberhuber and Kofler, 2000). The effects of the physiological drought, which occurs when water is not sufficient to sustain plant needs, are dampened in locations where soil water storage capacity is higher (Meusburger et al., 2022). Spatially variable soil characteristics and depths can result in variable degrees of water stress for the same forest species at the same site (Tai et al., 2017). With the expected increase in frequency and intensity of drought events, topography-related changes in soil moisture availability (Hawthorne and Miniat, 2018) and a changing land-surface energy balance (Dobrowski, 2011) may lead

45 to a gradient of water stress in the vegetation increasing from the lower to the higher parts of the hillslope catena. During dry periods, topographic factors may amplify the response of transpiration to soil water limitation (Renner et al., 2016).~~However,~~ Greater water availability in concave areas does not necessarily translate into high tree growth because persistently saturated conditions in the subsurface restrict root expansion to the vadose zone above the water table (Fan et al., 2017). Bosch et al. (2014) found that landscape position, and subsequently access to groundwater, did not appear to strongly influence sap flow

50 rates. Instead, sap flow rates were mainly influenced by water content in the vadose zone (Bosch et al., 2014). Similarly, Fabiani et al. (2022b) found that a high, steady groundwater table does not necessarily enhance sap velocity in two co-occurring species in a temperate forest. Low oxygen levels in saturated soil or regolith can hamper root functioning and development in trees sensitive to anaerobic conditions and force them to rely on shallow soil water and use little groundwater (Thorburn et al., 1993). Inter-annual meteorological variability represents another potentially important control on the patterns of plant physiological

activity (Murphy et al., 2020). Vegetation can deploy physiological (i.e. stomatal conductance) and structural (i.e. leaf area, crown architecture, rooting depth) adaptations to acclimate to changing hydrometeorological conditions at annual to decadal timescales (Grossiord et al., 2017a; McDowell et al., 2008).

European beech (*Fagus sylvatica* L.) is among those species that do not grow roots in the saturated zone and mainly relies on water stored in the shallow soil (Gessler, 2021; Kreuzwieser and Rennenberg, 2014). European beech is a key component of the European mesic forests, with a distribution range covering wide climatic and geological settings (Durrant et al., 2016). In the last decade, its physiological activity (i.e. leaf phenology and cambial activity) has been mildly to severely restricted by droughts in 2003, 2015, and 2018 (Cavin and Jump, 2017; Obladen et al., 2021; Salomón et al., 2022a; Walthert et al., 2021). It is expected that European beech will face high mortality rates with the predicted increase of heatwaves. The hydraulic system of beech trees can show pronounced modifications in response to drought (Zimmermann et al., 2021), but it is still unclear how beech trees will cope with a future increase in VPD and REW ~~climate aridity when rainfall deficits are associated with high atmospheric dryness~~. So far, site-specific case studies with contrasting results have offered a limited understanding of how hillslope scale processes ~~hydrological processes occurring at the hillslope scale~~ affect tree water use in complex terrain. This information cannot be retrieved from larger scale approaches (Murphy et al., 2020). Therefore, detailed hillslope scale field studies are needed to identify where and when tree physiological activity is more constrained by increasing VPD and REW. This can support the development of management practices suited for locations at risk. So far, ecohydrological studies have predominantly concentrated on variations in water use between species, with limited attention given to within-species dynamics (Li and Knighton, 2023), constraining our ability to understand how diverse climates influence physiological responses of a species. Through a cross-site comparison, we aim to advance our knowledge of water use strategies of beech trees under different climatic and topographic conditions in order to allow for a better understanding of the ecohydrological functioning of forest ecosystems. For this reason, we set up a comparative study on a gentle hillslope in the Weierbach catchment in Luxembourg (oceanic climate) and a steep hillslope in the Lecciona catchment in Italy (Mediterranean climate). These sites differed in steepness, climate, geology, and soil characteristics, but beech is the dominant species in both. We combined sap velocity and isotope measures with environmental monitoring to capture beech trees' water response to environmental variables along hillslope transects. While sap velocity measurements allow a continuous assessment of the tree's physiologic response to environmental drivers, stable isotopes of xylem water offer insights into the origin of the water utilized. We hypothesize that (i) the physiological response of beech trees varies as a function of topography-driven changes in water availability, (ii) at the Mediterranean site, characterized by an uneven precipitation regime and high summer evaporative demand, the physiological activity of beech trees is more constrained compared to the stand growing in the Luxembourgish site. We test these hypotheses by posing the following research questions: (i) does topography drive different water uptake strategies along two contrasting hillslopes? and (ii) does hillslope topography increase tree sensitivity to a seasonal decrease in soil water supply ~~water limitation~~?

2 Materials and methods

2.1 Study sites

The Weierbach catchment: study area and environmental monitoring

90   The experiment was carried out during two consecutive growing seasons (March-October 2019 and 2020) at a transect along a south-facing forested hillslope ranging from 485 m to 515 m a.s.l. in the Weierbach catchment, 42 ha, in Luxembourg (Fig. 1) (Hissler et al., 2021; Pfister et al., 2023). The site description and characterization of plateau, midslope and footslope location has been provided ~~described~~ in detail by Fabiani et al. (2022b). Here we report only the key details of the study site (Table 1). The hillslope transect is 380 m long and spans from the stream bank to a plateau area with an average slope of

95   10 degrees. Based on the results of a forest survey conducted in the study site, the forest consists of European beech trees (*Fagus sylvatica* L.) (78% of trees, 60% in basal area) and pedunculate and sessile oak hybrid trees (22% of trees, 40% in basal area). The moderate, oceanic climate in the region is largely influenced by air masses from the Northern Atlantic Ocean (Hissler et al., 2021). Long-term annual precipitation (2007-2020) is approximately 801 mm at the Roodt weather station (3.5 km from the study site), of which 452 mm falls during the growing season (01 April - 31 October) (Fig. 1). The mean annual

100   air temperature during the growing season from 2007 to 2020 was 8.3°C. Volumetric soil moisture was measured at the plateau at 10, 20, 40, and 60 cm depth with water content reflectometers (CS650, Campbell Scientific, UK). Groundwater wells were installed along the hillslope transect in the plateau, midslope, and hillfoot locations. Groundwater table depth was monitored with water pressure transducers (Orpheus Mini, OTT, Germany) recording data at 15 min logging intervals.

The Lecciona catchment: study area and environmental monitoring

105   Lecciona (Fig. 1) is a subcatchment (31 ha) of the Re della Pietra experimental catchment (2 km²) located in the Apennines, in Tuscany, central Italy. We selected a north-facing hillslope transect ranging from 940 to 970 m a.s.l. with an average slope of 30° (Table 1). The selected hillslope spanned from the stream to the highest point of each catchment to address the extreme locations and the progressive edaphic and environmental changes. We defined as hilltop the highest point in the slope (close to the catchment ridgeline), the footslope location in the proximity of the stream, and the midslope location as situated between

110   the two. The hillslope is covered by a pure stand of beech trees with sparse oak individuals at the ridge top. Understory and tree regeneration are absent, and a thick litter layer of leaves washed off the upper portion of the slope accumulates downslope. At the ridgeline, trees are replaced by Scotch broom bushes (*Cytisus scoparius L.*), a species that typically grows in dry and sunny sites in secondary succession stages. The climate in the study area is typical of Mediterranean mountain environments with long-term annual precipitation (2001-2021) of 1265 mm, of which 590 mm falls during the growing season (April - October),

115   as recorded at Consuma weather station (ca. 10 km from the study site, managed by the regional meteorological service). The meteorological station at the study site has been installed in late 2018, and records mean air temperature during the growing season of 15.1°C (01 April-31 October) over 2018 - 2021. The lithology consists of "Macigno" sandstone, a turbidite unit with pelitic dominant lithofacies and a reduced thickness. Soil texture was assessed on 11 samples distributed along the hillslope. Sand content ranged between 57% and 76%, and clay content ranged between 4% and 11%. Soil texture in all samples resulted

120   in sandy loam, according to the USDA (1999) classification. Volumetric soil moisture was measured at the midslope, footslope,

and riparian area at 15 and 35 cm depth with water content reflectometers (TEROS 10, Meter Group). The standard calibration for organic soils recommended by the manufacturer was applied to the soil moisture probes. As the analyses in this work focused on the dynamics of soil moisture and not on the absolute values of soil moisture, the lack of a specific soil calibration did not affect the data interpretation and the results. Groundwater wells were drilled in 2019 at the footslope and in the riparian area. Wells were equipped with water pressure transducers (Orpheus Mini, OTT, Germany) recording data at 15 min logging intervals. Meteorological data (precipitation, air temperature, air relative humidity, wind speed, wind direction and radiation) were monitored at 5 min resolution in an open area at the top of the hillslope, at 991 m a.s.l.

Based on long-term records, the Lecciona catchment consistently receives more precipitation than the Weierbach catchment, both annually and throughout the growing season. While precipitation is evenly distributed across seasons in the Weierbach catchment, it falls mostly during the dormant season in the in the Lecciona catchment, typical of a Mediterranean climate (data not shown).

2.2 Relative extractable water (REW) and vapour pressure deficit (VPD)

~~Soil water retention curves are not available to compare soil water supply to plants in the two study sites. Therefore,~~ In order to account for inter-site differences in soil properties and facilitate the inter-site comparison we estimated the daily relative extractable water (REW, unitless) (Granier et al., 1999) over all monitored depth classes at each site, calculated as (Eq. 1):

$$REW = \frac{SM - SM_{min}}{SM_{95^{th}} - SM_{min}} \tag{1}$$

where SM is the daily soil moisture obtained by averaging data from all sensors, and $SM_{95^{th}}$ and SM_{min} are the site-specific soil moisture approaching field capacity and minimum values, respectively. REW varies between 0 ~~(i.e., permanent wilting point)~~ and 1 ~~(i.e., field capacity)~~ and represents the ratio between available soil water and maximum extractable water. REW was calculated for the Weierbach catchment based on soil moisture records from 2012 to 2020 and for the Lecciona catchment from 2020 to 2021. Following Salomón et al. (2022a), we chose the 95th percentile, and not the maximum value, to exclude heavy rain events that may result in soil saturation. REW has been quantified in previous studies to characterize soil drought intensity (Bréda et al., 2006; Grossiord et al., 2017b) and to carry out inter-site comparison (Salomón et al., 2022b; Granier et al., 2007).

For each study site, we computed the daily mean vapour pressure deficit (VPD, kPa), calculated as (Eq. 2):

$$VPD = 0.61375 \cdot e^{17.502 \cdot \frac{T}{240.97 + T}} \cdot (1 - \frac{RH}{100}) \tag{2}$$

where T and RH are air temperature and relative air humidity recorded from the weather station at each study site (Fig. 1).

2.3 Measurement of sap velocity

At each site we defined three monitoring locations corresponding to different topographic positions: plateau, midslope, and footslope in the Weierbach catchment; and hilltop, midslope, footslope in the Lecciona catchment (Fig 1). For each monitoring location, we selected one tree in the Weierbach catchment and three trees in the Lecciona catchment (Fig 1). By evaluating the

Table 1. Summary of the characteristics of the instrumented hillslopes

Site	Altitude m (a.s.l)	Slope (degrees)	Aspect	Soil	Geology	Stand
Weierbach	485-515	10	south	loam	slate	beech-oak mixture
Lecciona	910-990	30	north	sandy-loam	sandstone	beech-pure

Table 2. Average precipitation (mm), temperature (°C), VPD (kPa), radiation (W/m^2), soil moisture (m3/m3), and mean REW (relative extractable water) of the growing season (1 April - 31 October) in the Weierbach and the Lecciona catchment.

	Site	Year	Precipitation (mm)	T (°C)	RH (%)	VPD (kPa)	Radiation (W/m^2)	Soil moisture (m^3/m^3)	mean REW
Growing season	Weierbach	2019	506	13.8 ± 4.3	73.4±8.5	0.53 ± 0.3	231 ± 84	0.202	0.491
		2020	423	14.4 ± 3.6	68.6±11.9	0.63 ± 0.3	197 ± 74	0.185	0.398
	Lecciona	2021	466	15.1± 5.8	66.6±5.4	0.72± 0.3	190.7± 58	0.199	0.541

forest stand characteristics and the crown structure, we selected mature trees with approximately the same phytosociological positions and diameters in each site to exclude tree-size related effects (diameters between 30 and 32 cm in both sites). The selected trees were equipped with heat pulse sap flow sensors (SFM1, ICT International Pty Ltd., Australia), which record sap velocity at distances of 12.5 and 27.5 mm from the bark. The sensors were installed before leaves flushed and remained in place until leaves had fallen. In 2020, the installation in the Weierbach catchment was delayed due to COVID-19 restrictions that prevented field work. In the Weierbach catchment, we positioned the sap flow sensors on the north-east side of the trunk at 1.3 m height. In the Lecciona catchment, we opted to install them were installed on the west side to avoid placement prevent installation in tension wood, which is characterized by lower lignification and eccentric growth in grown by hardwood species on steep slopes. The heat pulse technique uses heat as a tracer to determine sap velocity. Briefly, a heater and two temperature sensors are inserted into holes drilled horizontally into the sapwood, with the sensors at fixed distance above and below the heater (5 mm). More details on the method can be found in Burgess et al. (2001). The mechanical damage of sensors installation induces xylem wounding interrupting the water flowpath (Barrett et al., 1995) and an increase in the proportion of non-conducting tissue. In order to account for this effect, we applied a wound correction factor of 0.13 cm (Green et al., 2003). We averaged sap velocities measured at an hourly basis by the inner and outer thermistor, and then we calculated a daily mean sap velocity, which is used as a proxy of tree transpiration (Smith and Allen, 1996). We filled the data gaps due to power malfunctioning via linear interpolation with sensors at the same location (Table A1, Fig.A1).

2.4 Wood core, soil, and water sampling

We sampled tree xylem water for analysing its isotopic composition biweekly over the 2019 and 2020 growing seasons in the Weierbach catchment (26 sampling campaigns) and in 2021 in the Lecciona catchment (11 sampling campaigns). The trees
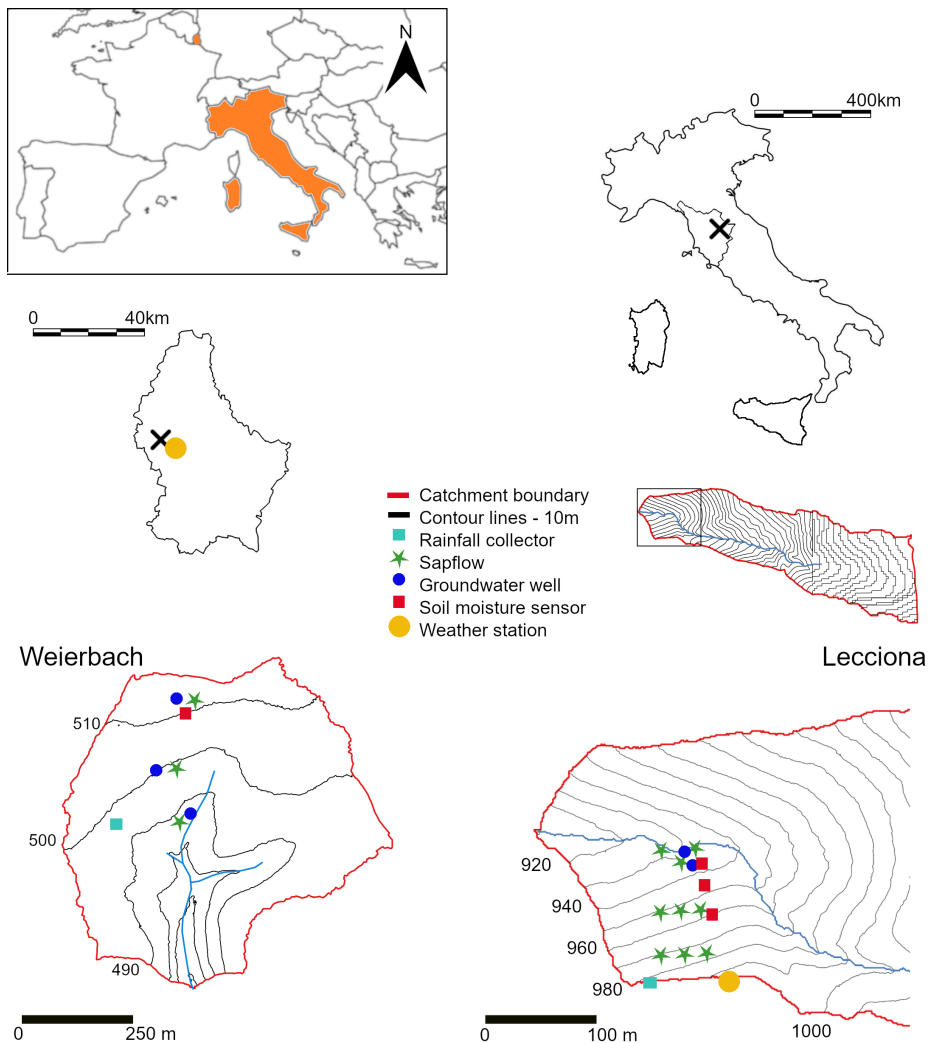
Figure 1. Sites overview with sensors in place: on the left the Weierbach catchment, Luxembourg, and on the right the Lecciona catchment in Tuscany, Italy. In the Weierbach, we monitored groundwater level (blue dot) and sap velocity (green star) in one beech tree at each hillslope position, and soil moisture (red square) at the plateau. In the Lecciona catchment, we measured sap velocity (green star) in three trees, and soil moisture content (red square) at midslope, footslope location and riparian area, and groundwater level (blue dot) was recorded at the footslope and in the riparian area.

selected for xylem sampling were in the same diameter range as the trees equipped with sap flow sensors and in close proximity to each other (within 25 m). Tree cores encompassing only the sapwood (ca. the outer 3.5 cm of xylem) were collected around the stem circumference with a Pressler borer. We avoided sampling above or below previous cores to minimize possible disturbances in sampled trees due to prior wounding. Xylem samples were quickly placed in glass vials, capped, and sealed

175 with Parafilm©. We simultaneously sampled soil cores to determine the soil water isotopic composition. At each sampling area, we extracted three soil cores from the uppermost 60 cm with a soil auger and divided them into five depth classes (0–5, 5–10, 10–20, 20–40, and 40–60 cm). Soil samples were collected in laminated aluminium bags, which have proven to be effective in minimizing evaporation even several days after the soil sample collection (40 days) (Gralher et al., 2021), and heat-sealed all bags upon arrival at the laboratory at the Luxembourg Institute of Science and Technology (LIST). The Weierbach soil samples

180 were processed and analysed upon arrival at the laboratory. More details are reported in Fabiani et al. (2022b). Lecciona soil samples were kept frozen at -10° and shipped to the laboratory at the end of the growing season 2021, and they were kept frozen until analysis. The freezing process prior to analysis reduces the microbial activity and the associated buildup of CO_2 (Gralher et al., 2021). We sampled groundwater at the sampling areas in the Weierbach catchment and rainfall bi-weekly with an evaporation-protected rainfall collector (Palmex Ltd.) placed in a clearing at both sites (Fig 1). In the Lecciona catchment,

185 groundwater was sampled on two occasions in 2022 (24 March and 5 October) due to logistical difficulties.

2.5 Laboratory ~~Isotopic~~ analyses

Xylem water was extracted via a cryogenic water extraction line (Orlowski et al., 2016) at LIST (Luxembourg Institute of Science and Technology). Briefly, samples were submerged in a 100°C oil bath for 3 h under a vacuum (0.03 hPa), and the resulting water vapour was collected in U-shaped tubes placed in liquid nitrogen (-197°C). We assessed the gravimetric water

190 content for xylem samples by weighing them before and after cryogenic water extraction. We quantified the wood moisture content (%) as the ratio of the weight of extracted water (liquid mass) to the weight of dry wood after cryogenic water extraction (Peck, 1953; Steppe et al., 2010; Fabiani et al., 2022a). ~~We assessed the wood moisture content defined as the ratio of the weight of extracted water to the weight of dry wood after cryogenic water extraction.~~ The isotopic composition (δ^2H and δ^{18}O) of the extracted water was analysed using a Picarro cavity ring-down spectrometer (CRDS) (L2140-i, Picarro, USA) coupled

195 with a Micro-Combustion ModuleTM (MCM) to remove organic compounds (ethanol, methanol and/or other biogenic volatile compounds). To detect possible organic contamination, xylem samples were screened with ChemCorrectTM (Picarro Inc., Santa Clara, CA, United States) software, which attempts to identify contamination by fitting to a known library of spectral features. No organic contamination was found in any sample. To minimize the memory effect, each sample was analysed 10 times and only the last 5 readings were saved and averaged (Penna et al., 2012). We analysed the isotopic composition of soil

200 samples with the direct liquid-water-vapour equilibration method (Wassenaar et al., 2008). We let the samples thaw for 2 days while equipping the aluminium bags with silicon blots. 48 hours were sufficient to ensure the hardening of the silicone and minimize the risk of outgassing volatile organic compounds from freshly applied silicone (Gralher et al., 2021). We inflated the bags with dry air by puncturing the hardened silicon blots, and we let them equilibrate for 48h at a constant temperature for isothermal equilibration. Headspace vapour was sampled directly with a needle connected to the Picarro analyser coupled

205 with MCM for the samples and the five bags with known isotopic composition (ranging between -16.2 - -2.9 in δ^{18}O and -123.7 - -9.9 in δ^2H). Water vapour concentrations were always above 28000 ppm where the concentration-dependent deviation becomes low and thus measurement precision is not compromised. The local meteoric water line (LMWL) at the Weierbach catchment is δ^2H = 7.4 δ^{18}O + 7.4, and is based on biweekly precipitation samples collected from 2011 to 2020. This rather

low slope is characteristic of the region (Klaus et al., 2015). The LMWL at the Lecciona catchment is δ^2H = 6.2 δ^{18}O + 7.0 and is based on biweekly to monthly samples of precipitation collected from 2018 to 2021.

2.6 Data analysis

We applied linear mixed effects models (LMEM) with lme4 package (Bates et al., 2015) to determine the combined effect of environmental variables (VPD, REW, and radiation W) and topographic positions on sap velocity over the course of the growing season. We fitted a LMEM for each study site to identify the most important predictors of monthly transpiration. Sap velocity was used as dependent variable, with VPD, W, and REW as environmental predictors. Individual trees were used as the random-effects term included in all models. Furthermore, since we were interested in the response of sap velocity to environmental conditions (i.e., REW and VPD) as an indicator for stomatal control, we normalised daily mean sap velocities between 0 and 1, where 0 and 1 were the minimum and maximum daily mean velocities recorded by each tree over the entire growing season. This procedure facilitates the comparison between the two study sites as shown elsewhere (Gimenez et al., 2019). Comparisons of sap velocities between locations were analysed with the Pairwise Wilcox test. The Pairwise Wilcox 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 locations were analysed via the non-parametric Mann–Whitney test. The significance level was set to $\alpha \leq 0.05$ to determine which year or location ~~zone~~ was statistically different from each other. For all our analyses we used R software, version v. 4.2.0 (R Core Team, 2022).

3   Results

3.1   Environmental conditions across years and sites

In the Weierbach catchment, the 2020 growing season was characterized by drier conditions compared to 2019, and below the long-term average (2007-2019) of 451 mm (Schoppach et al., 2021). Despite the lower average solar radiation in 2020 than in 2019 (Table 2, Fig. 2c), the 2020 growing season was characterized by higher evaporative demand concurrently with reduced precipitation input (Table 2, Fig. 2a) and lower soil moisture (Table 2, Fig. 2e) compared to 2019. The lowest REW value within the period 2002-2020 was reached in 2020 in the second half of September (data not shown). However, the daily maximum VPD was higher in 2019 with 3 kPa compared to 2020 when VPD reached 2.5 kPa. In the hydrometeorological space, defined by the relationship between REW and VPD (Salomón et al., 2022a) each month of the 2020 growing season was characterized by lower REW but higher VPD than in 2019, except for June and July when VPD was higher in 2019 (Fig. 3). This general dry-out of the system was also observed in the groundwater table that progressively declined (Fig. 2g) up to 5.58 and 6.50 m in depth in 2020 compared to 4.98 and 5.65 m in 2019 in the plateau and midslope, respectively. The maximum and minimum groundwater table depth did not vary between the two years at the footslope location (Fig. 2g). The decline of soil moisture was accompanied by a progressive dehydration of xylem (Fig. A3) leading to a significant relationship between soil moisture and wood moisture content (Fig. 4). In the Weierbach catchment, there were no statistical differences in wood

240 water content between the 2019 and 2020 growing seasons, or when values of each month were compared (Kruskal-Wallis, p>0.05). However, wood moisture was significantly lower in trees located at the plateau (Kruskal-Wallis, p=0.04) compared to trees growing in the other locations.

In the Lecciona catchment, the 2021 growing season was characterized by a higher average temperature compared to the Weierbach catchment (Table 2) but with a similar precipitation amount. Soil moisture content was on average similar between
245 the two sites (Table 2). In the Lecciona catchment, soil moisture decreased from June until September, when precipitation events replenished the soil water content. Soil moisture at the midslope and footslope decreased simultaneously, while soil moisture in the riparian area decreased to a lesser extent and remained higher and steadier (Fig. 2f). The groundwater table at the footslope location was rather constant with an average depth of 4.1 m, and responded only after major rainfall events (Fig. 2h). There was no statistical difference in wood moisture content among locations in the Lecciona catchment (Kruskal-Wallis,
250 p=0.72). By comparing the hydrometeorological space between the two study sites, we found slightly higher REW in the Lecciona catchment, and higher VPD compared to the Weierbach catchment (Fig. 3). The progressive decrease in precipitation input over the growing season affected not only soil moisture but also the wood water content (Fig. A3). There was a significant relationship between soil moisture and wood moisture content at all locations (Fig. 4) and a marked temporal variability (Fig. A3). According to hydrometeorological space (Fig. 3), we selected the months with more contrasting environmental conditions
255 (i.e. June, August, September) in terms of water availability relative to the maximum extractable water (REW) and evaporative demand (VPD). To investigate tree physiological response from the site-specific environmental stress and compare between locations, we plotted the normalised sap velocity against site daily VPD and REW for the selected months (Fig. 3).

3.2 Sap velocity

In the Weierbach catchment, there was a consistent pattern in sap velocity between the consecutive monitoring years with
260 monthly sap velocities being higher in June compared to other months (data not shown), but daily sap velocity peaking in July (Fig. 5). Sap velocity was significantly higher (Kruskal-Wallis test, p<0.001) at the midslope location than at other locations followed by plateau and footslope when both years were considered (Fig. 5). Sap velocities were statistically higher in 2020 than in 2019 in May and September at all locations. Despite the early yellowing and shedding of leaves observed in August 2020, symptoms of partial dysfunction of the hydraulic system, sap velocities were not lower than in 2019.

265 In the Lecciona catchment, there were no statistical differences in overall mean velocity among locations (Wilcoxon test, p>0.3) (Fig. 5b). However, there was a location-specific behaviour by month. All trees shared a common pattern for the first part of the growing season: after leaf-out (19-26 April), sap velocity increased for all trees and locations and peaked toward the end of June (Fig. 5). From August onwards, sap velocity markedly dropped in plants at the hilltop (Fig. 5, see arrow). In contrast, sap velocity remained high and did not vary between July and August at the footslope. Trees at the midslope
270 location displayed a behaviour in between the other locations. In September, the sap velocity of trees located at the footslope was significantly higher than at the other locations (Kruskal-Wallis, p<0.05) and 2- and 4-fold higher compared to midslope and hilltop, respectively. The growing season (leaf-out) started later in the Lecciona catchment compared to the Weierbach
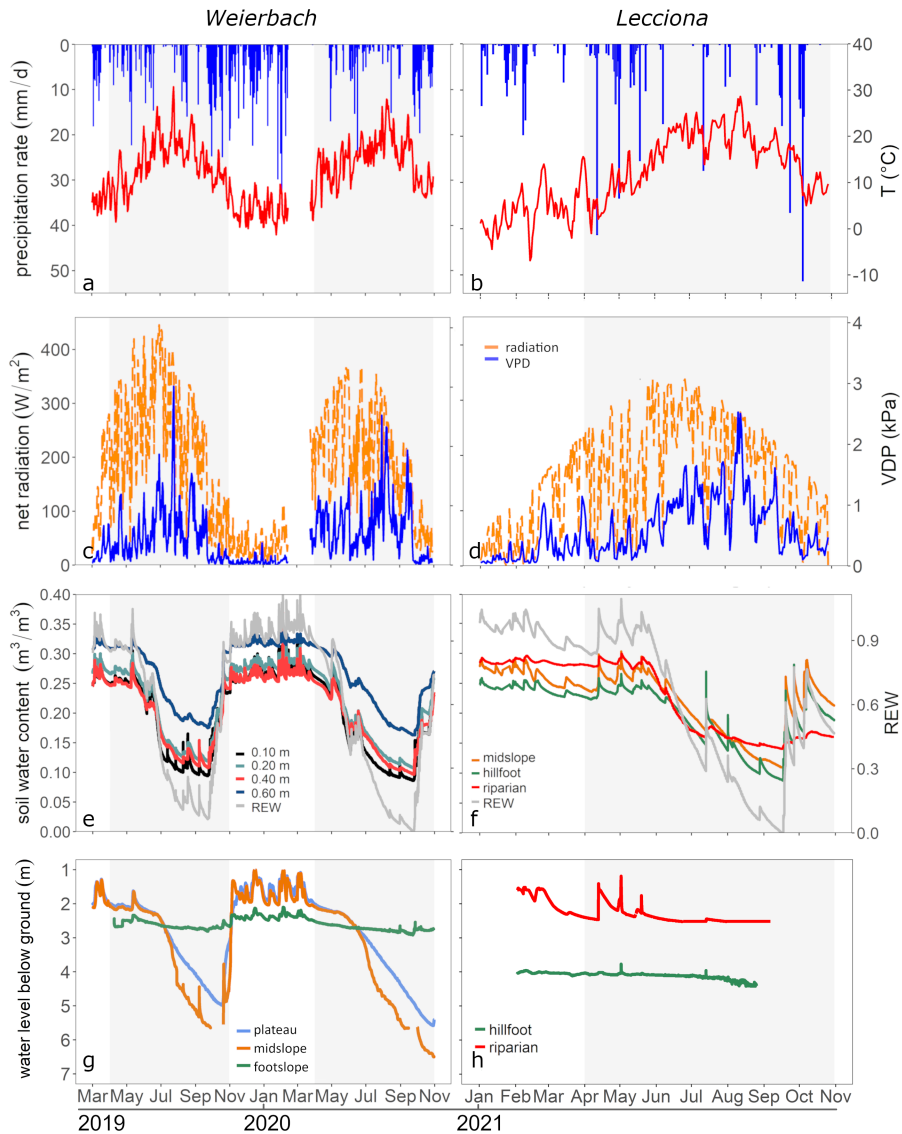
Figure 2. Daily total precipitation amount (mm/d) and daily mean air temperature (°C), and daily mean radiation (W/m²) and daily mean vapour pressure deficit (VPD) (kPa) observed at the Roodt (left plots, a, and c) weather station and the Lecciona catchment (right plots, b and d). Volumetric soil water content (m³/m³) and REW (relative extractable water) in the Weierbach (e) and the Lecciona catchment (f). Soil moisture in the Weierbach catchment was measured at four depths in the plateau location. In the Lecciona catchment, soil moisture was recorded in three topographic positions at two depths, which are averaged in the plot. Groundwater level below ground surface (m) in the Weierbach (g) and the Lecciona catchment (h). The shaded area represents the growing season.
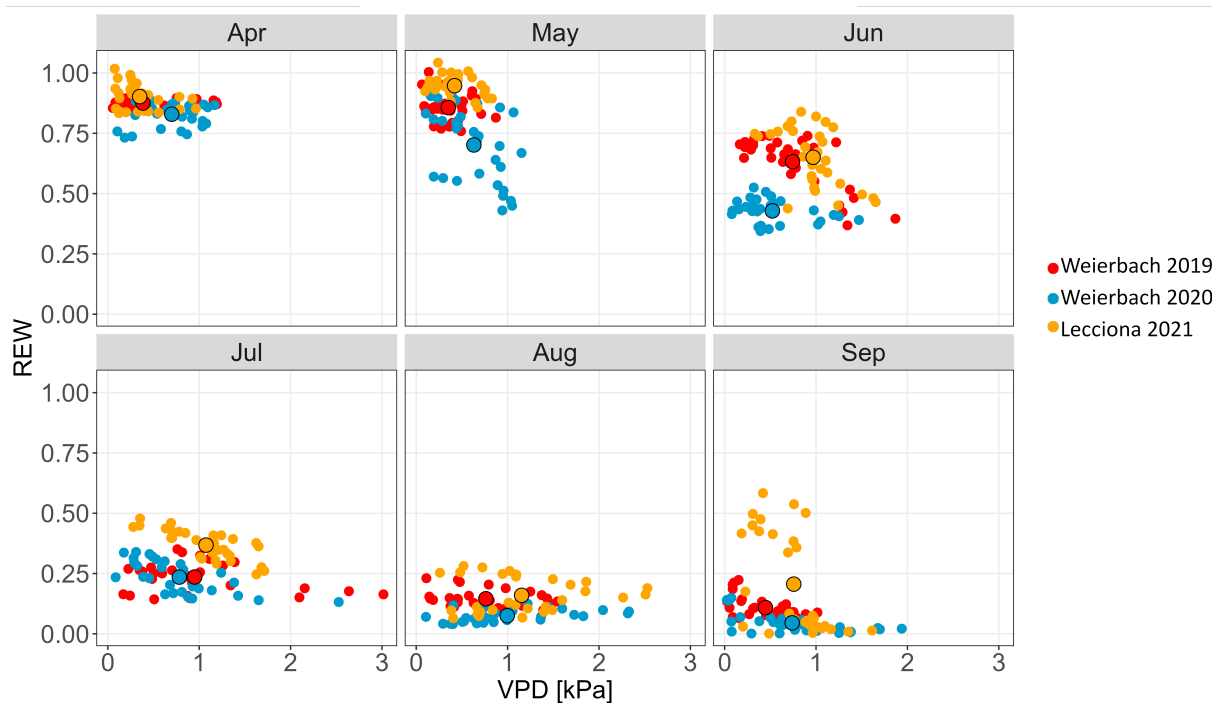
Figure 3. Relationship between VPD (kPa) and REW over the growing season (2019-2020) in the Weierbach catchment and (2021) in the Lecciona catchment. Full dots with black outlines represent monthly means.

catchment; data are not available from the late season (October onwards) to compare the duration of the growing season between the two sites.

275   In the Weierbach catchment, sap velocity was always positively correlated with an increase in VPD (p<0.01) and W (p<0.01) from June onwards (Fig. A2). High REW values were followed by a decrease in sap velocity (p<0.01) only in the early phases of the growing season, and later on by an increase in sap velocity. LMME analyses showed that hillslope position did not explain sap velocity variation both in 2019 and 2020. In the Lecciona catchment, VPD and W were the best predictor explaining an increase in sap velocity (p<0.01). However, LMMEs showed that hillslope position (p<0.01) and W (p<0.01) explained most

280   of the variability in sap velocity in September (Fig. A2).

3.3   Sap velocity response to VPD and REW

The relationship between normalised sap velocity and VPD in the growing season did not differ between locations and years in the Weierbach catchment (Fig. 6). However, for the same VPD values, sap velocity was lower in August and September at the footslope compared to the other locations indicating a stronger stomatal control on transpiration fluxes. There was a progressive

285   decline of sap velocity throughout the growing season despite similar monthly VPD (Fig. 3). In both years, maximum sap velocities were reached when VPD ranged between 1.0 and 1.4 kPa (data not shown). In the Lecciona catchment, there was
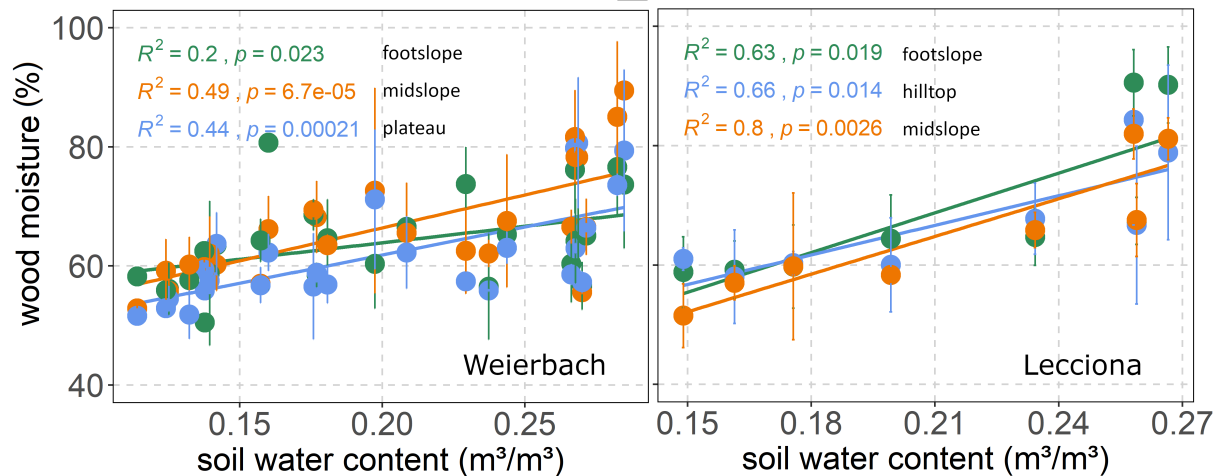
Figure 4. Relationship between wood moisture content (%) and volumetric soil moisture content of the xylem sampling date in the Weierbach catchment (left side) and the Lecciona catchment (right side). Solid dots represent the mean of xylem moisture, the whiskers indicate the confidence interval (95%). In the Weierbach catchment, we used the average soil moisture content over the four depths, while in the Lecciona catchment, we used the average soil moisture over the two monitored depths and the three locations

a strong differentiation of sap velocity response to VPD across the topographic sequence (Fig. 6). For the first months of the growing season, sap velocity response to VPD was consistent among hillslope positions. In August, trees at the footslope maintained a high sap velocity even when daily mean VPD values were 2.7 kPa, the highest value of the season (Fig. 2d). On the other hand, sap velocity of trees at the hilltop and midslope declined progressively in August and ceased in September, while remaining high at the footslope. There was no difference in the relationship between normalised sap velocity and REW among hillslope positions and over the years in the Weierbach catchment (Fig. 7). Following the reduction in REW over the months, sap velocity was progressively reduced at all locations (Fig. 7). In the Lecciona catchment, although REW reduction influenced sap velocity, its effect on sap velocity varied between locations likely resulting from the different soil moisture content between locations. In June, the high REW did not cause any differentiation in sap velocity response among locations, but in August with reduced REW, sap velocity at the hilltop and midslope decreased but not at the footslope. In September, despite the recharge of soil moisture by precipitation (Fig. 2f), sap velocity remained high only at the footslope and approached minimum values at the hilltop.

3.4 The isotopic composition of xylem, soil, groundwater, and precipitation

In the Weierbach catchment, xylem isotopic composition (157 samples, see Table A2) ranged between -8.8 and -3.1 ‰ in δ^{18}O and -76.6 and -39.3‰ in δ^2H. The mean isotopic composition was -6.4 ± 1.0 ‰ and -63.7 ± 7.1 ‰ in δ^{18}O and δ^2H, respectively. There was a marked temporal variability at all locations with a typical higher isotopic composition during the sampling date from the dormant season (Fig. A4). We did not find any statistical difference in xylem isotopic composition
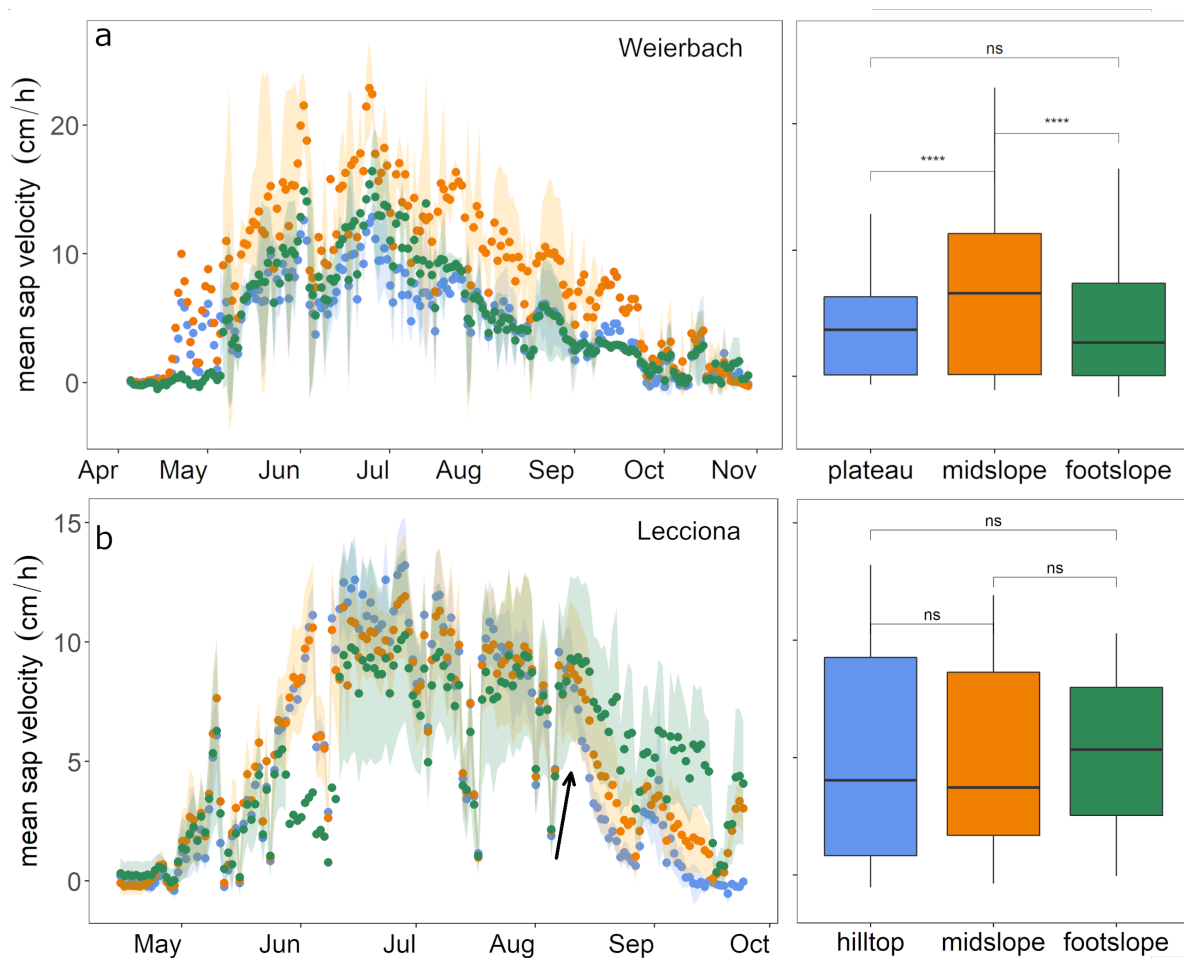
Figure 5. Daily mean sap velocity (cm h⁻¹) of Weierbach (a) and Lecciona (b) trees. ~~In this Figure, the Weierbach catchment~~ ~~D~~data ~~from the Weierbach catchment cover~~ were averaged between the 2019 and 2020 growing seasons ~~(April–October)~~, while data from the Lecciona catchment cover the 2021 growing season ~~(mid-April – September)~~. Each color corresponds to location (green = footslope, orange = midslope, blue = hilltop/plateau). The area inside the colored lines is the mean average deviationamong ~~between~~ trees at the same location for the Lecciona catchment and between monitored years in the Weierbach catchment. Boxplots on the right side show the average sap velocity by location. The whiskers indicate points within 1.5 times the interquartile range above or below the median. Above each boxplot, asterisks (symbols "*" and "ns" correspond to p-values ≤ 0.05 or > 0.05, respectively) denote significant statistical differences between locations (Wilcoxon test).

between sampling locations (p=0.2 for δ^{18}O, p=0.5 Kruskal-Wallis test) (Fig. 8). Soil water δ^{18}O and δ^2H showed the typical
305   depth-gradient with heavier isotopic composition in the shallow layers (mean -5.5 ± 1.6 ‰ δ^{18}O, -38.7 ± 9.6 ‰ δ^2H) and lighter values in the deeper one (-8.5 ± 1.4 ‰ δ^{18}O, -55.7 ± 8.9 ‰ δ^2H). The groundwater isotopic composition was stable over time and was statistically significantly lighter at the footslope (mean -8.5 ± 0.1 ‰ δ^{18}O, -54.3 ± 1.1 ‰ δ^2H) compared
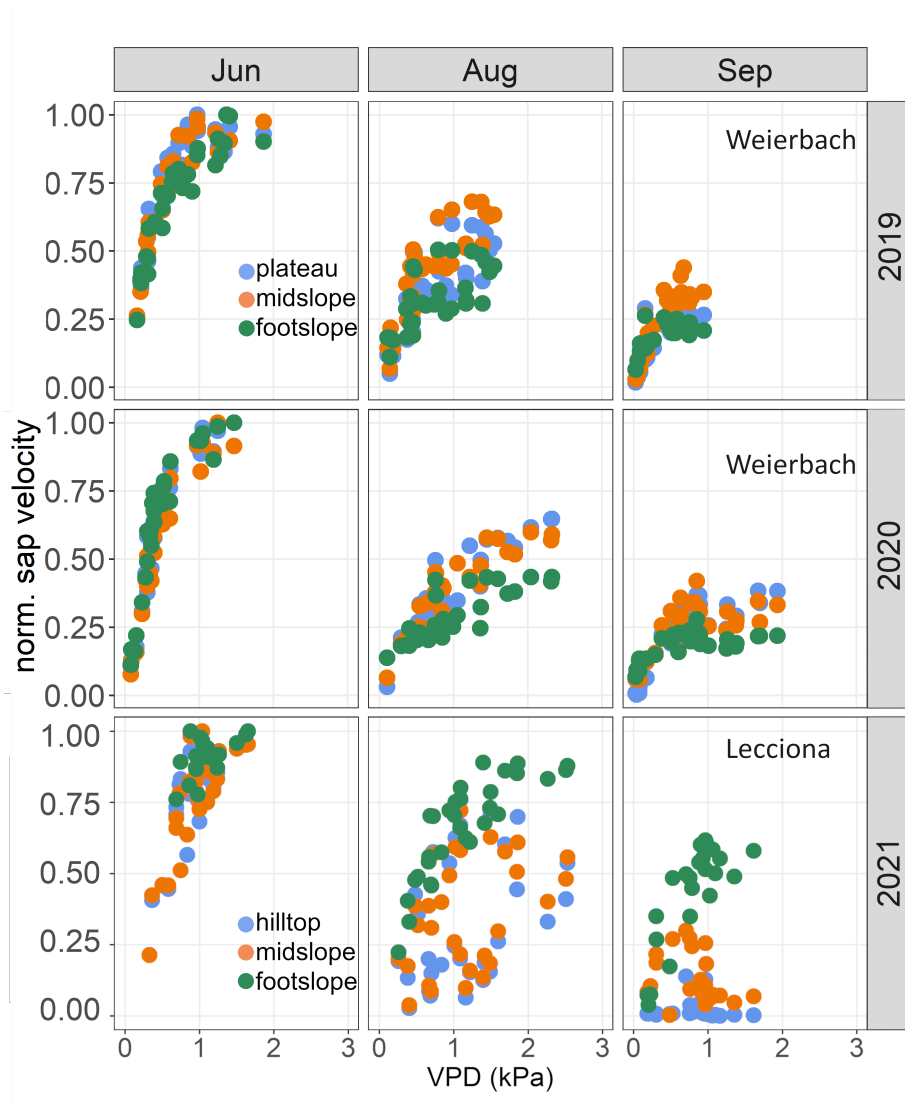
Figure 6. Relationship between normalised mean sap velocity and daily vapour pressure deficit (VPD) (kPa) at different hillslope positions in June, August, and September 2019 and 2020 in the Weierbach catchment (left and central column)and 2021 in the Lecciona catchment (right column).

to the midslope (mean -8.3 $\pm$ 0.3 ‰ δ^{18}O, -56.9 $\pm$ 1.8 ‰ δ^2H) and plateau (mean -8.5 $\pm$ 0.3 ‰ δ^{18}O, -52.6 $\pm$ 2.3 ‰ δ^2H) (p<0.05, Kruskall-Wallis test).

310   In the Lecciona catchment, xylem water (96 samples, see Table A2) showed values between -8.0 and -3.5 ‰ in δ^{18}O and -65.9 and -42.3 ‰ in δ^2H. During the growing season, xylem water displayed a strong temporal pattern (Fig. A4, A5). From May onwards, xylem water became heavier in both isotopes over time. After reaching the heaviest values on June 11, it
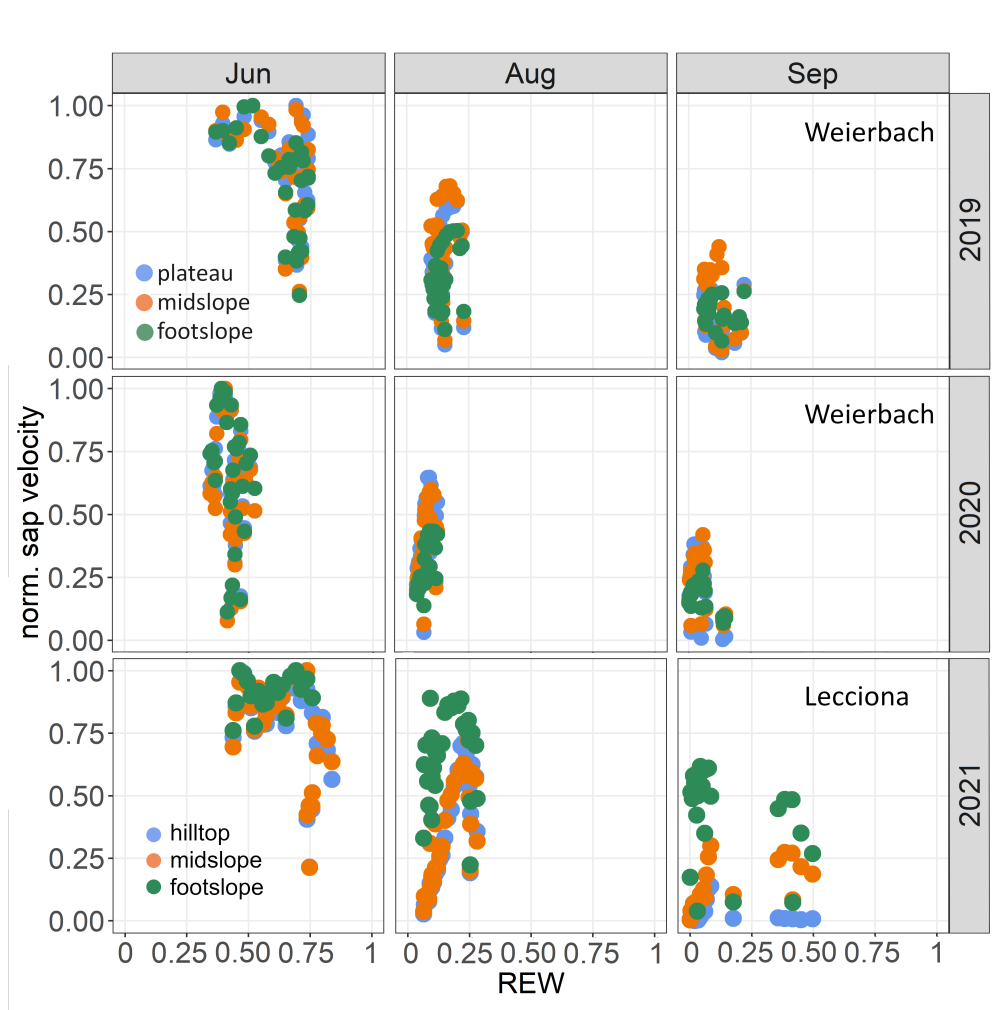
Figure 7. Relationship between normalised mean sap velocity and relative extractable water (REW) at different hillslope positions in June, August, and September of 2019 and 2020 in the Weierbach catchment ~~(left and central column)~~ and 2021 in the Lecciona catchment ~~(right column)~~.

progressively became lighter (Fig. A4, A5). Xylem water of trees located at the footslope (mean -6.5 ‰ δ^{18}O and -57.6 ‰ in δ^2H) was significantly lighter in both isotopes (p<0.01 δ^{18}O, p<0.02 δ^2H, Pairwise Wilcox test) compared to trees at the

315 midslope (mean -5.9 ‰ δ^{18}O and -53.9 ‰ in δ^2H) and hilltop (mean -5.4 ‰ δ^{18}O and -51.6 ‰ in δ^2H) (Fig. 8). Soil water in Lecciona showed a marked depth gradient and no statistical difference among locations (data not shown)~~(Fig. 8)~~. Soil isotopic composition plotted above the LMWL, reflecting the heavy isotopic composition of the summer precipitation. Although we followed standard protocol for this analysis and soil isotopic composition tracked the isotopic composition of precipitation, potential artefacts in the direct vapour equilibration method may have influenced these results. During the analyses, water

320 vapour concentrations were above 28000 ppm and no methane was detected as an indication of potential microbial activity,

both factors should ensure a reliable performance of the analysis (Gralher et al., 2021). However, we cannot exclude that shipping and storing procedures may have influenced the isotopic composition of soil samples. The isotopic composition of the groundwater sampled at the footslope displayed an average isotopic composition of -8.5 δ^{18}O and -50.3 δ^2H.

While topsoil (0-5 cm) isotopic composition displayed an average isotopic composition of -3.6 $\pm$ 1.9 ‰ in δ^{18}O and -16.8
325 $\pm$ 13.9‰ in the δ^2H, the deepest soil depth sampled (40-60 cm) had an average isotopic composition of -6.5 $\pm$ 1.8 ‰ in δ^{18}O and -31.9 $\pm$ 14.1 ‰ in δ^2H. As in the Weierbach catchment, we did not find significant differences in soil water isotopic composition between sampling locations (p>0.05, Wilcoxon rank sum test). At both sites, xylem water did not overlap with the potential water sources sampled (Fig.8), but we observed a stronger deviation between xylem water and soil water in the Lecciona catchment (Fig.8).
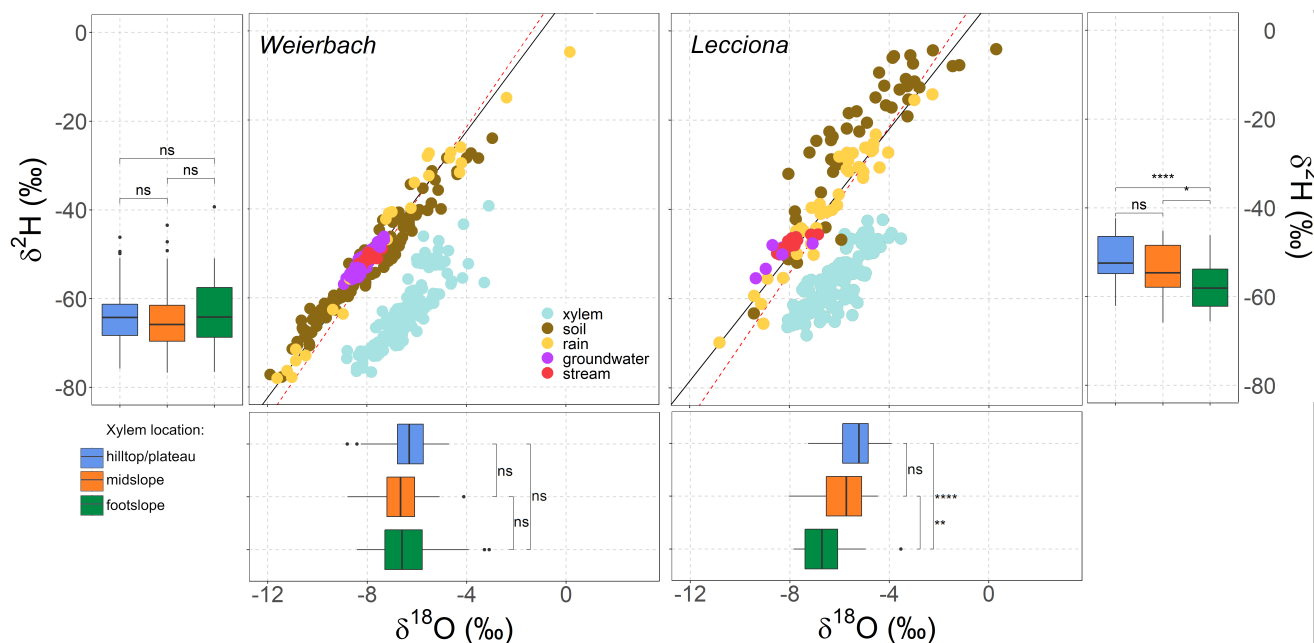
Figure 8. Dual isotope plots showing soil water, rain, groundwater, stream, and xylem water isotopic composition sampled in the Weierbach catchment (left panel) and the Lecciona catchment (right panel). The boxplot shows the median (black line in the box), the interquartile range (extent of the box), the range (whiskers), and outliers (points) for xylem isotopic composition for the three sampling locations. The dashed and solid lines represent the global meteoric water line (GMWL) and local meteoric water line (LMWL) for each site.

4 Discussion

4.1 Drier conditions did not increase tree sensitivity to topography in the Weierbach catchment

According to our results, a lower availability of soil water~~water availability~~ in the Weierbach catchment in the 2020 growing season compared to the 2019 growing season - ~~which was also the lowest recorded in the last eight years in the Weierbach~~which also marked the lowest recorded in the past eight years - did not lead to a stronger sensitivity (i.e. stronger stomatal control and therefore reduced sap velocity) of tree water use to topography (Fig. A2). Instead, environmental controls (VPD, radiation and REW) were the main predictors controlling sap velocity (Fig. A2). The 2020 growing season was characterized by lower precipitation ~~drier~~ and warmer compared to 2019 (Table 2, Fig. 2), which is in line with the general drying and warming trend observed over the last decade in the catchment (Schoppach et al., 2021). Despite this, sap velocity in 2020 did not decrease compared to 2019, and sap velocities were even higher in May and September at all locations in 2020. Similarly, Gutierrez Lopez et al. (2021) found that in Sweden drier conditions did not affect transpiration compared to a wetter previous year because small precipitation events were sufficient enough to recharge soil moisture. The gradual decrease in soil moisture content concurrently with an increase in VPD caused a reduction in normalised sap velocity, especially at the footslope location in both years (Fig. 6 and 7). We found that maximum sap velocities were reached for the same VPD range (1.0-1.5 kPa). However, the number of days with VPD higher than 1.5 kPa doubled in 2020, which, coupled with the depletion in soil water, might be the cause for the early leaf yellowing and defoliation observed from mid-August at our site. According to Walthert et al. (2021), early defoliation in beech can be used as a predictor for crown die-back in the following year. In fact, the effects of water shortage cannot be confined to the study year alone because the carry-over effects from current conditions will be expressed over the next seasons (Walthert et al., 2021).

Consistent with previous observations at the study site for 2019 (Fabiani et al., 2022b), the high vertical hydraulic conductivity in the Weierbach catchment (Glaser et al., 2016; Gourdol et al., 2021) does not promote shallow lateral subsurface flow from the plateau to the footslope (Fig. 9). Instead, deeper hydrological flow paths dominate (Rodriguez and Klaus, 2019) leading to a shallow and rather stable groundwater table at the footslope (Fabiani et al., 2022b). However, groundwater proximity to the soil surface did not have any influence on tree physiological response even during the dry conditions in 2020 (Fig. 2g). The 2019 minimum groundwater table depths at the plateau and midslope locations fell below in 2020, reaching a level below the typical rooting depth of *F. sylvatica* (0.83±0.46) (Fan et al., 2017). ~~Close proximity of the groundwater table to the soil surface for long duration leads to anoxic conditions that limit tree root development (Phillips et al., 2016).~~ This evidence, combined with the lack of statistical difference in xylem isotopic composition among locations (Fig. 8), supports the conclusion that there is a negligible role of groundwater as a water source for beech trees in the Weierbach catchment. Similarly, at a different study site, Weemstra et al. (2013) did not observe any impact of interannual variation in groundwater depth on beech growth rates. Although plants can grow roots deeper in the soil profile as a response to water limitation (Bréda et al., 2006), beech trees show little plasticity and rely on shallow soil storage regardless of the drought condition (Gessler et al., 2022; Volkmann et al., 2016). This result emphasizes the importance of occasional rainfall to wet the topsoil, where most of the fine roots of *F. sylvatica* are located (Coners and Leuschner, 2005; Meier and Leuschner, 2008).

Another potential water source to buffer water shortage is stem water (Tyree and Yang, 1990). The progressive dehydration of the xylem from winter to summer suggests that the stem internal water storage may have acted as an additional water source for tree transpiration (Fig. 4 and A3). Seasonal changes in stem water content resulting from the use of storage water have already been observed in other studies with progressive water depletion over summer and refill after leaf fall (Tyree and Zimmermann, 2002; Fabiani et al., 2022a). The relevance of stem-stored water has already been highlighted in other studies which showed that the internal water plays a crucial role in the water balance of beech trees, improving their ability to cope with water stresses (Betsch et al., 2011; Köcher et al., 2013; Matheny et al., 2017). Although we did not observe a statistical difference in wood moisture among locations and years (Fig. 4 and A3), we acknowledge that our measurements provided only snap-shots of xylem water status and cannot capture fine-scale differences that could exist across the landscape. A clearer understanding of the role of stem water reserves on tree hydraulic integrity can be better addressed in future studies with the deployment of band dendrometers combined with point dendrometers (e.g. Dietrich et al., 2018; , 2022a) allowing to discriminate between xylem and bark hydration.

4.2 Topography influences the duration of the growing season in the Lecciona catchment

In contrast to the Weierbach catchment, the topography in the Lecciona catchment had a significant effect on sap velocity, but only towards the end of the growing season when the system was dry (Fig. A2). We observed that sap velocity remained significantly higher at the footslope compared to other locations during this time. This evidence supports our hypothesis that the combination of steep topography and subsurface characteristics that promote fast and shallow subsurface flow at the Lecciona study site (Mary et al., 2023) enhances the variability in energy and water inputs (Fig.9). The higher soil moisture content at the bottom of the slope than at the upslope locations in the Lecciona catchment (Fig. 2f) leads to spatially different physiological responses in trees. Additionally, the thick litter accumulated downslope from the upper slope (Fig.9) might have acted as a barrier reducing soil evaporation at the footslope. In the Lecciona catchment, until July, the relationship between sap velocity and VPD was similar among hillslope positions (Fig. 7 and 6) suggesting that soil water supply was sufficient to compensate for evapotranspiration losses (Bréda and Granier, 1996). However, in August the reduced soil water availability at the hilltop and midslope resulted in a down-regulation of sap velocity (Fig. 7 and 6). When more favourable conditions were restored from rainfall events in September that recharged the upper soil (Fig. 2f), sap velocities at the hilltop and midslope locations did not recover the pre-drought transpiration (Fig. 7 and 6). At this time, hillslope topography had a positive significant effect on sap velocity leading to sustained transpiration at the footslope (Fig. A2). This result supports the anticipated effects of landscape characteristics on tree transpiration, leading to more conservative hydraulic behaviour in upper topographic positions due to the xeric conditions at the Lecciona catchment (Kumagai et al., 2008; Song et al., 2022). We also observed that the decrease in soil water content at the upslope location led to a progressively shorter vegetative season moving for upper slope positions at the Lecciona footslope (Fig. 5). This result might also be interpreted as evidence for the physiological acclimation of beech trees located at the hilltop and midslope locations. The drier and more evaporative-demanding conditions given by the higher solar radiation at the midslope and hilltop areas compared to the footslope (Méndez-Toribio et al., 2017), could cause trees in higher topographic positions to experience shorter growing season to withstand decreasing water supply water limitations (Fig.

5). Similarly, Méndez-Toribio et al. (2017) observed a shorter growth time window in the upper part of slopes as a strategy to mitigate drought via leaf shedding or by the use of internal water storage. The statistical difference in xylem isotopic composition between locations observed in the Lecciona but not in the Weierbach catchment (Fig.8) might suggest ~~support the hypothesis~~ that ~~to withstand the spatial changes in water availability,~~ trees ~~are adapted to~~ capitalize on different water sources with ~~different~~ contrasting isotopic composition to adapt to spatial changes in water availability. We found significantly heavier xylem isotopic composition at the hilltop and midslope compared to the footslope location in the Lecciona catchment (Fig. **??** and Fig. **??**), but no differences in the soil isotopic composition suggesting that the difference in xylem isotopes is not related to spatial differences in soil isotopes of the upper 60 cm of the soil. This might indicate ~~suggesting~~ a greater use of shallow water sources in the upslope locations due to inaccessibility to the deep aquifer. However, from the soil isotopic composition (Fig. 8), we cannot confirm this interpretation due to the large offset between xylem and soil, groundwater and stream water isotopic composition, as it has been commonly observed in other studies (Barbeta et al., 2019; Poca et al., 2019; de la Casa et al., 2022; Schreel et al., 2023). This topic has received increasing attention in recent literature, but no ubiquitous explanations have been confirmed. In the Lecciona catchment, we suggest that footslope trees compared to those at upslope locations benefit from the greater accessibility and availability to water stored in the deeper soil layers and in the weathered bedrock, which generally displays lighter isotopic composition compared to shallow soil water.

We observed that transpiration responses to VPD differed between the two study sites despite a similar soil moisture range. This is because different soil texture leads to different water availability for plant water use. The loamy soil texture in the Weierbach catchment translates into more negative soil water potential compared to the sandy-loam in the Lecciona catchment for similar soil moisture content values. For this reason, since soil moisture retention curves are missing at our study sites, we rely on REW to compare the Lecciona and Weierbach catchment. While maximum sap velocities were markedly reduced for VPD above 1.5 kPa in the Weierbach catchment (Fig. 7), in the Lecciona catchment sap velocity at the hilltop remained high even for VPD values above 2 kPa (Fig. 3). This suggests that trees at the footslope location in the Lecciona catchment were not water limited and likely had access to water stored in deep soil or saprolite. When compared to other species, *F. sylvatica* is generally considered to have an isohydric behaviour (Fabiani et al., 2022b; Gessler, 2021; Magh et al., 2020; Martínez-Vilalta and Garcia-Forner, 2017), which means that with decreasing VPD, beech trees tend to close their stomata to minimize water loss (Grossiord et al., 2017b). However, the different sap velocity response to VPD observed at our sites (Fig. 7 and 6) suggests that the hydraulic behaviour of this species could also change from site to site as an adaptation to hydro-meteorological conditions and landscape features. Indeed, water-use strategies within the same species can vary both spatially and temporally according to the coupling between soil moisture, atmospheric driver, and morphological adjustments (Kannenberg et al., 2022). Additionally, as already pointed out by Hochberg et al. (2018), when comparing data from multiple sites, we do not always have the capability to separate environmental and genotypic variability. The wide distribution range occupied by *F. sylvatica* in Europe results from the high plasticity of this species and the phenotypic variation including those relating to drought resistance (Stojnić et al., 2018). Previous literature has already emphasized that trees' hydraulic strategy should not be considered strictly as a dichotomy between iso- and anisohydric behaviour, but rather a continuum between the two (Martínez-Vilalta et al., 2014). Despite some evidence on the ~~high~~ adaptation potential of beech trees ~~to changing~~

environmental conditions has also been speculated in a study that revealed the high plasticity capacity of the stem hydraulic system in *F. sylvatica* over decades (Zimmermann et al., 2021), However, it remains unclear how a long-term increase in soil

435   and air dryness may impact this species, vulnerable to drought (Walthert et al., 2021), across its wide distribution range.
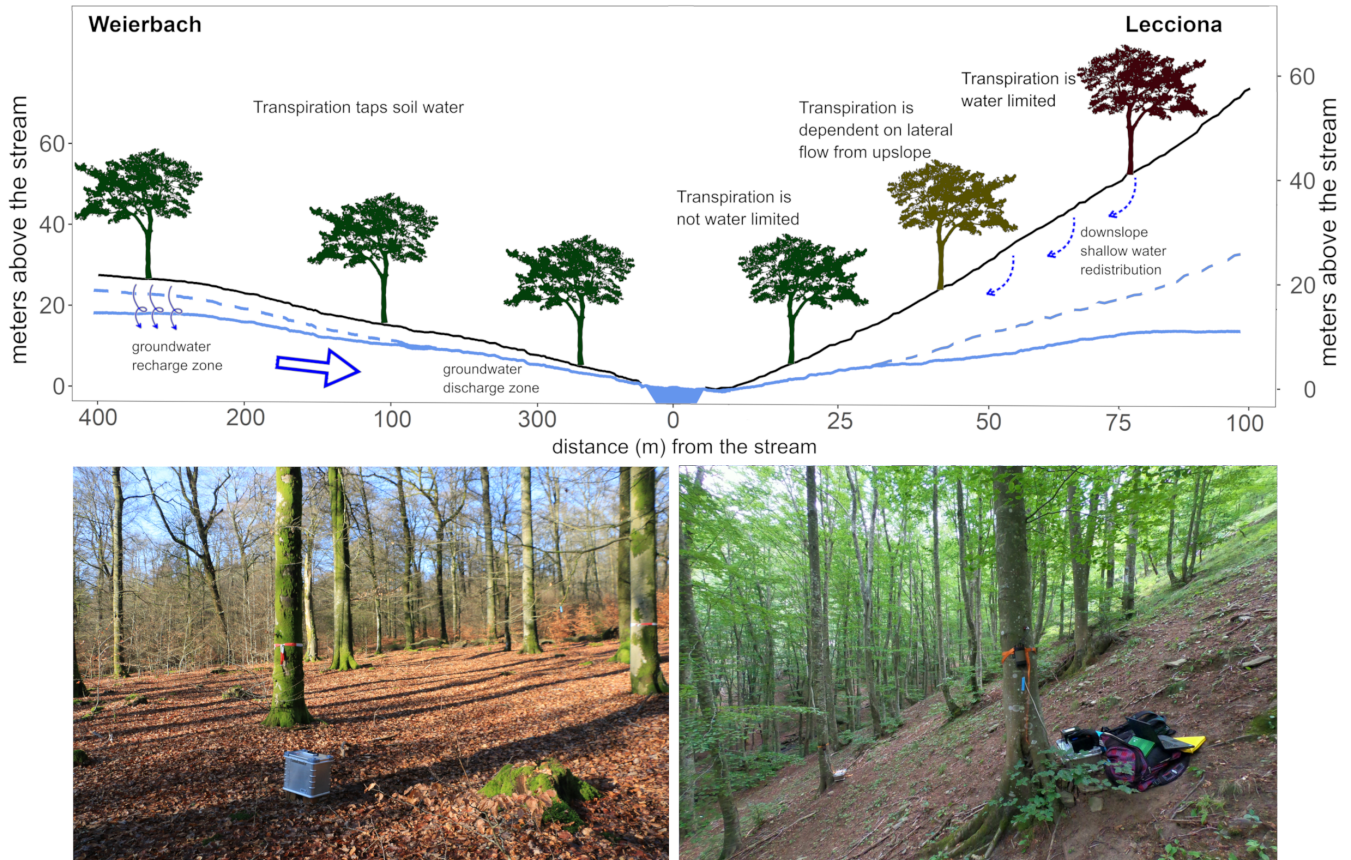
Figure 9. Conceptual graph showing the individual monitoring locations at each catchment and the ecohydrological processes taking place. Photos of the hillslopes are also shown for each study site from the plateau and hilltop positions. The terrain profiles were extracted from the digital terrain model (DEM grid size 5 and 10 m in the Weierbach and the Lecciona catchment, respectively). In the Weierbach catchment, the homogeneous edaphic conditions lead to a lack of statistical difference in transpiration across the landscape. On the contrary, in the Lecciona catchment, the subsurface structure combined with the steep slope creates a gradient of water stress (represented as a coulor gradient in the trees).

5   Conclusions

~~So far, there has been a lack of consistent studies on how hillslope position controls tree water use.~~ So far, no study has explored the influence of topography on tree water use within the same species growing in diverse climatic settings. In the present study, we found that surface topography and hillslope structure results in varying sap velocity responses to environmental controls (VPD and REW), but not consistently across landscapes (Fig. 9) as initially hypothesised. In the Weierbach catchment, the homogeneous growing conditions across the slope and the vertical connectivity of the subsurface structure result in uniform physiological responses to environmental controls among trees, even during the drier conditions of 2020 compared to 2019. Contrary, in the Lecciona catchment we observed a stronger edaphic and environmental gradient across the hillslope topography, where upslope locations become water limited by the interplay of multiple factors. In the Lecciona catchment, water redistribution downslope through shallow subsurface flow results in a longer growing season for trees located at the footslope, where growing conditions are more favourable. These contrasting results in the two investigated slopes suggest that in landscapes where the hydraulic and climatic gradients are stronger, the physiological response of the same forest species among locations may ~~will~~ be more spatially variable. Contrary to what was initially hypothesised, the physiological activity of beech trees was not constrained when compared to the central European population in the Weierbach catchment likely due to the plasticity of this species. Therefore, the present work contributes to emphasising that different environmental conditions drive different physiological responses in space and time within the same species. Future work carrying out a cross-site comparison may take into account the effect of genotypic variability, which may lead to differing physiological responses for similar environmental conditions. Having information on the drought resistance traits across a species distribution range will be crucial to assess species ~~performance~~ responses in face of the current climate change ~~crisis~~.

Table A1. Data gaps filled. Color corresponds to the color code of Fig. S2.

Sensor	Color	Gap filled	R^2	p-value
Hilltop 3	pink	2021-04-21 – 2021-05-13	0.93	<0.01
Midslope 2	blue	2021-05-15 – 2021-06-10	0.88	<0.01
Midslope 3	pink	2021-06-14 – 2021-06-22, 2021-09-21 – 2021-10-03	0.92	<0.01
Midslope 1	black	2021-04-15 – 2021-04-22, 2021-05-29 – 2021-06-10	0.92	<0.01
Footslope 3	pink	2021-04-15 – 2020-04-29, 2021-06-11 – 2021-07-20, 2021-09-22 – 2021-10-04	0.93	<0.01
Footslope 2	blue	2021-05-15 – 2021-05-28	0.93	<0.01
Footslope 1	black	2021-05-15 – 2021-05-27	0.96	<0.01

Table A2. Number of total samples collected at each site.

Site	Xylem samples	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm
Weierbach	157	95	95	95	95	95
Lecciona	96	27	27	27	27	27
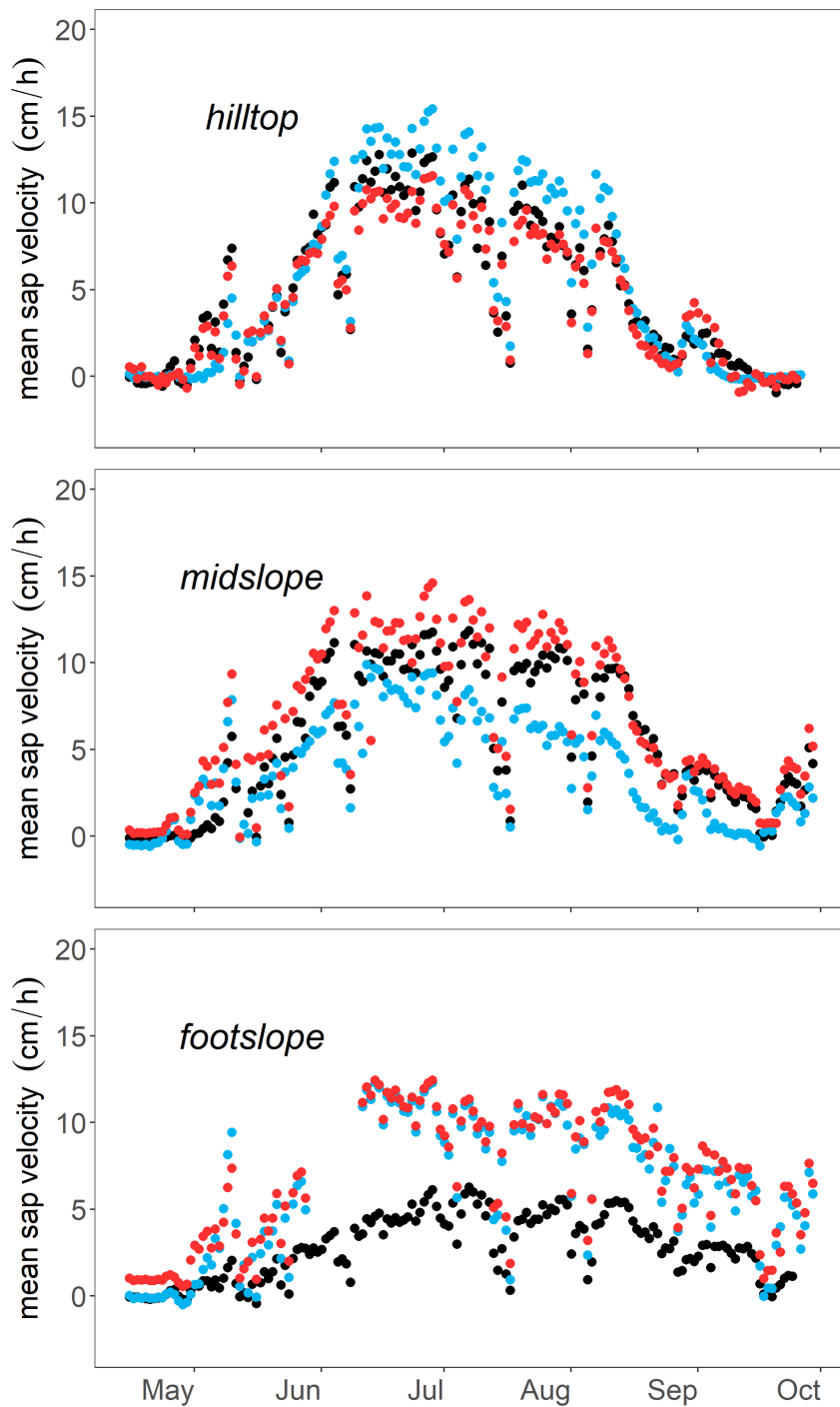
Figure A1. Sap velocity (cm h⁻¹) of beech at three sampling areas (hilltop, midslope, footslope) in the Lecciona catchment; each colour corresponds to one equipped tree. Missing data are the result of power interruption. When possible, data gaps were filled by interpolation, details are reported in Table A1.

Figure A2. Summary of significant predictors explaining the variability in sap velocity for the Weierbach and the Lecciona catchment. Significancy of the predictors has been evaluated with linear mixing model analysis. Fixed effects used in the model include topographic location (hilltop/plateau, midslope, footslope), relative extractable water (REW), radiation (W/m^2), and vapour pressure deficit (VPD). + and - signs correspond to a significant increase or decrease, respectively, of sap velocity following the increase of the predictor.
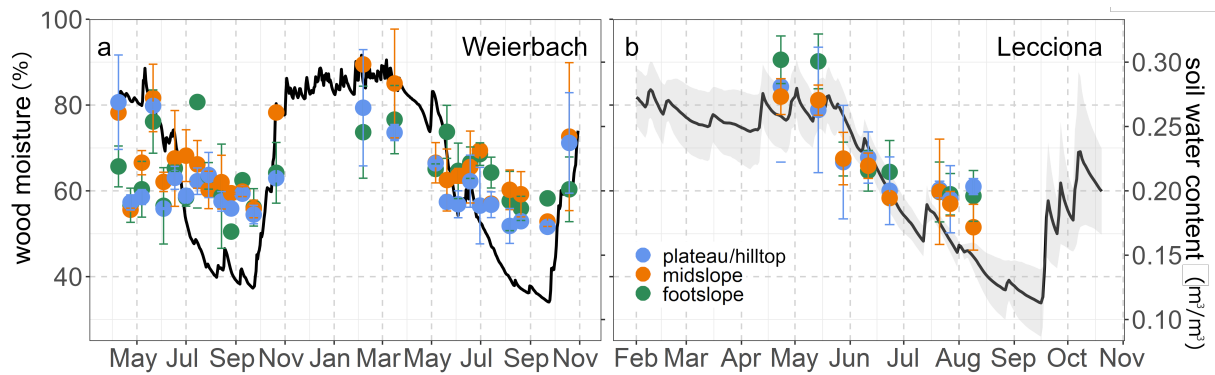
Figure A3. Temporal pattern of wood moisture content (%) and volumetric soil moisture content in the Weierbach catchment (a) and in the Lecciona catchment (b). Solid dots represent the mean, the whiskers indicate the confidence interval (95%) ~~each color corresponds to sampling locations (blue= plateau, orange= midslope, green= footslope, red= riparian)~~. In the Weierbach catchment we used the average soil moisture content over the four depths, while in the Lecciona catchment, we used the average soil moisture over the three monitored locations ~~the two monitored depths recorded at each location~~.
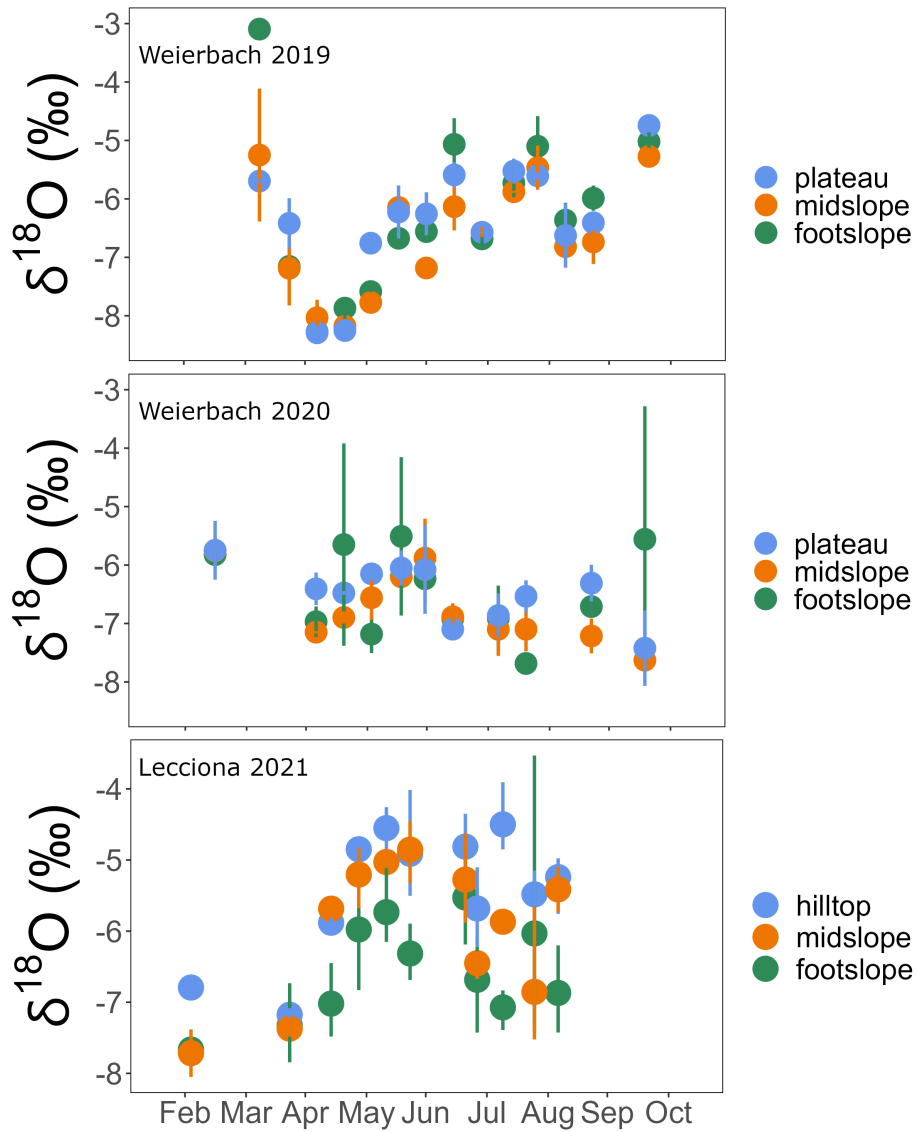
Figure A4. δ^{18}O of xylem water for each sampling campaign across 2019 and 2020 growing season in the Weierbach catchment and 2021 in the Lecciona catchment. Data were averaged by location. Solid dots represent the mean, the whiskers indicate the confidence interval (95%).
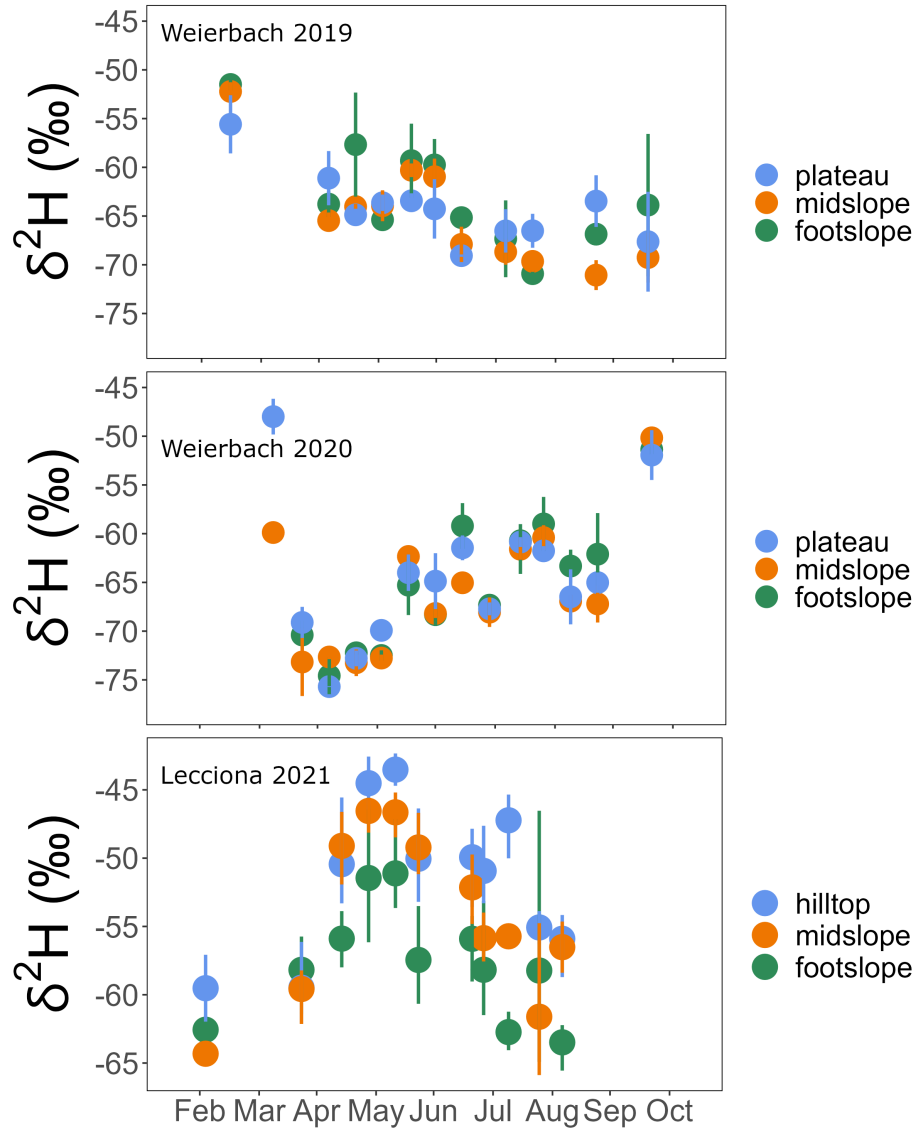
Figure A5. δ^2H of xylem water for each sampling campaign across 2019 and 2020 growing season in the Weierbach catchment and 2021 in the Lecciona catchment. Data were averaged by location. Solid dots represent the mean, the whiskers indicate the confidence interval (95%).

Data availability. The data that support the findings of this study are available for the Lecciona catchment (Fabiani et al., 2023b) and the Weierbach catchment (Fabiani et al., 2023a) in Zenodo repositories.

Author contributions. Ginevra Fabiani: conceptualisation, funding acquisition, investigation, formal analysis, visualisation and writing–original draft. Julian Klaus: conceptualisation, funding acquisition, supervision, validation, writing–review and editing and project administration.
460 Daniele Penna: conceptualisation, funding acquisition, supervision and writing–review and editing.

Competing interests. 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.

Acknowledgements. This work was supported by the Luxembourg National Research Fund (AFR/STEP-UP ID 12546983), the Italian Minister for University and Research (WATZON-grant 2017SL7ABC, WATERSTEM-grant 20202WF53Z), and the National Research Council
465 - CNR (Carbon and water cycles interactions during drought and their impact on WAter and ForEst Resources in the Mediterranean region -WAFER). We thank Enrico Bonanno, Adnan Moussa, Remy Schoppach, Jean Francois Iffly, Laurent Gourdol, Cyrille Tailliez, Matteo Verdone, Francesca Sofia Manca di Villahermosa, Andrea Dani, Ilaria Zorzi for their help during the field work and fruitful discussion. We express our sincere gratitude to Richard Keim, Ilja van Meerveld, Claudia Cocozza, Adrià Barbeta, and Laurent Pfister for their invaluable insights on this manuscript, which enhanced the quality of this work.

References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-h., Allard, G., Running, S. W., Semerci, A., and Cobb, N.: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, Forest Ecology and Management, 259, 660–684, https://doi.org/10.1016/j.foreco.2009.09.001, 2010.

Barbeta, A., Jones, S. P., Clavé, L., Wingate, L., Gimeno, T. E., Fréjaville, B., Wohl, S., and Ogée, J.: 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, 2019.

Barrett, D. J., Hatton, T. J., Ash, J. E., and Ball, M. C.: 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, 1995.

Bates, D., Mächler, M., Bolker, B., and Walker, S.: Fitting Linear Mixed-Effects Models Using lme4, Journal of Statistical Software, 67, https://doi.org/10.18637/jss.v067.i01, 2015.

Betsch, P., Bonal, D., Breda, N., Montpied, P., Peiffer, M., Tuzet, A., and Granier, A.: Drought effects on water relations in beech: The contribution of exchangeable water reservoirs, Agricultural and Forest Meteorology, 151, 531–543, https://doi.org/10.1016/j.agrformet.2010.12.008, 2011.

Bosch, D. D., Marshall, L. K., and Teskey, R.: Forest transpiration from sap flux density measurements in a Southeastern Coastal Plain riparian buffer system, Agricultural and Forest Meteorology, 187, 72–82, https://doi.org/10.1016/j.agrformet.2013.12.002, 2014.

Bréda, N. and Granier, A.: 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, 1996.

Bréda, N., Huc, R., Granier, A., and Dreyer, E.: Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences, Annals of Forest Science, 63, 625–644, https://doi.org/10.1051/forest:2006042, 2006.

Cavin, L. and Jump, A. S.: Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree Fagus sylvatica L. not the equatorial range edge, Global Change Biology, 23, 362–379, https://doi.org/10.1111/gcb.13366, 2017.

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global convergence in the vulnerability of forests to drought, Nature, 491, 752–755, https://doi.org/10.1038/nature11688, 2012.

Coners, H. and Leuschner, C.: 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, 2005.

de la Casa, J., Barbeta, A., Rodríguez-Uña, A., Wingate, L., Ogée, J., and Gimeno, T. E.: Isotopic offsets between bulk plant water and its sources are larger in cool and wet environments, Hydrology and Earth System Sciences, 26, 4125–4146, https://doi.org/10.5194/hess-26-4125-2022, 2022.

Dietrich, L., Zweifel, R., and Kahmen, A.: Daily stem diameter variations can predict the canopy water status of mature temperate trees, Tree Physiology, 38, 941–952, https://doi.org/10.1093/treephys/tpy023, 2018.

Dobrowski, S. Z.: A climatic basis for microrefugia: The influence of terrain on climate, Global Change Biology, 17, 1022–1035, https://doi.org/10.1111/j.1365-2486.2010.02263.x, 2011.

Elliott, K. J., Miniat, C. F., Pederson, N., and Laseter, S. H.: Forest tree growth response to hydroclimate variability in the southern Appalachians, Global Change Biology, 21, 4627–4641, https://doi.org/10.1111/gcb.13045, 2015.

510   Fabiani, G., Penna, D., Barbeta, A., and Klaus, J.: Sapwood and heartwood are not isolated compartments: Consequences for isotope ecohydrology, Ecohydrology, pp. 0–2, https://doi.org/10.1002/eco.2478, 2022a.

Fabiani, G., Schoppach, R., Penna, D., and Klaus, J.: Transpiration patterns and water use strategies of beech and oak trees along a hillslope, Ecohydrology, 15, 1–18, https://doi.org/10.1002/eco.2382, 2022b.

Fabiani, G., Schoppach, R., Moussa, A., Pfister, L., Penna, D., and Klaus, J.: STEP UP project: the Weierbach dataset 2019-2020,
515   https://doi.org/10.5281/ZENODO.8326112, 2023a.

Fabiani, G., Verdone, M., Manca di Villahermosa, F. S., Pfister, L., Klaus, J., and Penna, D.: STEP UP project: the Lecciona dataset 2021, https://doi.org/10.5281/ZENODO.8328006, 2023b.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., and Otero-Casal, C.: Hydrologic regulation of plant rooting depth, Proceedings of the National Academy of Sciences of the United States of America, 114, 10 572–10 577, https://doi.org/10.1073/pnas.1712381114,
520   2017.

Gessler, A.: Water transport in trees—the importance of radial and circumferential transport, Tree Physiology, pp. 1–3, https://doi.org/10.1093/treephys/tpab131, 2021.

Gessler, A., Bächli, L., Rouholahnejad Freund, E., Treydte, K., Schaub, M., Haeni, M., Weiler, M., Seeger, S., Marshall, J., Hug, C., Zweifel, R., Hagedorn, F., Rigling, A., Saurer, M., and Meusburger, K.: Drought reduces water uptake in beech from the drying topsoil, but no
525   compensatory uptake occurs from deeper soil layers, New Phytologist, 233, 194–206, https://doi.org/10.1111/nph.17767, 2022.

Gimenez, B. O., Jardine, K. J., Higuchi, N., Negrón-Juárez, R. I., Sampaio-Filho, I. d. J., Cobello, L. O., Fontes, C. G., Dawson, T. E., Varadharajan, C., Christianson, D. S., Spanner, G. C., Araújo, A. C., Warren, J. M., Newman, B. D., Holm, J. A., Koven, C. D., McDowell, N. G., and Chambers, J. Q.: Species-specific shifts in diurnal sap velocity dynamics and hysteretic behavior of ecophysiological variables during the 2015–2016 el niño event in the amazon forest, Frontiers in Plant Science, 10, 1–16, https://doi.org/10.3389/fpls.2019.00830,
530   2019.

Giménez, C., Gallardo, M., and Thompson, R.: Plant–Water Relations, in: Reference Module in Earth Systems and Environmental Sciences, May, pp. 1–8, Elsevier, https://doi.org/10.1016/B978-0-12-409548-9.05257-X, 2013.

Glaser, B., Klaus, J., Frei, S., Frentress, J., Pfister, L., and Hopp, L.: 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,
535   https://doi.org/10.1002/2015WR018414, 2016.

Gourdol, L., Clément, R., Juilleret, J., Pfister, L., and Hissler, C.: 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, 2021.

Gralher, B., Herbstritt, B., and Weiler, M.: Technical note: Unresolved aspects of the direct vapor equilibration method for stable isotope
540   analysis (δ18O, δ2H) of matrix-bound water: Unifying protocols through empirical and mathematical scrutiny, Hydrology and Earth System Sciences, 25, 5219–5235, https://doi.org/10.5194/hess-25-5219-2021, 2021.

Granier, A., Bréda, N., Biron, P., and Villette, S.: A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands, Ecological Modelling, 116, 269–283, https://doi.org/10.1016/S0304-3800(98)00205-1, 1999.

Granier, A., Reichstein, M., Bréda, N., Janssens, I. A., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buch-
mann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Köstner, B., Lagergren, F., Lindroth, A., Long-
doz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J.,
Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., and Wang, Q.: Evidence for soil water control on car-
bon and water dynamics in European forests during the extremely dry year: 2003, Agricultural and Forest Meteorology, 143, 123–145,
https://doi.org/10.1016/j.agrformet.2006.12.004, 2007.

Green, S., Clothier, B., and Jardine, B.: Theory and Practical Application of Heat Pulse to Measure Sap Flow, Agronomy Journal, 95,
1371–1379, https://doi.org/10.2134/agronj2003.1371, 2003.

Grossiord, C., Sevanto, S., Borrego, I., Chan, A. M., Collins, A. D., Dickman, L. T., Hudson, P. J., McBranch, N., Michaletz, S. T., Pockman,
W. T., Ryan, M., Vilagrosa, A., and McDowell, N. G.: Tree water dynamics in a drying and warming world, Plant Cell and Environment,
40, 1861–1873, https://doi.org/10.1111/pce.12991, 2017a.

Grossiord, C., Sevanto, S., Dawson, T. E., Adams, H. D., Collins, A. D., Dickman, L. T., Newman, B. D., Stockton, E. A., and McDowell,
N. G.: Warming combined with more extreme precipitation regimes modifies the water sources used by trees, New Phytologist, 213,
584–596, https://doi.org/10.1111/nph.14192, 2017b.

Gutierrez Lopez, J., Tor-ngern, P., Oren, R., Kozii, N., Laudon, H., and Hasselquist, N. J.: How tree species, tree size, and topographical
location influenced tree transpiration in northern boreal forests during the historic 2018 drought, Global Change Biology, 27, 3066–3078,
https://doi.org/10.1111/gcb.15601, 2021.

Hahm, W. J., Dietrich, W. E., and Dawson, T. E.: Controls on the distribution and resilience of Quercus garryana: ecophysiological evidence
of oak's water-limitation tolerance, Ecosphere, 9, https://doi.org/10.1002/ecs2.2218, 2018.

Hawthorne, S. and Miniat, C. F.: Topography may mitigate drought effects on vegetation along a hillslope gradient, Ecohydrology, 11, e1825,
https://doi.org/10.1002/eco.1825, 2018.

Hissler, C., Martínez-Carreras, N., Barnich, F., Gourdol, L., Iffly, J. F., Juilleret, J., Klaus, J., and Pfister, L.: 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, 2021.

Hochberg, U., Rockwell, F. E., Holbrook, N. M., and Cochard, H.: Iso/Anisohydry: A Plant–Environment Interaction Rather Than a Simple
Hydraulic Trait, Trends in Plant Science, 23, 112–120, https://doi.org/10.1016/j.tplants.2017.11.002, 2018.

Hogg, E. H., Brandt, J. P., and Michaelian, M.: Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian
aspen forests, Canadian Journal of Forest Research, 38, 1373–1384, https://doi.org/10.1139/X08-001, 2008.

Hoylman, Z. H., Jencso, K. G., Hu, J., Martin, J. T., Holden, Z. A., Seielstad, C. A., and Rowell, E. M.: Hillslope Topography
Mediates Spatial Patterns of Ecosystem Sensitivity to Climate, Journal of Geophysical Research: Biogeosciences, 123, 353–371,
https://doi.org/10.1002/2017JG004108, 2018.

Jencso, K. G., McGlynn, B. L., Gooseff, M. N., Wondzell, S. M., Bencala, K. E., and Marshall, L. A.: Hydrologic connectivity between
landscapes and streams: Transferring reach- and plot-scale understanding to the catchment scale, Water Resources Research, 45, 1–16,
https://doi.org/10.1029/2008WR007225, 2009.

Kannenberg, S. A., Guo, J. S., Novick, K. A., Anderegg, W. R., Feng, X., Kennedy, D., Konings, A. G., Martínez-Vilalta, J., and
Matheny, A. M.: Opportunities, challenges and pitfalls in characterizing plant water-use strategies, Functional Ecology, 36, 24–37,
https://doi.org/10.1111/1365-2435.13945, 2022.

Klaus, J. and Jackson, C. R.: 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, 2018.

Klaus, J., Chun, K. P., and Stumpp, C.: Temporal trends in $\delta 18O$ composition of precipitation in Germany: Insights from time series modelling and trend analysis, Hydrological Processes, 29, 2668–2680, https://doi.org/10.1002/hyp.10395, 2015.

Klaus, J., Monk, W. A., Zhang, L., and Hannah, D. M.: Ecohydrological interactions during drought, Ecohydrology, 15, 1–7, https://doi.org/10.1002/eco.2456, 2022.

Köcher, P., Horna, V., and Leuschner, C.: Stem water storage in five coexisting temperate broad-leaved tree species: Significance, temporal dynamics and dependence on tree functional traits, Tree Physiology, 33, 817–832, https://doi.org/10.1093/treephys/tpt055, 2013.

Kreuzwieser, J. and Rennenberg, H.: Molecular and physiological responses of trees to waterlogging stress, Plant, Cell & Environment, pp. n/a–n/a, https://doi.org/10.1111/pce.12310, 2014.

Kumagai, T., Tateishi, M., Shimizu, T., and Otsuki, K.: 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, 2008.

Li, K. and Knighton, J.: Characterizing the heterogeneity of eastern hemlock xylem water isotopic compositions: Implications for the design of plant water uptake studies, Ecohydrology, pp. 1–12, https://doi.org/10.1002/eco.2571, 2023.

Magh, R.-k., Eiferle, C., Burzlaff, T., and Dannenmann, M.: Competition for water rather than facilitation in mixed beech-fir forests after drying-wetting cycle, Journal of Hydrology, 587, 124 944, https://doi.org/10.1016/j.jhydrol.2020.124944, 2020.

Martínez-Vilalta, J. and Garcia-Forner, N.: Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept, Plant Cell and Environment, 40, 962–976, https://doi.org/10.1111/pce.12846, 2017.

Martínez-Vilalta, J., Poyatos, R., Aguadé, D., Retana, J., and Mencuccini, M.: A new look at water transport regulation in plants, New Phytologist, 204, 105–115, https://doi.org/10.1111/nph.12912, 2014.

Matheny, A. M., Garrity, S. R., and Bohrer, G.: The calibration and use of capacitance sensors to monitor stem water content in trees, Journal of Visualized Experiments, 2017, 1–10, https://doi.org/10.3791/57062, 2017.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., and Yepez, E. A.: Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?, New Phytologist, 178, 719–739, https://doi.org/10.1111/j.1469-8137.2008.02436.x, 2008.

Meier, I. C. and Leuschner, C.: Belowground drought response of European beech: Fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient, Global Change Biology, 14, 2081–2095, https://doi.org/10.1111/j.1365-2486.2008.01634.x, 2008.

Méndez-Toribio, M., Ibarra-Manríquez, G., Navarrete-Segueda, A., and Paz, H.: Topographic position, but not slope aspect, drives the dominance of functional strategies of tropical dry forest trees, Environmental Research Letters, 12, https://doi.org/10.1088/1748-9326/aa717b, 2017.

Meusburger, K., Trotsiuk, V., Schmidt-Walter, P., Baltensweiler, A., Brun, P., Bernhard, F., Gharun, M., Habel, R., Hagedorn, F., Köchli, R., Psomas, A., Puhlmann, H., Thimonier, A., Waldner, P., Zimmermann, S., and Walthert, L.: Soil-plant interactions modulated water availability of Swiss forests during the 2015 and 2018 droughts, Global Change Biology, pp. 0–3, https://doi.org/10.1111/gcb.16332, 2022.

Murphy, P. C., Knowles, J. F., Moore, D. J., Anchukaitis, K., Potts, D. L., and Barron-Gafford, G. A.: Topography influences species-specific patterns of seasonal primary productivity in a semiarid montane forest, Tree Physiology, 40, 1343–1354, https://doi.org/10.1093/TREEPHYS/TPAA083, 2020.

Oberhuber, W. and Kofler, W.: Topographic influences on radial growth of Scots pine (Pinus sylvestris L.) at small spatial scales, Plant Ecology, 146, 231–240, 2000.

Obladen, N., Dechering, P., Skiadaresis, G., Tegel, W., Keßler, J., Höllerl, S., Kaps, S., Hertel, M., Dulamsuren, C., Seifert, T., Hirsch, M., and Seim, A.: Tree mortality of European beech and Norway spruce induced by 2018-2019 hot droughts in central Germany, Agricultural and Forest Meteorology, 307, 108 482, https://doi.org/10.1016/j.agrformet.2021.108482, 2021.

Orlowski, N., Breuer, L., and Mcdonnell, J. J.: Critical issues with cryogenic extraction of soil water for stable isotope analysis, Ecohydrology, 9, 3–10, https://doi.org/10.1002/eco.1722, 2016.

Peck, E. C.: The sap of moisture in wood, 1953.

Penna, D., Borga, M., Norbiato, D., and Dalla Fontana, G.: 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, 2009.

Penna, D., Stenni, B., S˚anda, M., Wrede, S., Bogaard, T. A., Michelini, M., Fischer, B. M., Gobbi, A., Mantese, N., Zuecco, G., Borga, M., Bonazza, M., Sobotková, M., Čejková, B., and Wassenaar, L. I.: Technical note: Evaluation of between-sample memory effects in the analysis of δ2H and δ18O of water samples measured by laser spectroscopes, Hydrology and Earth System Sciences, 16, 3925–3933, https://doi.org/10.5194/hess-16-3925-2012, 2012.

Pfister, L., Bonanno, E., Fabiani, G., Gourdol, L., Hissler, C., Huck, V., Iffly, J. F., Keim, R., Martínez-Carreras, N., Mestdagh, X., Montemagno, A., Penna, D., Schymanski, S., and Zehe, E.: Fast motion view of a headwater creek—A hydrological year seen through time-lapse photography, Hydrological Processes, 37, 1–10, https://doi.org/10.1002/hyp.15026, 2023.

Phillips, R. P., Ibáñez, I., Orangeville, L. D., Hanson, P. J., Ryan, M. G., and Mcdowell, N. G.: Forest Ecology and Management A belowground perspective on the drought sensitivity of forests : Towards improved understanding and simulation q, Forest Ecology and Management, 380, 309–320, https://doi.org/10.1016/j.foreco.2016.08.043, 2016.

Poca, M., Coomans, O., Urcelay, C., Zeballos, S. R., Bodé, S., and Boeckx, P.: 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, 2019.

Renner, M., Hassler, S. K., Blume, T., Weiler, M., Hildebrandt, A., Guderle, M., Schymanski, S. J., and Kleidon, A.: 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, 2016.

Rodriguez, N. B. and Klaus, J.: 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, 2019.

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G. W., Stegehuis, A. I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B. J. W., Lindner, M., Martinez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bär, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiller, D., Blaženec, M., Čada, V., Carraro, V., Cecchini, S., Chan, T., Conedera, M., Delpierre, N., Delzon, S., Ditmarová, , Dolezal, J., Dufrêne, E., Edvardsson, J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Güney, A., Heinrich, I., Hentschel, R., Janda, P., Ježík, M., Kahle, H.-P., Knüsel, S., Krejza, J., Kuberski, , Kučera, J., Lebourgeois, F., Mikoláš, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbel, I., Rathgeber, C. B. K., Salmon, Y., Saunders, M., Scharnweber, T., Sitková, Z., Stangler, D. F., Stereńczak, K., Stojanović, M., Střelcová, K., Světlík, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavrčík, H., Vejpustková, M., Walthert, L., Wilmking, M., Zin, E., Zou, J., and Steppe, K.: The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests, Nature Communications, 13, 28, https://doi.org/10.1038/s41467-021-27579-9, 2022a.

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G. W., Stegehuis, A. I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B. J. W., Lindner, M., Martinez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bär, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiller, D., Blaženec, M., Čada, V., Carraro, V., Cecchini, S., Chan,

T., Conedera, M., Delpierre, N., Delzon, S., Ditmarová, , Dolezal, J., Dufrêne, E., Edvardsson, J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Güney, A., Heinrich, I., Hentschel, R., Janda, P., Ježík, M., Kahle, H.-P., Knüsel, S., Krejza, J., Kuberski, , Kučera, J., Lebourgeois, F., Mikoláš, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbel, I., Rathgeber, C. B. K., Salmon, Y., Saunders, M., Scharnweber, T., Sitková, Z., Stangler, D. F., Stereńczak, K., Stojanović, M., Střelcová, K., Světlík, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavrčík, H., Vejpustková, M., Walthert, L., Wilmking, M., Zin, E., Zou, J., and Steppe, K.: The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests, Nature Communications, 13, 28, https://doi.org/10.1038/s41467-021-27579-9, 2022b.

Schoppach, R., Chun, K., He, Q., Fabiani, G., and Klaus, J.: Species-specific control of DBH and landscape characteristics on tree-to-tree variability of sap velocity, Agricultural and Forest Meteorology, 307, 108 533, https://doi.org/10.1016/j.agrformet.2021.108533, 2021.

Schreel, J. D. M., Steppe, K., Roddy, A. B., and Poca, M.: Does back-flow of leaf water introduce a discrepancy in plant water source tracing through stable isotopes ?, Hydrology and Earth System Sciences, pp. 1–20, https://doi.org/doi.org/10.5194/hess-2023-13, 2023.

Schwantes, A. M., Parolari, A. J., Swenson, J. J., Johnson, D. M., Domec, J. C., Jackson, R. B., Pelak, N., and Porporato, A.: Accounting for landscape heterogeneity improves spatial predictions of tree vulnerability to drought, New Phytologist, 220, 132–146, https://doi.org/10.1111/nph.15274, 2018.

Smith, D. and Allen, S.: Measurement of sap flow in plant stems, Journal of Experimental Botany, 47, 1833–1844, https://doi.org/10.1093/jxb/47.12.1833, 1996.

Song, L., Zhu, J., Li, X., Wang, K., Wang, G., and Sun, H.: Transpiration of Pinus sylvestris var. mongolica trees at different positions of sand dunes in a semiarid sandy region of Northeast China, Trees - Structure and Function, 36, 749–762, https://doi.org/10.1007/s00468-021-02247-z, 2022.

Steppe, K., De Pauw, D. J., Doody, T. M., and Teskey, R. O.: A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods, Agricultural and Forest Meteorology, 150, 1046–1056, https://doi.org/10.1016/j.agrformet.2010.04.004, 2010.

Stojnić, S., Suchocka, M., Benito-Garzón, M., Torres-Ruiz, J. M., Cochard, H., Bolte, A., Cocozza, C., Cvjetković, B., De Luis, M., Martinez-Vilalta, J., Ræbild, A., Tognetti, R., and Delzon, S.: Variation in xylem vulnerability to embolism in European beech from geographically marginal populations, Tree Physiology, 38, 173–185, https://doi.org/10.1093/treephys/tpx128, 2018.

Tai, X., Mackay, D. S., Anderegg, W. R. L., Sperry, J. S., and Brooks, P. D.: Plant hydraulics improves and topography mediates prediction of aspen mortality in southwestern <scp>USA</scp>, New Phytologist, 213, 113–127, https://doi.org/10.1111/nph.14098, 2017.

Thorburn, P. J., Hatton, T. J., and Walker, G. R.: Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests, Journal of Hydrology, 150, 563–587, https://doi.org/10.1016/0022-1694(93)90126-T, 1993.

Tijdeman, E., Blauhut, V., Stoelzle, M., Menzel, L., and Stahl, K.: Different drought types and the spatial variability in their hazard, impact, and propagation characteristics, Natural Hazards and Earth System Sciences, 22, 2099–2116, https://doi.org/10.5194/nhess-22-2099-2022, 2022.

Tromp-van Meerveld, H. J. and McDonnell, J. J.: 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, 2006.

Tyree, M. and Zimmermann, M. H.: Springer Series in Wood Science: Wood structure and enviroment, 2002.

Tyree, M. T. and Yang, S.: Water-storage capacity of Thuja, Tsuga and Acer stems measured by dehydration isotherms - The contribution of capillary water and cavitation, Planta, 182, 420–426, https://doi.org/10.1007/BF02411394, 1990.

Volkmann, T. H., Kühnhammer, K., Herbstritt, B., Gessler, A., and Weiler, M.: A method for in situ monitoring of the isotope composition of tree xylem water using laser spectroscopy, Plant Cell and Environment, 39, 2055–2063, https://doi.org/10.1111/pce.12725, 2016.

Walthert, L., Ganthaler, A., Mayr, S., Saurer, M., Waldner, P., Walser, M., Zweifel, R., and von Arx, G.: From the comfort zone to crown dieback: Sequence of physiological stress thresholds in mature European beech trees across progressive drought, Science of The Total Environment, 753, 141 792, https://doi.org/10.1016/j.scitotenv.2020.141792, 2021.

Wassenaar, L., Hendry, M., Chostner, V., and Lis, G.: High Resolution Pore Water δ 2 H and δ 18 O Measurements by H 2 O (liquid) -H 2 O (vapor) Equilibrium Laser Spectroscopy, Environmental Science & Technology, 42, 9262–9267, https://doi.org/10.1021/es802065s, 2008.

Weemstra, M., Eilmann, B., Sass-Klaassen, U. G., and Sterck, F. J.: Summer droughts limit tree growth across 10 temperate species on a productive forest site, Forest Ecology and Management, 306, 142–149, https://doi.org/10.1016/j.foreco.2013.06.007, 2013.

Western, A. W., Grayson, R. B., Blöschl, G., Willgoose, G. R., and McMahon, T. A.: Observed spatial organization of soil moisture and its relation to terrain indices, Water Resources Research, 35, 797–810, https://doi.org/10.1029/1998WR900065, 1999.

Xiao, D., Brantley, S. L., and Li, L.: Vertical Connectivity Regulates Water Transit Time and Chemical Weathering at the Hillslope Scale, Water Resources Research, 57, 1–21, https://doi.org/10.1029/2020WR029207, 2021.

Zimmermann, J., Link, R. M., Hauck, M., Leuschner, C., and Schuldt, B.: 60-year record of stem xylem anatomy and related hydraulic modification under increased summer drought in ring- and diffuse-porous temperate broad-leaved tree species, Trees, 35, 919–937, https://doi.org/10.1007/s00468-021-02090-2, 2021.