Contrasting water use strategies of beech trees along two hillslopes with different slope and climate

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Abstract. Understanding the interaction 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

5   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

10   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

15   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 performances.

1   Introduction

The ongoing climate crisis is strongly affecting forest ecosystems by exacerbating the environmental extremes, such as droughts

20   and heatwaves (Allen et al., 2010; Choat et al., 2012). The increasing atmospheric evaporative demand and reduced water availability in soils expose trees to water deficit risk (Salomón et al., 2022) impairing tree functioning (Giménez et al., 2013). The severity of water limitation is variable in space, time, and among domains of the hydrological cycle (Klaus et al., 2022; Tijdeman et al., 2022), and is expected to affect tree species performance not only at the limits but also at the centre of their distribution range (Parmesan, 2006), where trees are assumed to benefit from the most suited growing conditions. Multiple

25 studies that investigated the effect of water limitations on forest vulnerability have neglected landscape heterogeneity at fine

spatial resolutions, even though soil properties and topography are important abiotic factors for forest health (Schwantes et al., 2018). The interaction 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 (Dunne et al., 1975; Jencso et al., 2009; Xiao et al., 2021) resulting in different water availabilities in the subsurface,

30 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 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

35 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 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

40 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 to a gradient of water stress in the vegetation increasing from the lower to the higher parts of the hillslope catena. 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

45 appear to strongly influence sap flow 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). European beech (*Fagus sylvatica* L.) is among those species that do not grow roots

50 in the saturated zone, and this species mainly relies on water stored in the topsoil (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 forest droughts in 2003, 2015, and 2018 (Cavin and Jump, 2017; Obladen et al., 2021; Salomón et al., 2022; Walthert et al., 2021) and is expected to face high mortality rates with the future predicted

55 heatwaves. 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). 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

60   increase in 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 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 dryness. This can support the development of management practices suited for locations at risk. Through

65   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

70   measures with environmental monitoring to capture beech trees' water response to environmental variables along hillslope

transects. We hypothesize that (i) the physiological response of beech trees varies as a function of topography-driven changes

in water availability, (ii) in the Mediterranean site, 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

75   tree sensitivity to water limitation?

2   Materials and methods

2.1   Study sites

The Weierbach catchment: study area and environmental monitoring

The experiment was carried out during two consecutive growing seasons (March-October 2019 and 2020) at a transect along

80   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). The site has been described in detail by Fabiani et al. (2022b) and only the key details are reported here (Table 1). The

hillslope transect is 380 m long and spans from the stream bank to a plateau area with an average slope of 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,

85   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 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

90   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

Lecciona (Fig. 1) is a subcatchment (31 ha) of the Re della Pietra experimental catchment (2 km^2) 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

95 30° (Table 1). The hillslope is covered by a pure stand of beech trees with space 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, 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), as recorded at

100 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 in sandy

105 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

110 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.

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

115 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

120 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. (2022), we chose the 95th percentile, and not the maximum value, to exclude
heavy rain events that may result in soil saturation. REW is generally quantified to characterize soil drought intensity (Bréda
et al., 2006; Grossiord et al., 2017b).

125   For each study site, we computed the daily mean vapour pressure deficit (VPD), 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).

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

2.3 Measurement of sap velocity

    At each site we defined three monitoring locations corresponding to different topographic positions: plateau, midslope, and

130   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 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). The sensors

135   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 at the north-east side of the trunk at 1.3 m height. In the Lecciona catchment, the sensors were installed on the west side to avoid installing in tension wood, which is 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

140   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
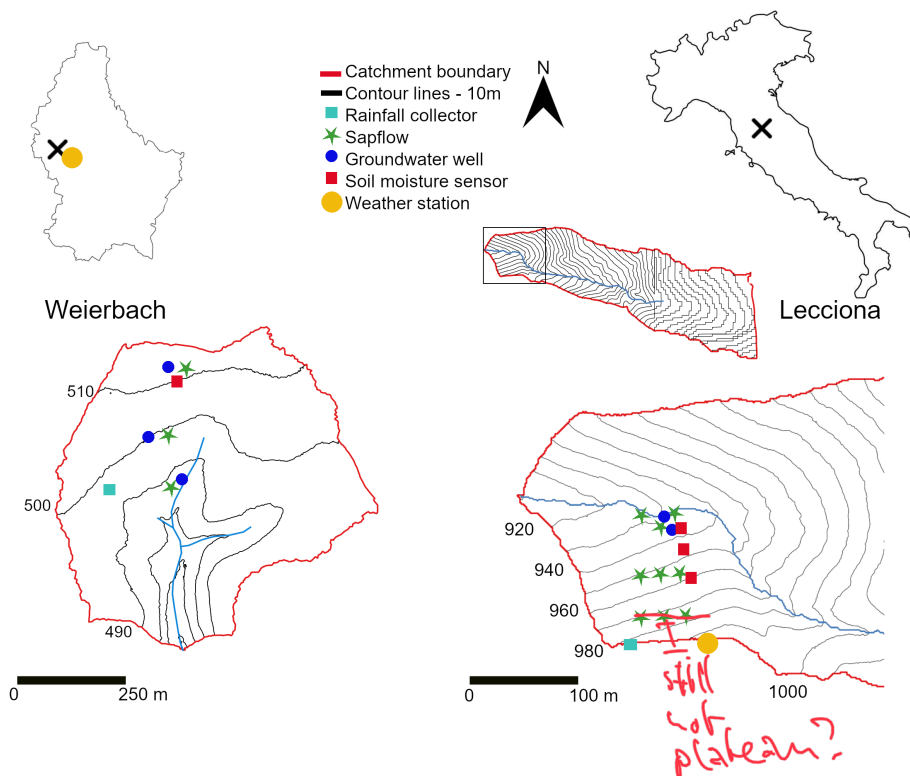
Figure 1. Sites overview with sensors in place: on the left the Weierbach catchment, Luxembourg, and on the right the Lecciona catchment in Tuscany, Italy. In the Weierbach, we monitored groundwater level (blue dot) and sap velocity (green star) in one beech tree at each hillslope position, and soil 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.

account for this effect, we applied a wound correction factor of 0.13 cm (Green et al., 2003). We filled the data gaps due to power malfunctioning via linear interpolation with sensors at the same location (Table A1, Fig.A1).

145 ## 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 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 were collected around the stem circumference with 150 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 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 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. In the Lecciona catchment, groundwater was sampled on two
occasions in 2022 (24 March and 5 October) due to logistical difficulties.

2.5 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 content and extraction yields for each xylem sample by weighting them before and after cryogenic water extraction. We
assessed the wood moisture content defined as the ratio of the weight of extracted water to the weight of dry wood (Berry
and Roderick, 2005; Peck, 1953; Siau, 1984; Steward, 1967) 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 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
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 and 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 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

190 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

195 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 zone was statistically different from each other. For all

200 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

205 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., 2022) each month of the 2020 growing season was

210 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

215 soil moisture and wood moisture content (Fig. 4). In the Weierbach catchment, there were no statistical differences in wood
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.

[handwritten annotations: "Fig 2 data does not look likel this - Is this an effect of the short time series? 2n winter are missing"]

The Lecciona catchment in 2021 was characterized by a higher average temperature compared to the Weierbach catchment
(Table 2) but a similar precipitation amount. Soil moisture content was on average similar between 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, 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 (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
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.

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

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
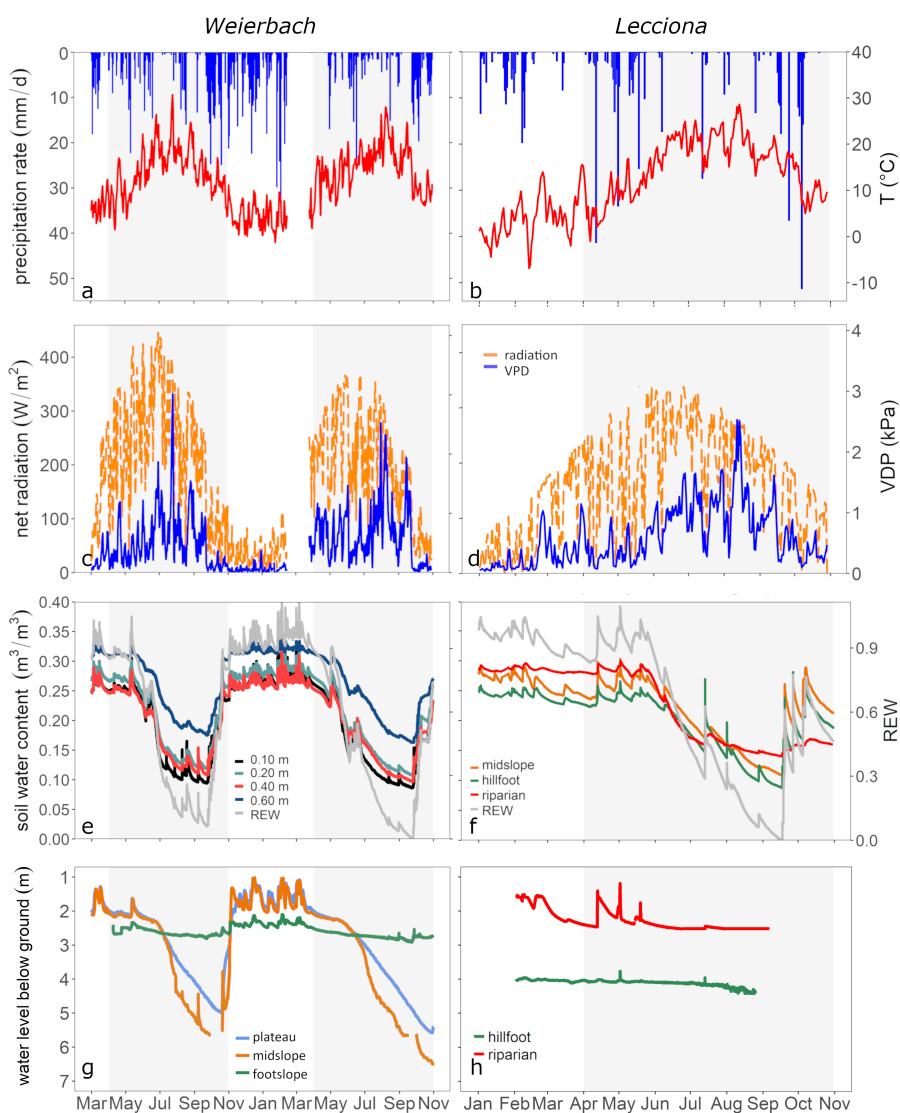
Figure 2. Daily total precipitation amount (mm/d) and daily mean air temperature (°C), and daily mean radiation (W/m²) and daily mean vapour pressure deficit (VPD) (kPa) observed at the Roodt (left plots, a, and c) weather station and the Lecciona catchment (right plots, b and d). Volumetric soil water 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.
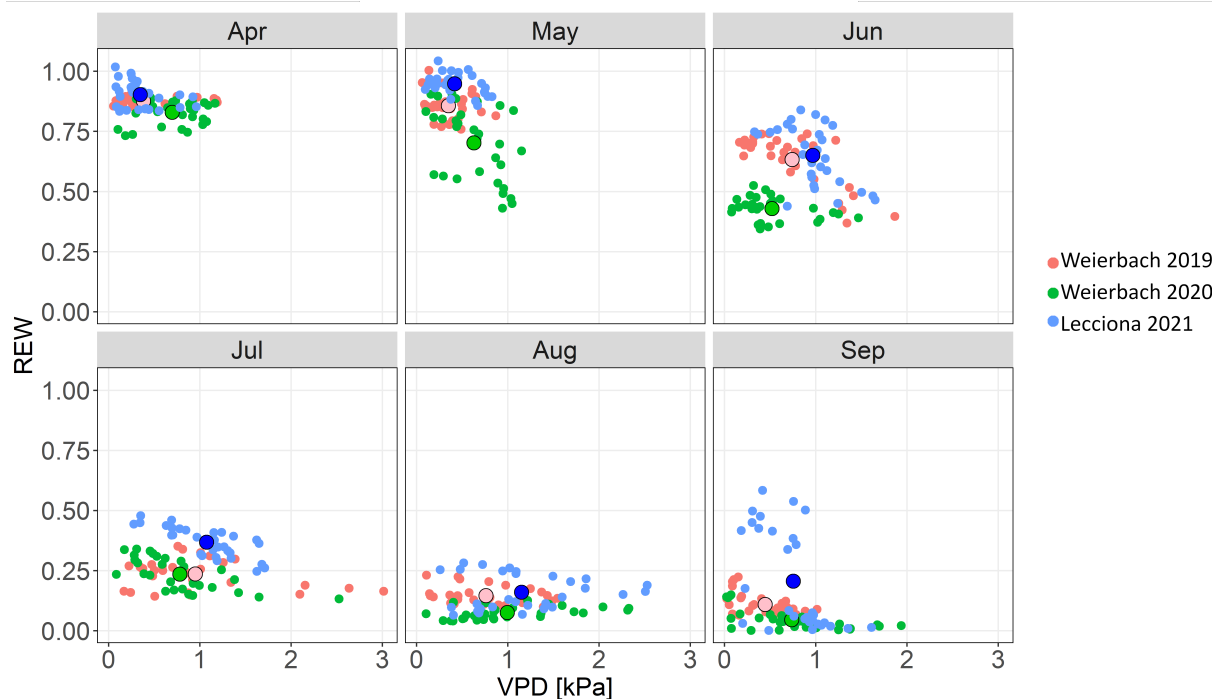
Figure 3. Relationship between VPD (kPa) and REW over the growing season (2019-2020) in the Weierbach catchment and (2021) in the Lecciona catchment. Full dots with black outlines represent monthly means.

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
255 increase in sap velocity (p<0.01). However, LMMEs showed that hillslope position (p<0.01) and W (p<0.01) explained most
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
260 footslope compared to the other locations indicating a stronger stomatal control on transpiration fluxes. There was a progressive
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
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
265 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,
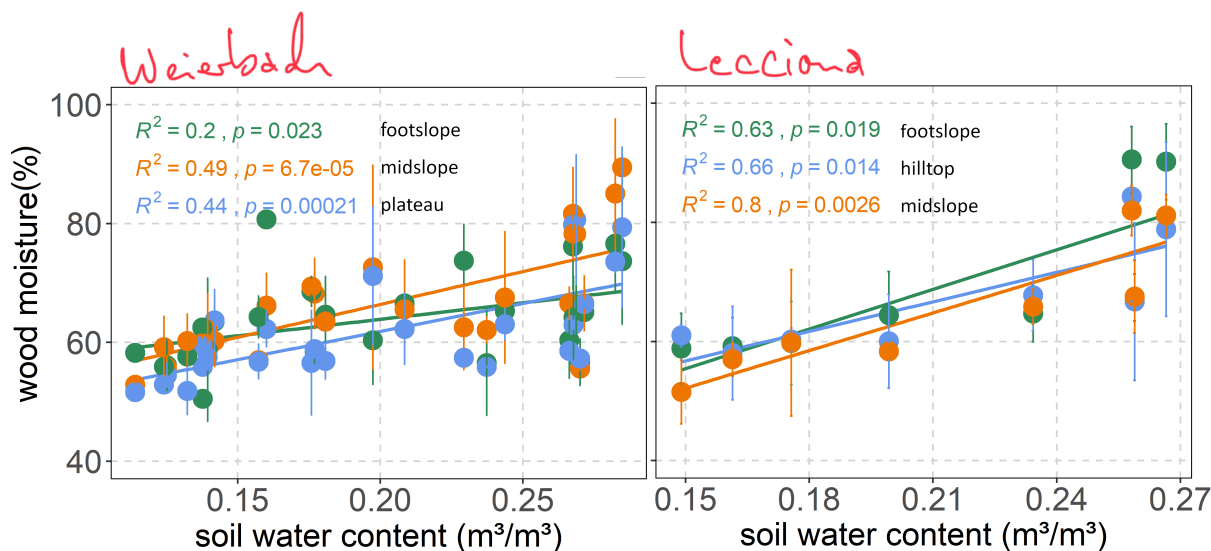
Figure 4. Relationship between wood moisture content (%) and volumetric soil moisture content of the xylem sampling date in the Weierbach catchment (left side) and the Lecciona catchment (right side). Solid dots represent the mean of xylem moisture, the whiskers indicate the confidence interval (95%). 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

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

270 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.

275 **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 $\delta^{18}O$ and -76.6 and -39.3‰ in δ^2H. The mean isotopic composition was -6.4 ± 1.0 ‰ and -63.7 ± 7.1 ‰ in $\delta^{18}O$ 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

280 between sampling locations (p=0.2 for $\delta^{18}O$, p=0.5 Kruskal-Wallis test) (Fig. 8). Soil water $\delta^{18}O$ and δ^2H showed the typical depth-gradient with heavier isotopic composition in the shallow layers (mean -5.5 ± 1.6 ‰ $\delta^{18}O$, -38.7 ± 9.6 ‰ δ^2H) and lighter values in the deeper one (-8.5 ± 1.4 ‰ $\delta^{18}O$, -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 ‰ $\delta^{18}O$, -54.3 ± 1.1 ‰ δ^2H) compared
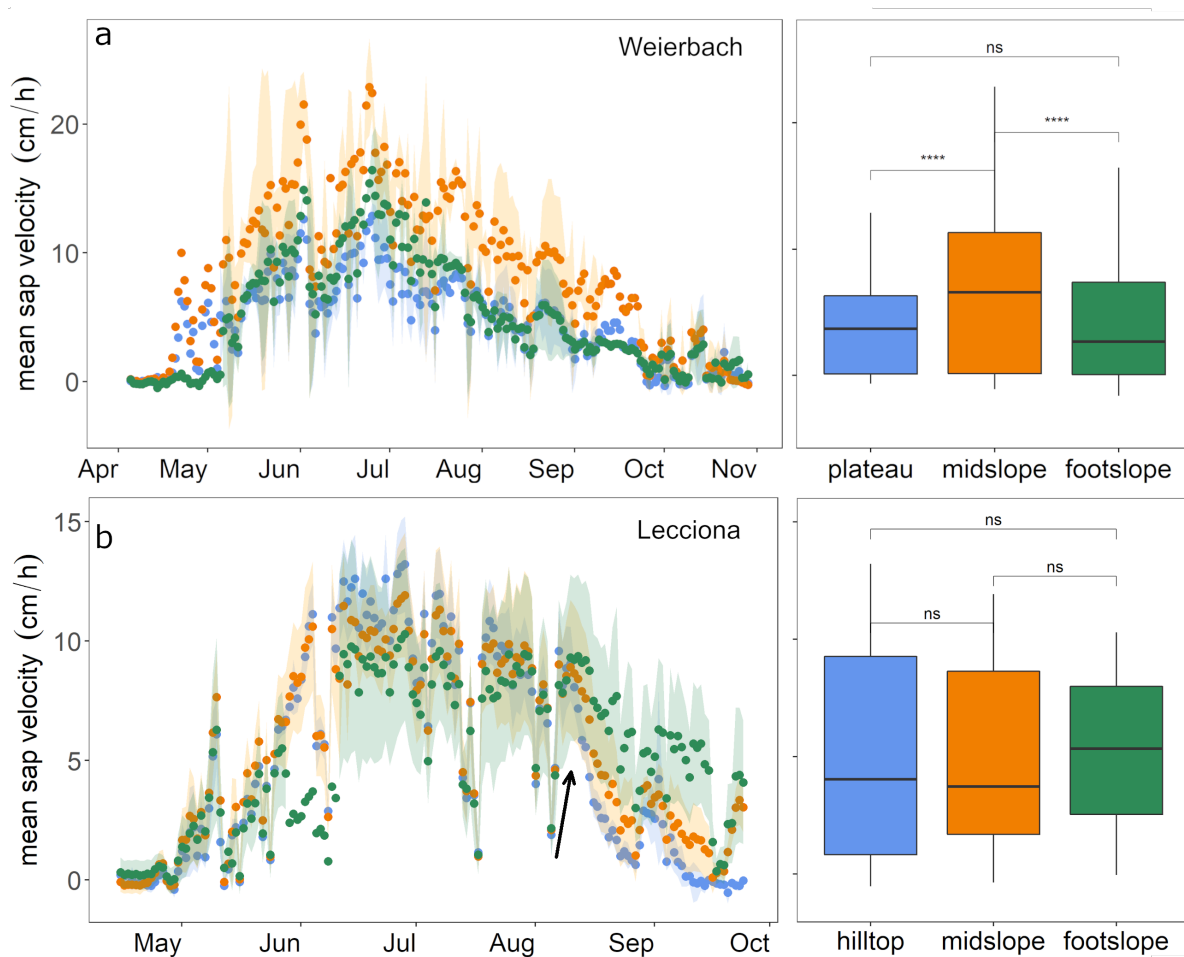
Figure 5. Daily mean sap velocity (cm h^{-1}) of Weierbach (a) and Lecciona (b) trees. Data from the Weierbach catchment cover the 2019 and 2020 growing seasons (April–October), while data from the Lecciona catchment cover the 2021 growing season (mid-April – September). Each color corresponds to location (green = footslope, orange = midslope, blue = hilltop/plateau). The area inside the colored lines is the mean average deviation between trees at the same location. 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).

to the midslope (mean -8.3 ± 0.3 ‰ δ^{18}O, -56.9 ± 1.8 ‰ δ^2H) and plateau (mean -8.5 ± 0.3 ‰ δ^{18}O, -52.6 ± 2.3 ‰ δ^2H)

285 (p<0.05, Kruskall-Wallis test).

In the Lecciona catchment, xylem water (96 samples, see Table S2) 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. A5). From May onwards, xylem water became heavier in both isotopes over time. After reaching the heaviest values on June 11, it progressively became lighter (Fig. A5). Xylem water of trees located at the footslope (mean -6.5 ‰ δ^{18}O and -57.6 ‰ in δ^2H)
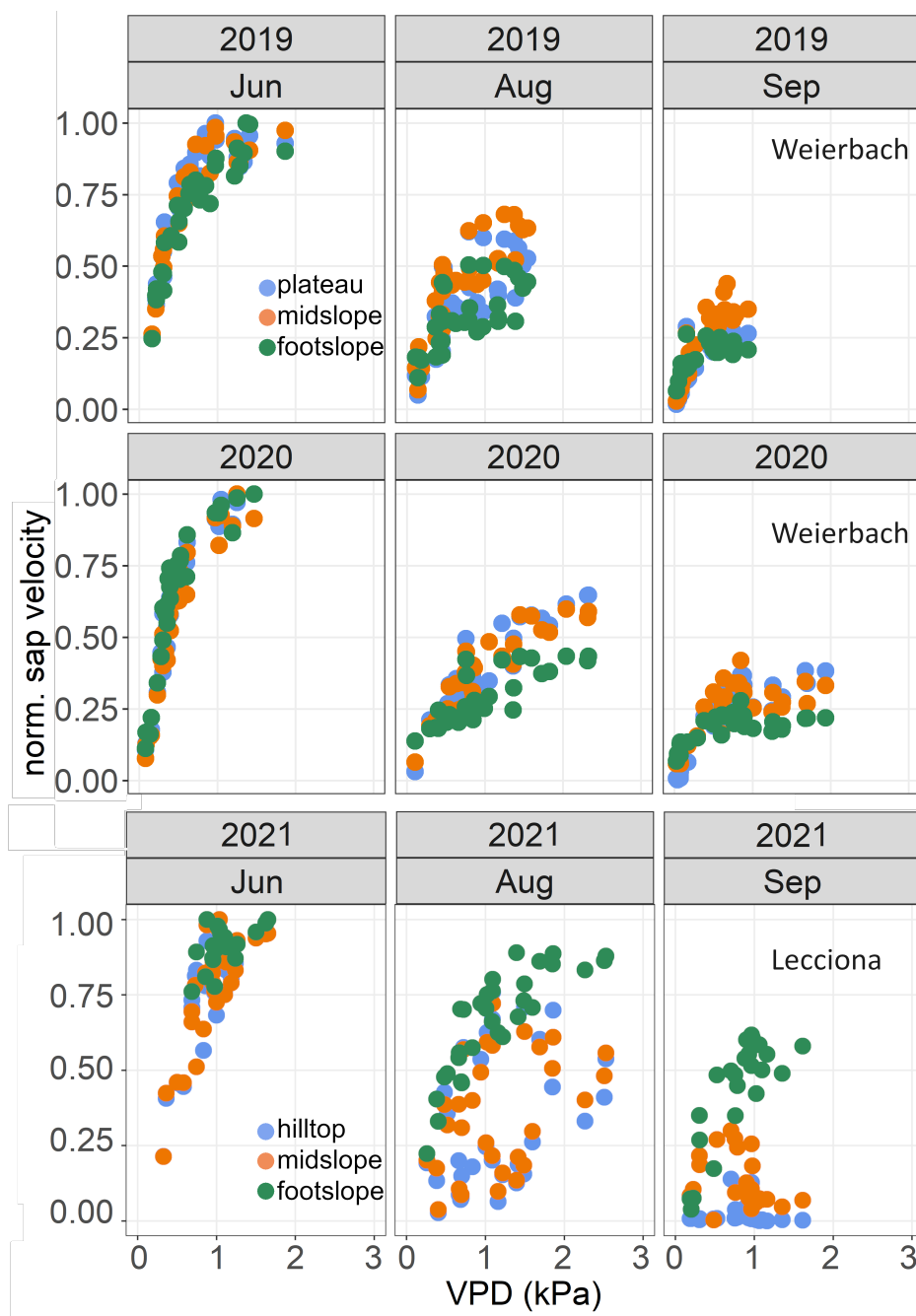
Figure 6. Relationship between normalised mean sap velocity and daily vapour pressure deficit (VPD) (kPa) at different hillslope positions in June, August, and September 2019 and 2020 in the Weierbach catchment (left and central column) and 2021 in the Lecciona catchment (right column).

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).

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 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 (Fig. 8). Soil isotopic composition plotted above the LMWL, reflecting the heavy isotopic

composition of the summer precipitation. 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.

295   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 $\pm$ 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

300   Lecciona catchment (Fig.8).
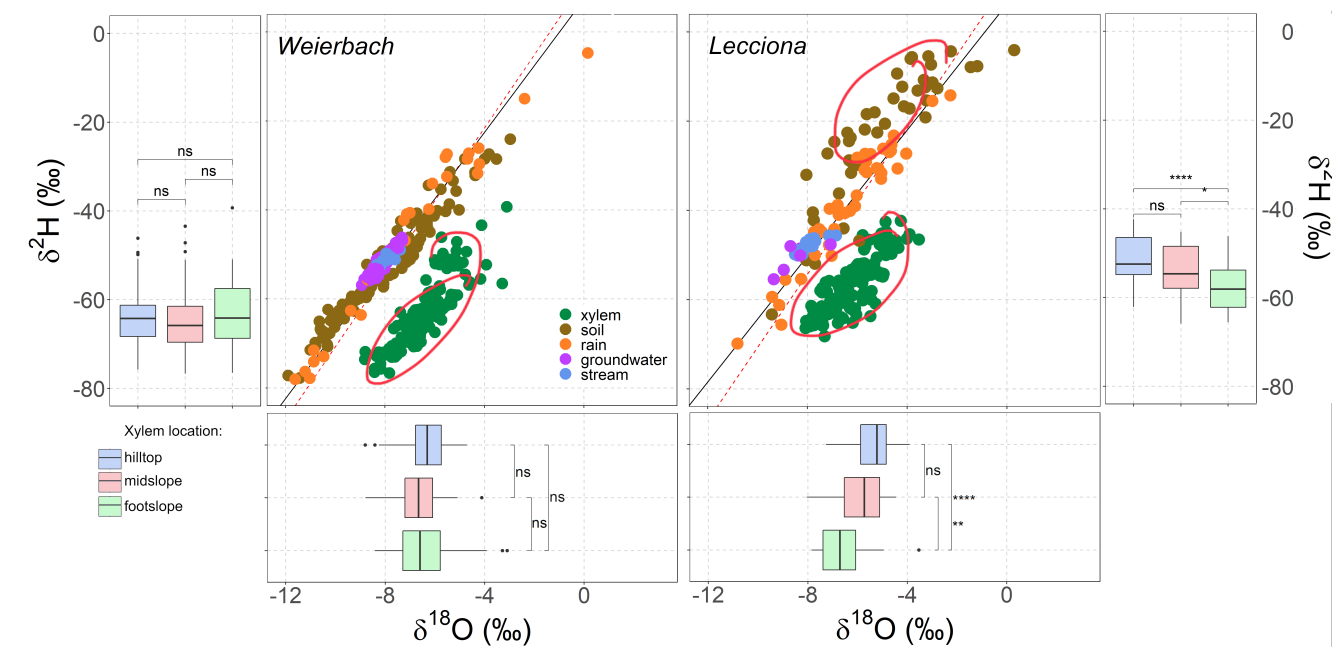
Figure 8. Dual isotope plots showing soil water, rain, groundwater, stream, and xylem water isotopic composition sampled in the Weierbach catchment (left panel) and the Lecciona catchment (right panel). The boxplot shows the median (black line in the box), the interquartile range (extent of the box), 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

According to our results, lower water availability in the 2020 growing season compared to 2019 in the Weierbach catchment - which was also the lowest recorded in the last eight years in the Weierbach - 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

305   (VPD, radiation and REW) were the main predictors controlling sap velocity (Fig. A2). The 2020 growing season was 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

310 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

315 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 from

320 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

325 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

330 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 acted as an additional water source for tree

335 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

340 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; Salomón et al., 2022) allowing to discriminate between xylem and bark hydration.

345   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

350   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

355   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

360   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

365   higher topographic positions to experience shorter growing season to withstand 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 support the hypothesis that to withstand the spatial changes in water availability, trees are adapted to capitalize water sources with different isotopic composition. We found

370   significantly heavier xylem isotopic composition at the hilltop and midslope compared to the footslope location in the Lecciona catchment (Fig. A5) suggesting a greater use of shallow water sources 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,

375   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
380 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
385 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
390 conditions and landscape features. 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
395 (Martínez-Vilalta et al., 2014). 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 and air dryness may impact this species, vulnerable to drought (Walthert et al., 2021), across its wide distribution range.

5 Conclusions

400 So far, there has been a lack of consistent studies on how hillslope position controls tree water use. 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 results in uniform physiological response to environmental controls among trees, even during the drier conditions of 2020 compared to 2019. Contrary, in the
405 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
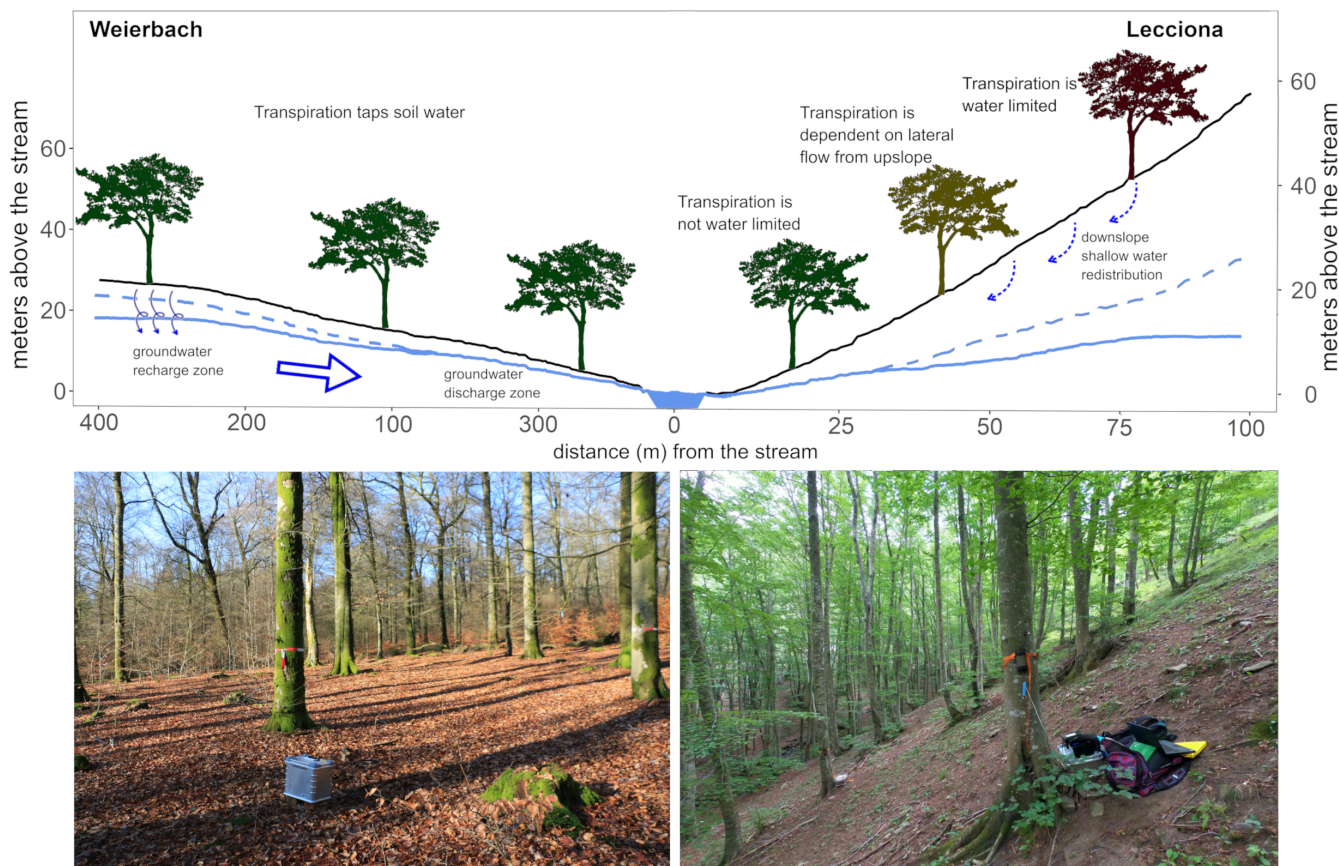
Figure 9. Conceptual graph showing the individual monitoring locations at each catchment and the ecohydrological processes taking place. Photos of the hillslopes are also shown for each study site from the plateau and hilltop positions. The terrain profiles were extracted from the digital terrain model (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).

and climatic gradients are stronger, the physiological response among locations will be more spatially variable. Contrary to
410   what was initially hypothesised, the physiological activity of beech trees was not constrained when compared to the central European population in the Weierbach catchment due to the plasticity of this 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 in face of the current climate crisis.

415 **Appendix A**

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

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

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
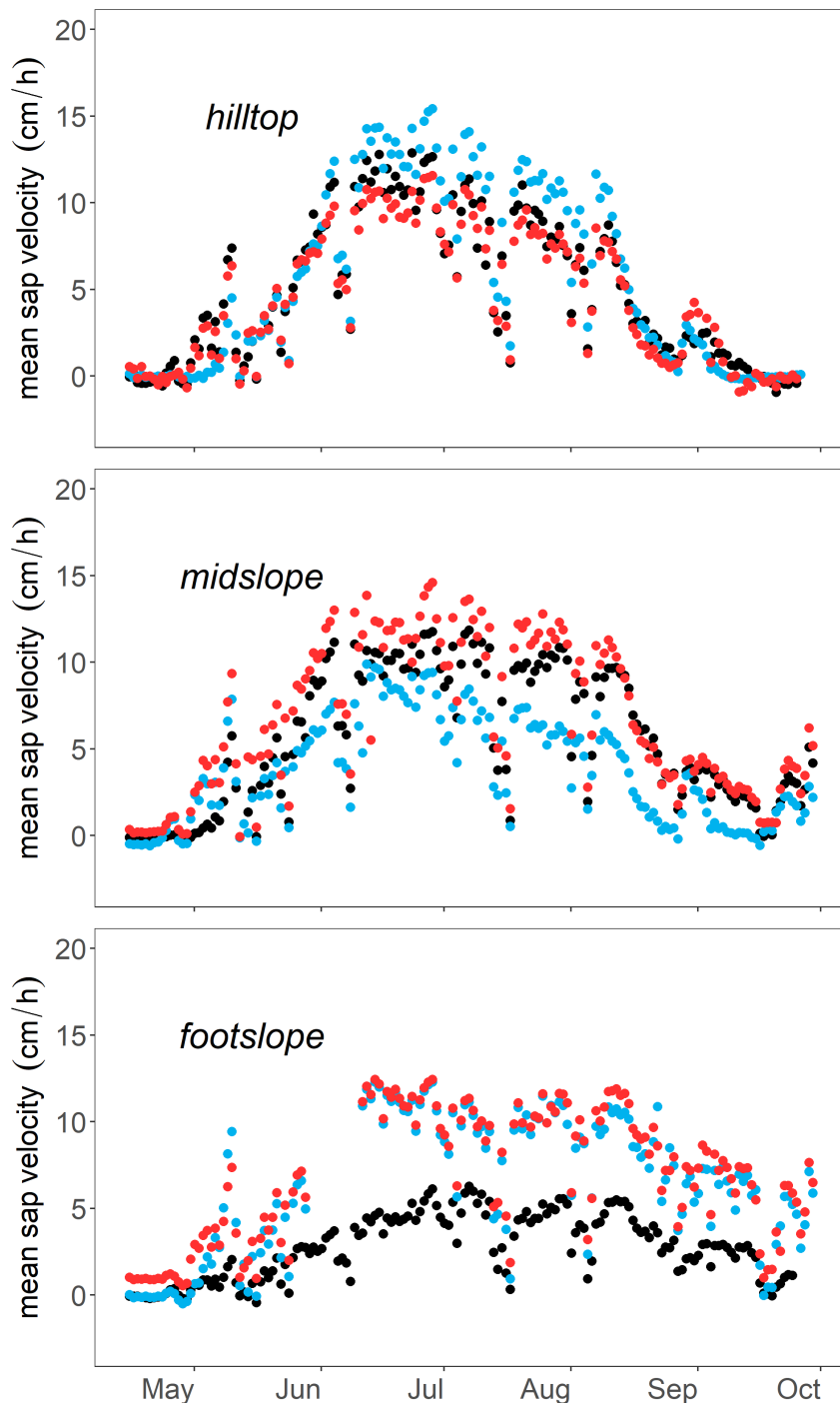
Figure A1. Sap velocity (cm h⁻¹) of beech at three sampling areas (hilltop, midslope, footslope) in the Lecciona catchment; each colour corresponds to one equipped tree. Missing data are the result of power interruption. When possible, data gaps were filled by interpolation, details are reported in Table 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.
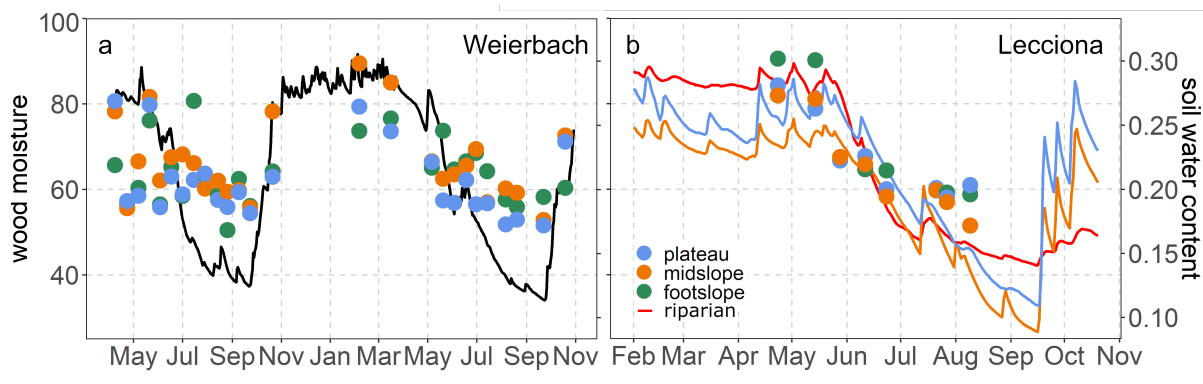
Figure A3. Temporal pattern of wood moisture content (%) and volumetric soil moisture content in the Weierbach catchment (a) and in the Lecciona catchment (b). Solid dots represent the mean, each color corresponds to sampling locations (blue= plateau, orange= midslope, green= footslope, red= riparian). 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 two monitored depths recorded at each location.
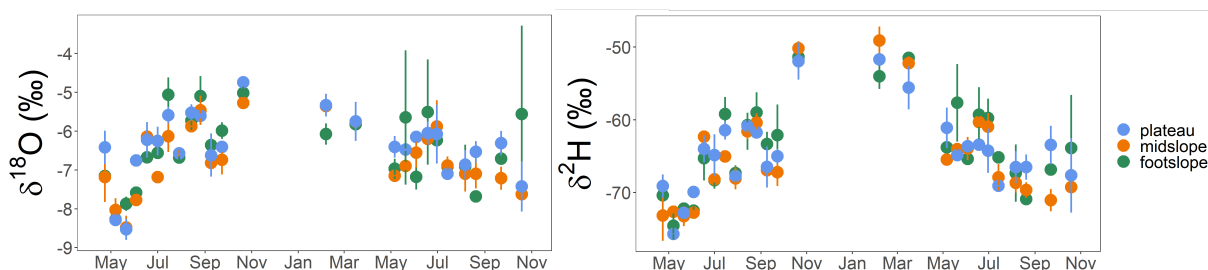
Figure A4. Isotopic composition of xylem water for each sampling campaign across 2019 and 2020 growing season in the Weierbach catchment. Data were averaged by location. Solid dots represent the mean, the whiskers indicate the confidence interval (95%).
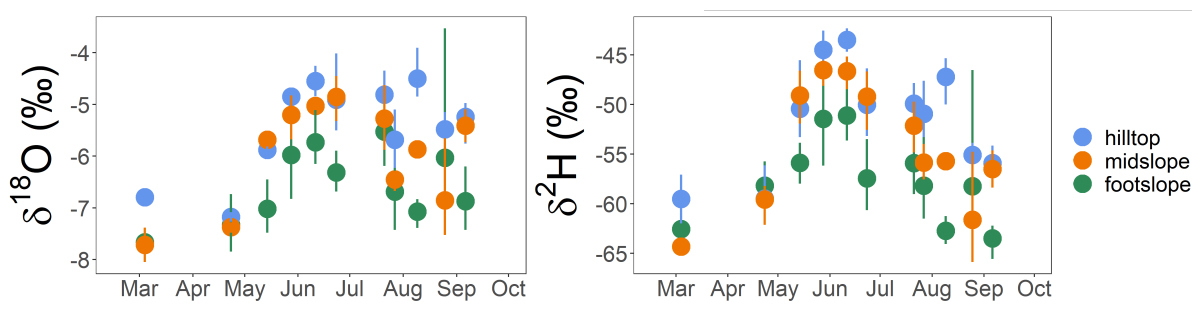
Figure A5. Isotopic composition of xylem water for each sampling campaign across the growing season in the Lecciona catchment. Data were averaged by location. Solid dots represent the mean, the whiskers indicate the confidence interval (95%).

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.

420 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.

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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.

Berry, S. L. and Roderick, M. L.: Plant–water relations and the fibre saturation point, New Phytologist, 168, 25–37, https://doi.org/10.1111/j.1469-8137.2005.01528.x, 2005.

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.

470 Dunne, T., Moore, T. R., and Taylor, C. H.: Recognition and prediction of runoff-producing zones in humid regions, Hydrol Sci BULL Sci Hydrol, 20, 305–327, 1975.

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.

Fabiani, G., Penna, D., Barbeta, A., and Klaus, J.: Sapwood and heartwood are not isolated compartments: Consequences for isotope ecohy-
475 drology, 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, https://doi.org/10.5281/ZENODO.8326112, 2023a.

480 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, 2017.

485 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 compensatory uptake occurs from deeper soil layers, New Phytologist, 233, 194–206, https://doi.org/10.1111/nph.17767, 2022.

490 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, 2019.

495 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, https://doi.org/10.1002/2015WR018414, 2016.

500 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 analysis (δ18O, δ2H) of matrix-bound water: Unifying protocols through empirical and mathematical scrutiny, Hydrology and Earth

505   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.

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.

510   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,

515   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.

Hawthorne, S. and Miniat, C. F.: Topography may mitigate drought effects on vegetation along a hillslope gradient, Ecohydrology, 11, e1825,

520   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

525   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,

530   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.

Klaus, J., Chun, K. P., and Stumpp, C.: Temporal trends in δ18O composition of precipitation in Germany: Insights from time series modelling

535   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.

540   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.

       Magh, R.-k., Eiferle, C., Burzlaff, T., and Dannenmann, M.: Competition for water rather than facilitation in mixed beech-fir forests after
545   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: decon-
          structing 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.

550   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.

555   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 domi-
          nance of functional strategies of tropical dry forest trees, Environmental Research Letters, 12, https://doi.org/10.1088/1748-9326/aa717b,
          2017.

560   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 influ-
          ences species-specific patterns of seasonal primary productivity in a semiarid montane forest, Tree Physiology, 40, 1343–1354,
565   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
570   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.

       Parmesan, C.: Ecological and evolutionary responses to recent climate change, Annual Review of Ecology, Evolution, and Systematics, 37,
          637–669, https://doi.org/10.1146/annurev.ecolsys.37.091305.110100, 2006.

575   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., S̊anda, 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.

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.

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, 2022.

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.

Siau, J. F.: Transport Processes in Wood, vol. 2 of *Springer Series in Wood Science*, Springer Berlin Heidelberg, Berlin, Heidelberg, https://doi.org/10.1007/978-3-642-69213-0, 1984.

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.

Steward, C. M.: Moisture content of living trees, Nature Publishing Group, 216, 615–616, 1967.

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.

615 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 ground-water 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,
620 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.

625 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.

630 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) Equilibration Laser Spectroscopy, Environmental Science & Technology, 42, 9262–9267, https://doi.org/10.1021/es802065s,
635 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.

640 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.