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Hydro-meteorological forcing modulates sap flux dynamics in beech trees along a steep Mediterranean hillslope

Jerzy Piotr Kabala [a], Ilenia Murgia [b,*], Matteo Verdone [b], Ginevra Fabiani [b,c,d], Ilaria Zorzi [b,e,f], Alessio Giovannelli [g], Giovanna Battipaglia [a], Daniele Penna [b,h], Claudia Cocozza [b]

[a] Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, University of Campania L. Vanvitelli, Caserta, Italy
[b] Dipartimento di Scienze e Tecnologie Agrarie, Alimentari, Ambientali e Forestali (DAGRI), Università degli Studi di Firenze, Firenze, 50145, Italy
[c] Swiss Federal Research Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, 8903, Switzerland
[d] Department of Environmental Research and Innovation, Luxembourg Institute of Science and Technology (LIST), Luxembourg
[e] Bluebiloba Startup Innovativa s.r.l., Via C. Salutati 78, Florence, 50126, Italy
[f] ForTech Laboratorio Congiunto, University of Florence, Florence, 50145, Italy
[g] Istituto di Ricerca Sugli Ecosistemi Terrestri (IRET), Consiglio Nazionale delle Ricerche, Via Madonna del Piano 10, Sesto Fiorentino, I-50019, Italy
[h] Oregon State University, Forest Engineering Resources and Management Department, Corvallis, OR, USA

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ABSTRACT

Understanding how forest ecosystems respond to environmental stressors is crucial for forest management strategies in the climate-sensitive Mediterranean region. This study examines the spatio-temporal variability of sap flux in response to hydro-meteorological drivers along a steep hillslope in a mountain Mediterranean forest. Sap flux rates and soil moisture were measured in a pure European beech stand (*Fagus sylvatica* L.) during the 2021 growing season (May-September) at three different locations along a steep hillslope in the Re della Pietra catchment, central Italy. Results indicated a distinct topographic gradient in physiological control. Transpiration in riparian trees was mainly limited by solar radiation and vapor pressure deficit, independent of soil moisture seasonality. Moving upslope, the trees shift from energy-limited to water-limited conditions as the growing season advances. By using an independent, replicated low-cost sensor network combined with moving-window correlation and regression-tree analysis, we determined soil moisture thresholds (0.15 m^3m^{-3} and 0.17 m^3m^{-3} at 15 and 35 cm depth, respectively) at which the relationship between sap flux and solar radiation decreased, making soil water availability the main factor influencing transpiration. Therefore, while soil moisture, mediated by topography, affected tree transpiration, emerging as the key predictor for hillslope positions, radiation was identified as the main factor influencing trees in the riparian position. Results show that forest stands act as a "dynamic ecohydrological mosaic" in which soil water redistribution dictates variability in ecological thresholds for the same species. This research emphasizes the importance of accounting for fine-scale topographic and soil moisture variations in hydrological models and precision forestry strategies to effectively forecast forest resilience under future climate change scenarios.

1. Introduction

Forest ecosystems play a vital and complex role in the Earth's water cycle through several mechanisms, such as rainfall interception by tree canopy, water storage within plant organs, and the return of water vapor to the atmosphere through evaporation and transpiration (Ellison et al., 2017; Goldstein et al., 1998; Penna, 2026; Wang et al., 2022). Specifically, transpiration represents a large component of the water budget in forest ecosystems (Oishi et al., 2010). It varies spatially and seasonally depending on local conditions like topography, soil properties, and water availability, as well as microclimate factors such as precipitation, temperature, and solar radiation (Emanuel et al., 2011, 2010; Fan et al., 2017; Renner et al., 2016). To better understand and consider all variables involved in the transpiration process and its responses to environmental conditions, it is necessary to adopt a multidisciplinary approach, bridging knowledge between tree ecophysiology and soil hydrology (Cocozza and Penna, 2022). This approach enables the identification of the most relevant meteorological forcings that influence plant growth and functionality (e.g., photosynthesis

* Corresponding author.
E-mail address: ilenia.murgia@unifi.it (I. Murgia).

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and transpiration), providing essential information to understand forest dynamics and support appropriate management strategies of forest resources (Vannoppen et al., 2018). In particular, understanding how forests respond to environmental changes and stresses, such as soil water deficit, provides insights into the sensitivity and potential for adaptation of forest ecosystems, which is crucial for informing forest management practices (Magh et al., 2019).

Recent studies have increasingly focused on understanding the effects of water stress on tree transpiration and factors that control it, as, at the ecosystem level, variations in soil moisture influence how water is partitioned between soil and atmospheric fluxes (Song et al., 2022). Xu et al. (2022), using a global analysis on eddy covariance evapotranspiration data collected across different biomes, highlighted reduced soil moisture as the main limiting factor for transpiration under seasonal drought conditions. However, an analysis performed on the AmeriFlux network found that evaporative demand was found to be more important than soil moisture (Novick et al., 2016). These contrasting results highlight the difficulty of disentangling multiple drivers, as trees operate at the continuum interface between soil and atmosphere. To cope with soil water deficits and high evaporative demand, trees have evolved strategies to minimize water loss through regulation of their stomatal conductance, which varies according to their position along the isohydric-anisohydric continuum (Klein, 2014). Specifically, isohydric species exert tighter control over their stomatal opening to maintain a constant level of leaf water potential, whereas anisohydric species enable a decline in leaf water potential through lighter stomatal conductance regulation in order to support carbon assimilation under limiting conditions (McDowell et al., 2008). Between these two strategies, there is a high degree of plasticity in how plants adapt to different environmental conditions, developing various water regulation strategies (Domec and Johnson, 2012).

One of the main local conditions influencing soil moisture distribution and, in turn, tree transpiration is the topographic gradient (e.g., local slope). Hillslope topography strongly impacts soil moisture redistribution by affecting water movement, storage, and availability at different positions, with areas near the upper part of a hillslope typically having shallower soils, causing rainwater to drain more quickly and resulting in lower soil moisture, in contrast with downslope areas which often have deeper soils and receive redistributed water from upslope, leading to higher soil moisture retention (Penna et al., 2009; Penna et al., 2013; Penna et al., 2015; Singh et al., 2021). This spatial variability in soil moisture conditions, driven by topography, can noticeably affect tree growth and transpiration (Moeslund et al., 2013). In a recent study conducted in the Krycklan catchment (Sweden), Larson et al., (2024) analysed the variation in tree growth potential across the landscape and its relation to soil moisture. They found a clear decrease in tree growth under the highest soil moisture conditions, although intermediate soil moisture conditions did not show clear differences in growth. More specifically, Malone et al. (2025) observed that trees located in high elevations, north-facing aspects, and convergent topographic positions in six hillslopes in the Lubrecht Experimental Forest (Montana, USA) were related to decreased temperatures, higher soil moisture, and limited vapor pressure deficits, leading to later growth cessation, but that, on the contrary, at the wettest positions, soil saturation led to earlier growth cessation. Spatial variations in soil moisture with depth were observed to cause differences in tree transpiration rates between upslope and midslope sections of a hillslope in the Panola Mountain Research Watershed (Georgia, USA). In the upper part of the hillslope, characterized by shallower soils, transpiration became limited by soil moisture, whereas in the midslope section with deeper soils, transpiration was not limited by soil moisture (Tromp-van Meerveld and McDonnell, 2006). The limiting effect of topography and soil moisture on tree transpiration at the smaller scale was also observed in a pure beech tree stand in the Lecciona hillslope, within the Mediterranean Re della Pietra experimental catchment (Central Italy): lower sap velocities during the hottest periods and shorter growing seasons were recorded in trees growing in the upper portions of the hillslope, related to water redistribution and different soil moisture along the hillslope catena. However, sap flux remained stable in the riparian trees, which responded more strongly to variations in vapor pressure deficit and air temperature than trees growing in upper hillslope positions (Fabiani et al., 2024; Verdone et al., 2025a). A subsequent wavelet-based analysis at the same site further showed that these topographic differences manifest as distinct lead-lag dynamics between soil moisture, precipitation, and vapor pressure deficit. While soil moisture at the hillslope position responded rapidly to individual rainfall events, riparian soil moisture stayed smoother and more buffered, and they identified a critical soil moisture threshold ($\approx$0.15 m^3 m^{-3}) below which both precipitation and sap flow responses were strongly constrained (Murgia et al., 2026).

These topographic controls on soil moisture are not merely local drivers of spatial variability but also critical mediators of tree resilience in environments characterized by increasingly frequent periods of water scarcity. In Mediterranean landscapes, where drought is becoming the dominant stressor, topographic positions and soil depth can either promote favorable micro-environments or high-stress hotspots, effectively setting the ecological threshold for sensitive species. While Mediterranean vegetation is adapted to seasonal multi-year time scales (Massari et al., 2022; La Jeunesse et al., 2016), climate projections indicate a future of even lower summer rainfall and more persistent drought periods (Tramblay et al., 2020). European beech (*Fagus sylvatica L.*), a prominent montane species in this region, exemplifies this vulnerability: despite its broad adaptability (Puchi et al., 2024), it remains exceptionally sensitive to the intensifying drought dictated by these topographic limits. Recent studies have observed the effects of drought on beech trees by analyzing sap flux, water potential, and stomatal conductance, as well as, in some cases, growing rates (Grams et al., 2021; Hesse et al., 2023, 2024). They observed that beech under recurring drought experiences reduced sap flux, increasingly negative water potentials, and strong stomatal down-regulation, leading to substantial reductions in growth. Nevertheless, water relations and leaf physiology recover quickly after re-wetting, sap flux and growth recover more slowly, indicating notable but not unlimited resilience to recurrent drought. Other researchers highlighted that beech is more sensitive to drought at the center of its distribution range and less at the edges, hypothesizing that either different local adaptations to climate or favorable soil conditions in more southern sites allow mitigating the strong effects of climate change (Klesse et al., 2024). A recent study analyzed the effects of the principal climatic drivers on beech tree growth at the southern distribution limit, utilizing a large dendrochronological database (Serrano-Notivoli et al., 2025). They found that precipitation and maximum temperature were the key drivers of tree growth across variable temporal windows, and that climatic effects were stronger and the critical response threshold commenced earlier in larger trees (Serrano-Notivoli et al., 2025). In the central Apennines, dendrochronological evidence from old-growth beech forests shows a decline in basal area increment over recent decades, driven by increasing drought. This trend is consistent with other Mediterranean mountains but contrasts with that reported for many Central European forests (Piovesan et al., 2008). However, most studies on beech adaptation have been conducted in Central Europe, while the Mediterranean area, which constitutes the southernmost part of the beech's distribution range, has been largely overlooked (Kabala et al., 2025). The uniqueness of the Mediterranean climate, characterized by frequent summer droughts due to high temperatures and scarce precipitation, raises questions about the physiological strategies employed by beech stands that persist in this region.

Nowadays, different monitoring systems have been widely used to investigate tree responses to climate change conditions (Peters et al., 2021) to gain information about environmental drivers and stressors (e.g., Camarero et al., 2021; Niccoli et al., 2024, 2023; Poyatos et al., 2016; Zweifel et al., 2005). These monitoring systems benefit from high temporal resolution in data acquisition, ranging from minutes to hours, to define daily, monthly, and/or seasonal behavioral processes (van der Maaten et al., 2018). In particular, transpiration is indirectly estimated using models applied to remote sensing data (Norman et al., 1995), or by physically based or semi-empirical methods, such as the “big leaf” approach

(Monteith, 1965; Priestley and Taylor, 1972). A wide array of direct methods also exists, including gravimetric analysis, heat pulse velocity (HPV), single-leaf, and whole-plant infrared gas-exchange measurements (Ferrara et al., 2003). The use of the HPV method to estimate transpiration through sap flux measurements within the plant stems has been successfully applied to define the relationship between tree growth and yield to soil moisture and climatic forcing variability (Boggs et al., 2021; Cocozza et al., 2015; Giovannelli et al., 2019; Oishi et al., 2010) or to manage crop irrigation (Fernández et al., 2001, 2008; Tognetti et al., 2009). While these traditional instrumentation suites are highly precise, their high cost often limits dense, large-scale spatial deployments. To address this, the TreeTalker (TT) has emerged as an affordable, IoT-enabled alternative that enables simultaneous, high-frequency monitoring of both plant physiology and surrounding microclimatic variables (Francini et al., 2021; Niccoli et al., 2023, 2024). Although the use of TT in eco-meteorological research remains a relatively small and emerging field, these devices enable the monitoring of biophysical and environmental processes, including plant-scale temperature, deviation from verticality (through a gyroscope), intensity of penetrating light, radial growth, and sap flux, at a lower cost than more expensive systems (Valentini et al., 2019; Vaglio Laurin et al., 2024; Niccoli et al., 2025). Ultimately, ground-based measurements of evaporative water flux on a very local scale, such as those provided by these refined TT networks, are highly useful for evaluating and improving model performance (Bittencourt et al., 2023; Saitta et al., 2020; Shuttleworth and Calder, 1979) in order to increase the accuracy of estimated values of biogeochemical cycle components (Kim et al., 2023). However, because these budget-friendly sensors generate raw signals that are highly sensitive to site conditions, they inherently demand more intensive pre-processing, calibration, and validation workflows to match the performance of premium instruments. This has driven a growing methodological focus on data curation pipelines and specialized software, such as the *ttprocessing* and *TreeTalkersCheck* R packages, to clean, filter, and standardize the raw datasets (Asgharinia et al., 2022; Tomelleri et al., 2022; Zorzi et al., 2021; Kabala et al., 2024).

While previous work at the Lecciona hillslope in the Re della Pietra catchment (central Italy) has established that topography modulates beech water-use strategies - through isotopic and growing-season evidence (Fabiani et al., 2024), hysteresis and time-lag analysis of sap velocity and VPD (Verdone et al., 2025a), and wavelet coherence/phase analysis of lead-lag dynamics among soil moisture, precipitation, VPD and sap flow (Murgia et al., 2026), none of these studies has tested the reproducibility of this gradient using an independent, spatially replicated, low-cost sensor network suitable for scaling to precision forestry applications, nor derived an explicit soil moisture threshold directly from a continuous bivariate relationship between sap flux and a competing energy-driven predictor (like radiation), together with the hierarchical structure of environmental drivers underlying this switch. Therefore, despite the extensive literature on this topic, a clear understanding of the combined influence of local conditions, primarily topography, and meteorological factors such as precipitation frequency and rate, as well as rising temperatures, and their impact on soil water redistribution and, consequently, on controlling tree transpiration in Mediterranean mountain forests is still lacking.

To address these gaps, this study introduces a distinct technological and analytical paradigm. While previous works at the Lecciona hillslope characterized spatial soil-water patterns and overall transpiration using traditional, decoupled instrumentation, we installed a network of TT devices across three hillslope positions, allowing to scale from isolated observations to a fully integrated, tree-scale view of the soil-plant-atmosphere continuum. This comprehensive integration allowed us to address previously unanswered questions regarding the complex, coupled feedbacks, thresholds, and time-lagged responses among dynamic meteorological forcing, soil water depletion, and trees' water use across the steep hillslope. Using the Penman-Monteith model to analyze these interactions, we assess whether the low-cost sensor network can capture the delicate intraseasonal ecophysiological dynamics with the same observational accuracy as traditional, high-cost instruments.

2. Materials and methods

2.1. Study area and forest characteristics

The Lecciona hillslope is located in the upper part of the Re della Pietra experimental catchment (Tuscany, central Italy; 43.878°N, 11.622°E), where the forest composition is mainly dominated by European beech (*F. sylvatica* L.) trees (Kaffas et al., 2025; Macchioli Grande et al., 2024; Verdone et al., 2025a;b). The Lecciona hillslope was historically managed as coppice for charcoal production. The study site has an average annual precipitation of about 1316 mm and a mean temperature of 10.7°C, based on data collected from 1992 to 2025 at a weather station 12 km south of the catchment area (elevation 955 m asl). Precipitation tends to be highest in autumn, with November recording the most rain at 185 mm, while July is the driest month with only 40 mm (see Fig. S1). Events with intensity above 1 mm also varied seasonally, with higher intensities from May to October (3.6 mm/h) than from October to May (2.1 mm/h). Although rare, snowfall occurred during December and January. The monitored hillslope lies between 920 and 970 m a.s.l., it has a NNW aspect and a mean slope of 30°. Precipitation, solar radiation, wind speed and direction, relative humidity, atmospheric pressure, and air temperature were collected at 5-minute timestep over the 2021 growing season (May-September) using a weather station (Davis Vantage Pro, Vernier, Oregon, USA) located in an open area at 991 m a.s.l. at the top of the study hillslope. The annual precipitation in 2021 was 928 mm, and the mean annual temperature was 10.9°C.

Vapor Pressure Deficit (VPD) was calculated according to the following equation (Murray, 1967):

$$VPD(kPa) = \left(1 - \frac{RH}{100}\right) * SVP \quad (1)$$

where SVP is the saturation vapor pressure of water calculated by the Tetens equation (Tetens, 1930):

$$SVP(kPa) = 0.61078 * e^{\frac{Tair*17.08}{234.175+Tair}} \quad (2)$$

Where *Tair* is air temperature expressed in °C and RH is the relative humidity.

Ten trees were selected at three hillslope locations, named riparian, midslope, and upslope (Fig. 1). We installed TTs in three trees at the upslope and midslope locations, and four at the riparian location. The size of the trees varies considerably along the hillslope, with an overall average diameter at breast height (DBH) of 29 ± 9 cm and an average height of 19.6 m. However, the monitored trees at the riparian position have a DBH of 36 ± 6 cm and a height of 18 m, those in the midslope position have a DBH of 41 ± 8 cm and a height of 19 m, and those at the upslope have a DBH of 32 ± 5 cm and a height of 24 m. The DBH was measured with a caliper, and height was measured with the Vertex IV device (Haglof, Sweden), which has an estimated uncertainty of 1–2% (Eriksson, 1970). Based on dendrochronological analysis of core samples from these 10 trees, we estimated the average age of the forest to be approximately 60 years. Canopy phenology across the site follows a distinct topographic gradient (Verdone et al., 2025a), with the start of canopy development in April and continuing through May, even if exhibiting an elevation-dependent lag. By early May, canopy cover reaches approximately 90% at lower-slope/riparian positions, whereas upper-slope trees lag behind at approximately 70% canopy cover before reaching full closure later in the season.

Soil texture on the hillslope was determined in the lab through the analysis of eleven soil samples collected in March 2021 at the riparian position (two samples at 0–20 cm, two samples at 20–40 cm, and one sample at 40–60 cm depth), and the midslope and upslope positions (one sample at 0–20 cm, 20–40 cm, and 40–60 cm depth for each

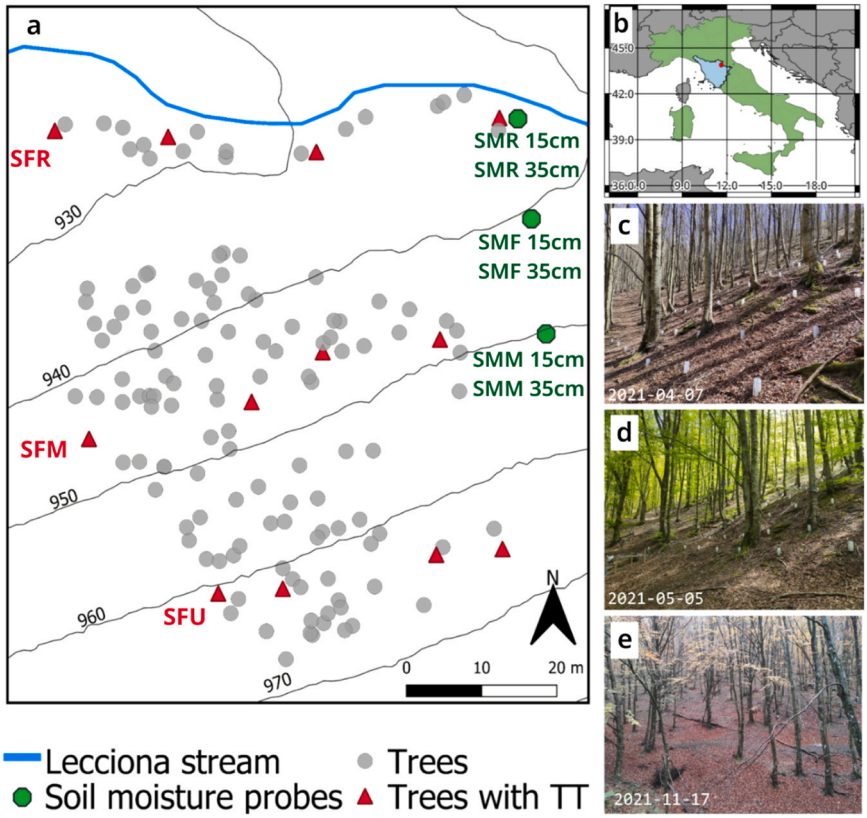

Fig. 1. a) Detailed representation of the Lecciona hillslope: red triangles are the trees where sap flux was measured (SFR: riparian trees, SFM: midslope trees, and SFU: upslope trees). All the other trees are indicated by grey circles. The positions of the soil moisture probes are indicated by the green circle: SMR is the riparian position, SMF the footslope position, and SMM the midslope position. In all positions, soil moisture was measured at 15 and 35 cm depth. b) Location of the study site (red circle) in Italy. c) Picture of the hillslope of the study site on the 7th of April 2021, d). The study area during the growing season (5th May 2021) and e) in fall (17th November 2021).

location). The analysis highlighted a uniform distribution of the same soil texture, specifically composed of sand content ranging from 57% to 76%, and clay content from 4% to 11%. According to the USDA classification (1999), the soil texture of the collected samples is sandy loam (Macchioli Grande et al., 2024).

2.2. Soil moisture measurements

Soil moisture has been monitored since August 2020 at three different points along a 30 m linear transect from the riparian area to the hillslope, specifically in the riparian (SMR), footslope (SMF), and midslope (SMM) positions, at depths of 15 and 35 cm (Kaffas et al., 2025; Fig. 1a). Measurements were taken using frequency-domain reflectometry probes (Teros 10, Meter®, Pullman, WA, USA) at 5-minute intervals. The raw probe values were converted to volumetric water content (m^3/m^3) using a standard calibration for mineral soils, as recommended by the manufacturer (reported precision ± 0.03 m^3/m^3).

2.3. Sap flux measurements

Sap flux data were collected by the 10 TT over the 2021 growing season (May 1st —September 30th), specifically from shortly after bud break to the end of the growing season. The installation was completed on April 1st, 2021, on the north face to prevent sunlight from affecting the measurements. To ensure the probes were inserted into the sapwood area, we extracted a wood core that reached the center of the plant on the eastern side of the trunk, thereby avoiding any potential interference with the sap flux measurement. Probes were installed at depths ranging from 0 to 2 cm in sapwood. The sapwood area was estimated in the field by measuring with a ruler the wet portion of the core, and we observed that trees at the riparian location (SFR) had higher surfaces than those at midslope (SFM) and upslope (SFU) locations, reaching 25%, 14%, and 8% of the total basal area, respectively.

The data of the first month of monitoring were discarded to avoid any wound effect on the data (Wiedemann et al., 2016). The TT sap flux density sensor works according to the principle of the Transient Thermal Dissipation method (Do et al., 2011; Granier, 1987), utilizing a single-probe setup with a cyclic heating system (Do and Rocheteau, 2002) that alternates between 10 min of heating and 50 min of cooling. This differs from the heat-pulse technique (SFM1 sensors) used in previous sap flow studies at this hillslope (Fabiani et al., 2024; Verdone et al., 2025b; Murgia et al., 2026), both in underlying physical principle and in sampling depth (0–2 cm sapwood vs. 12.5/27.5 mm from the bark). The Transient Thermal Index (K) was computed from the temperature after heating, and the result of the linear interpolation between the temperature before the heating and after the cooling phase, following Eqs. 4 and 5, to minimize the potential effect of natural temperature gradients (Ayutthaya et al., 2011), and then sap flux density (SFD, $gm^{-2}s^{-1}$) was computed according to Eq. 5 (Do et al., 2011).

$$K_i = \frac{\Delta T_{max}}{\Delta T_i} - 1 \tag{3}$$

$$\Delta T_i = Theat_i - linearInterpolation(Tcooling_{i-1}, Tcooling_i) \tag{4}$$

$$SDF\left(\frac{g}{m^2 * s}\right) = \frac{1}{3.6} * 12.95 * K * 100 \tag{5}$$

The system has an additional reference probe, located 10 cm below the heated one, and 2 cm to the side, which is not affected by heating. It measures sapwood and air temperature simultaneously, enabling

consistent process control. The computation was performed with the *ttprocessing* R package (Kabala et al., 2024, 2022).

2.4. Statistical analysis

The meteorological and soil moisture data were aggregated to an hourly timescale to allow the comparison with sap flux data. We considered cumulative precipitation, average radiation, and VPD values, as well as minimum, maximum, and mean air temperatures. Soil moisture data were also averaged hourly, yielding a time series of soil moisture dynamics on the slope. Since the sap flux time series was quite noisy, we smoothed the raw data using a three-hour moving average to remove off-scale peaks. Afterwards, to consider only stable signals from TT probes, rainy days (37 out of 153 monitoring days) were removed from the sap flux time series, as transpiration is reduced under lower VPD. Hourly sap flux was averaged between the trees equipped at each hillslope location. After testing for normality with the Jarque-Bera test ($p > 0.05$), an ANOVA and Tukey's Honestly Significant Difference post hoc test were used to compare sap flux values between locations for each month of the growing season ($\alpha = 0.05$).

To analyze the relationship between meteorological forcing, soil moisture, and sap flux, we considered SMR directly correlated with SFR, while for hillslope areas, soil moisture values from two positions (SMF and SMM) were averaged while maintaining vertical depth distinctions, and the values were subsequently correlated with sap flux data from the SFM and SFU positions.

We computed the Pearson correlation coefficient between the sap flux time series at each location and the meteorological variables and soil moisture. To assess whether correlations changed over the growing season, we employed a moving-window analysis (Polanco-Martínez, 2020) with a 30-day window, allowing us to examine how correlations shifted in response to fluctuating environmental conditions. All correlation values were tested for significance at the 0.05 alpha level.

Finally, to corroborate these findings and uncover potential non-linearities, regression tree models were fitted for each hillslope location using a parametric statistical approach (Breiman et al., 1984). The strength of this technique lies in avoiding the pre-specification of relationship types between predictors and the response variable. Its structure handles interactions and hierarchical interactions (Loh, 2014), recursively splitting the data into subgroups with similar response values. In this manner, the algorithm identifies the optimal split to minimize residual deviance (Rieger et al., 2017). The resulting tree structure predicts the response based on predictor values and can be graphically shown to reveal detected patterns (Schläppy et al., 2013). For our analysis, a regression tree was fitted to the dataset for each hillslope location, using 10-fold cross-validation to ensure consistency across locations. We considered the following variables as predictors, which are generally regarded as input parameters in physically based models for quantifying evapotranspiration: radiation, wind speed, atmospheric pressure, VPD, relative humidity, and soil moisture.

For the fitted regression trees, goodness of fit was assessed using the percentage of variance explained, and predictor feature importance was computed. The statistical analyses were performed in the R 4.3 environment, using the *Hmisc* package to compute correlations and the *rpart* package to fit regression trees.

3. Results

3.1. Meteorological variables, soil moisture dynamics, and sap flux

During the 2021 growing season (considered here as May 1st – September 30th), we observed the typical precipitation pattern of Mediterranean regions, with prolonged events during autumn and spring, while intense and short storm events occurred during the dry period, which generally featured long intervals of no precipitation (blue bars in Fig. 2a). The cumulative precipitation for the investigated growing season was 284 mm, with a monthly maximum of 113 mm in May and a minimum of 19 mm in June, while the highest value of daily rainfall was recorded on September 26^{th,} with 36.55 mm. The mean air temperature (dark red line) was about 17.9 °C, ranging from a maximum daily value of 38.8 °C recorded on August 14th to a minimum of 4.5 °C registered on May 15 (Fig. 2a). Compared to the previous 30 years, the investigated growing season experienced positive temperature anomalies, while the cumulative precipitation in 2021 was 9% lower than the 30-year average (Supplementary figure S1). The daily relative humidity (Fig. 2b) showed a general, gradual decrease during the hottest period of summer, with spikes corresponding to precipitation events. VPD gradually increased during the summer as temperatures rose, reaching a peak of 2.52 kPa on August 12th (Fig. 2c). Finally, solar radiation (Fig. 2d) showed a highly variable pattern, characterized by rapid fluctuations between maximum and minimum values. Several peaks approaching or reaching 30 MJm^{-2} occurred during summer days with clear skies, while minimum values of radiation reaching or falling below 5 MJm^{-2} occurred on days with heavy cloud cover or during precipitation events. In addition, regarding the seasonal trend in radiation, we observed high values corresponding to the maximum summer solar potential in the Mediterranean regions (June and July), followed by a slight but clear decreasing trend starting in mid-August, suggesting the transition to autumn. We observed a remarkably stable baseline of near-zero daily wind speed from June through September, punctuated only by a single, sharp spike reaching approximately 2.5 kmh^{-1} in late July.

Soil moisture showed the typical decreasing trend of Mediterranean zones, with similar dynamics across all locations (Fig. 2a). At the SMR and SMM positions, moisture values at the two depths were very similar and identical during the dry season for the riparian probes. In contrast, soil moisture values measured at the SMF were higher at 35 cm than at 15 cm throughout the growing season. This offset reflects local variability in soil bulk density and pore structure at the probe location. In fact, although soil texture was classified as uniformly sandy loam across the hillslope, the bulk density measurements at this same hillslope confirmed non-negligible differences in soil structure among positions and depths (Kaffas et al., 2025). The data show a sharp, immediate spike in shallow-layer moisture following precipitation at both the SMF and SMM positions, while the deeper soil layers exhibit a more attenuated, gradual rise. However, we observed a distinct seasonal shift: during wet periods, the shallow-layer peaks preceded those of the deeper layers, whereas in summer the deeper-layer response preceded the shallow-layer response.

The sap flux in May and June was higher at SFU compared to SFM and SFR (Fig. 3b; Tukey HSD test, $p < 0.05$). We observed similar seasonal trends in the SFR and SFM, with flux values starting low in early summer, gradually increasing and stabilizing at approximately 800 $Lm^{-2}day^{-1}$, and then decreasing in autumn as temperature and VPD declined. In contrast, SFU sap flux peaked early in the growing season, exceeding the maximum values at the other two lines before steadily declining. By July, SFU sap flux values were statistically comparable to those of the other positions, but by August and September, they had fallen significantly below those of the other positions ($p < 0.05$). While these position-level trends represent the average behavior of the trees monitored at each location, a complementary pairwise analysis of individual-tree sap flux (Supplementary Fig. S3) showed that, although trees within the same position were on average more synchronous with one another than with trees at other positions, the strength of this synchrony varied among individuals, indicating that effects on transpiration processes due to hillslope-scale seasonal patterns coexist with the tree-level heterogeneity.

3.2. Correlation analysis during the growing season

The correlation analysis revealed distinct patterns in the hydro-meteorological controls of sap flux across the three study locations (Fig. 3). Atmospheric drivers, specifically solar radiation, air temperature, and VPD, exhibited strong positive correlations for all positions. Among these, radiation was the highest, peaking in the riparian zone (about 0.75) and remaining high at the midslope and upslope positions (about 0.40 and 0.45, respectively). Conversely, relative humidity exhibited a consistent

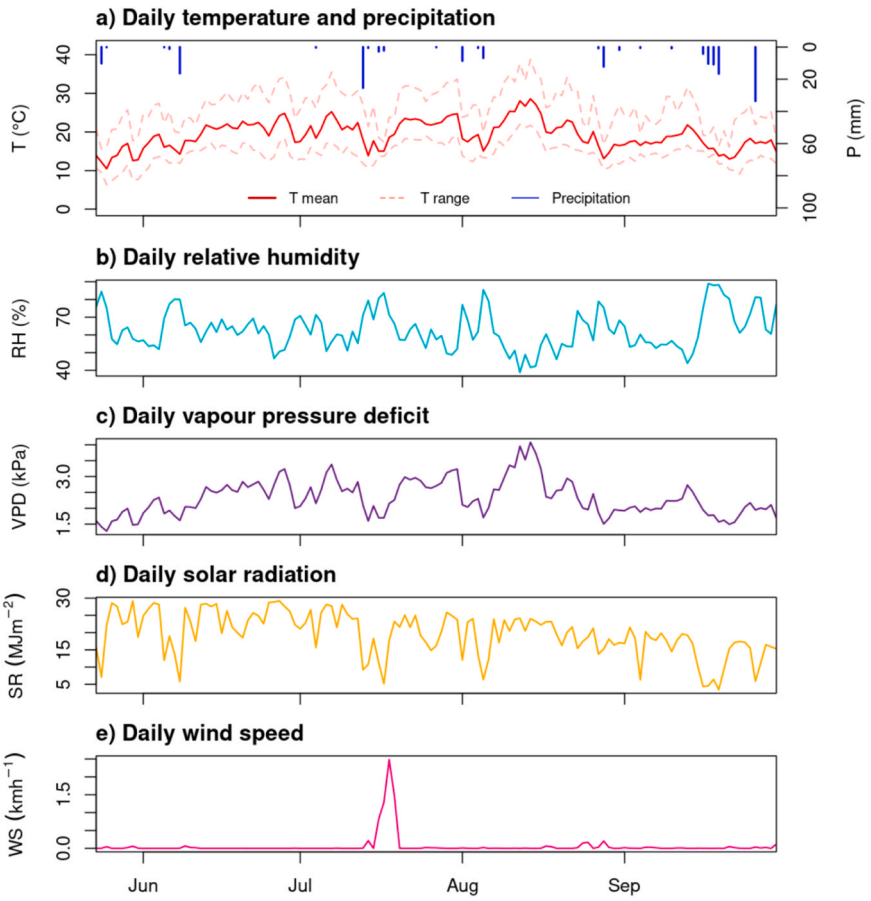

Fig. 2. Meteorological variables: a) daily air temperature (°C; mean in dark red and ranges in light red) and daily total precipitation (mm/day; in blue); b) daily relative humidity (%); c) daily vapour pressure deficit (kPa); d) daily solar radiation (MJm^{-2}); e) daily wind speed (Kmh^{-1}).

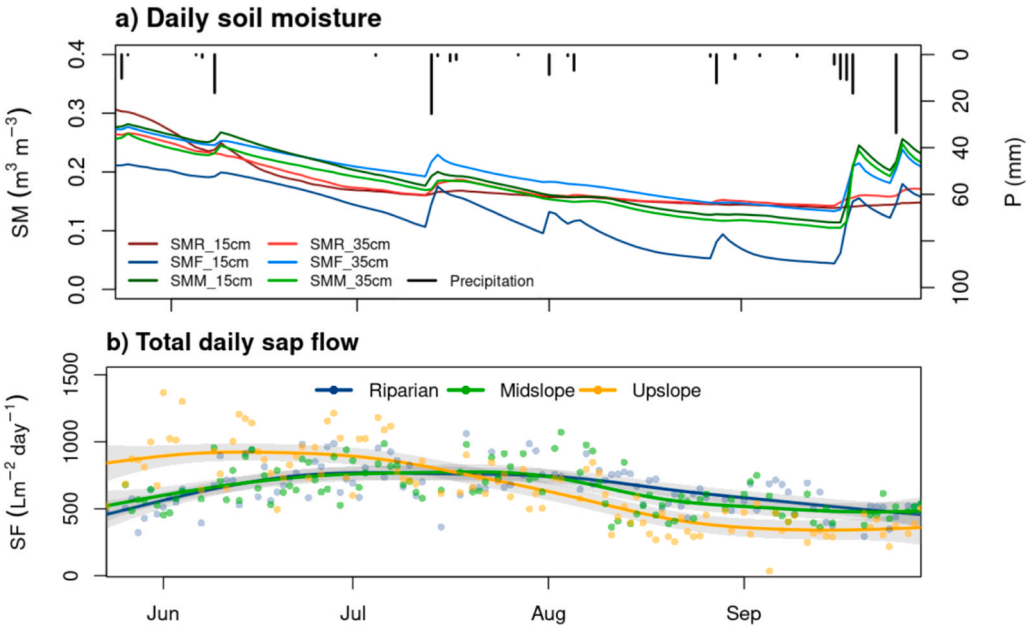

Fig. 3. a) Daily soil moisture (m3m-3) recorded by the different probes: SMR is the riparian position at depths of 15 and 35 cm, respectively; SMF is the footslope position at depths of 15 and 35 cm, respectively; SMM is the midslope position at depths of 15 and 35 cm, respectively. b) Total daily sap flux per square meter of sapwood (Lm-2day-1)) (average for each of the three slope locations) during rainless days, with trend displayed as a GAM (generalized additive model) line (dashed line) to fit smooth, non-linear trendlines through the noisy daily sap flow data across the growing season. The 95% confidence interval is highlighted in the grey shaded band.

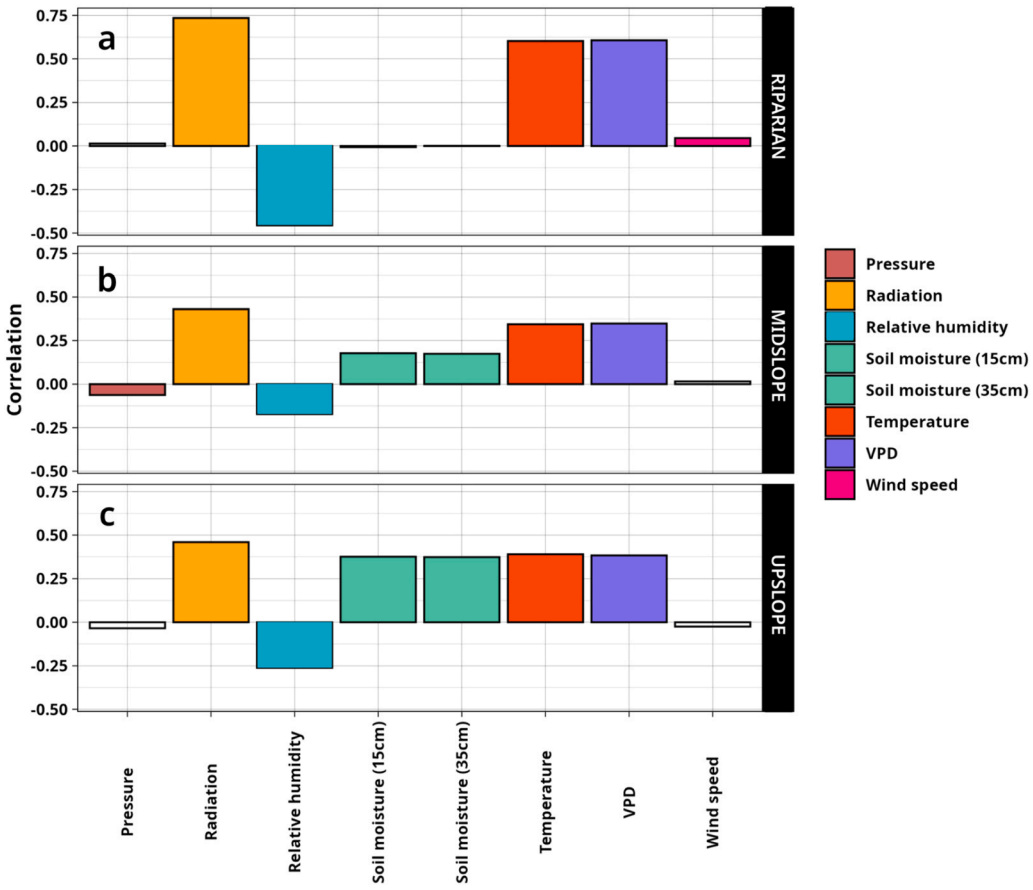

Fig. 4. Pearson correlation between the average hourly sap flux at each TT monitored location along the hillslope and the hydro-meteorological variables. Colour bars are unfilled when the correlation was not statistically significant. Critical values for correlation are identified by the horizontal dashed lines.

negative correlation along the entire hillslope, showing clear differences in hydrological control between the riparian zone and the two hillslope positions. In the riparian zone, soil moisture at both measured depths showed negligible correlation with sap flux, suggesting that transpiration in this area was not limited by water availability. However, when moving upslope, the influence of soil moisture increased significantly. At the midslope and upslope positions, soil moisture at both depths exhibited moderate positive correlations (ranging from 0.20 to 0.40), indicating a transition toward soil-moisture-limited conditions in higher topographic positions. Other meteorological variables, including atmospheric pressure and wind speed, exhibited near-zero or negligible correlations across all sites, suggesting they played a minor role in driving diurnal sap flux variations in our study area. Correlation values among the hydro-meteorological variables are reported in Fig. S4 and S5.

The moving-window correlation analysis (Fig. 5) revealed distinct temporal patterns in the sensitivity of sap flux to hydro-meteorological variables between the riparian and hillslope positions. In the riparian zone, the coupling between sap flux and atmospheric drivers remained remarkably stable throughout the growing season. VPD, temperature, and radiation maintained consistently strong positive correlations (r about 0.36–0.86) from May through September, while relative humidity exhibited a persistent negative correlation. The frequent lack of statistical significance for soil moisture (indicated by gray intervals) reinforces the interpretation that riparian transpiration is primarily energy-limited and decoupled from soil moisture fluctuations. However, a shift in soil moisture sensitivity was observed: a brief negative correlation in May transitioned to a positive correlation following the rise in temperature and VPD after July 20th, which lasted until mid-September (Fig. 5). By the end of the summer season, sap flux in the riparian site showed a positive correlation with soil moisture at 15 cm and a negative correlation with moisture at 35 cm.

In contrast, the midslope and upslope positions displayed a pronounced seasonal shift in hydro-meteorological control, showing a slight difference in the timing of the change from positive to negative correlations, with upslope lagging. During the early-to-mid growing season (May–July), responses to atmospheric demand at these locations were identical to those in the riparian zone (Fig. 5). However, during August and September, the strength of these atmospheric correlations decreased significantly, often losing statistical significance or trending toward zero. At the same time, soil moisture at 15 cm showed a stronger and more persistent correlation with sap flux during the mid-summer period, particularly at the upslope site. This transition suggests a seasonal switch from energy-limited to water-limited conditions. As shallow soil water was depleted, the physiological control of transpiration shifted from atmospheric demand to soil water supply, leading to the observed late-season breakdown in the sap flux-VPD relationship. Across all positions, both wind speed and atmospheric pressure were only occasionally significantly correlated during the growing season.

To investigate whether temporal variability in the correlation coefficients could be attributed to changes in environmental forcing, we analyzed the relationship between these coefficients and soil moisture availability (Fig. 6). Specifically, the moving-window correlation values, representing the coupling between radiation and sap flux (Fig. 6a, b) and between soil moisture and sap flux (Fig. 6c, d), were analyzed against the corresponding average soil moisture measured at depths of 15 cm and 35 cm. This approach allowed us to identify potential soil moisture thresholds where the hydro-meteorological control of sap flux shifts from atmospheric demand to soil moisture limitation. A different critical soil moisture threshold was identified for the two investigated depths, specifically 0.15 m^3m^{-3} for the shallow layer and 0.17 m^3m^{-3} for the deeper layer. Above this threshold, the correlation between sap flux and

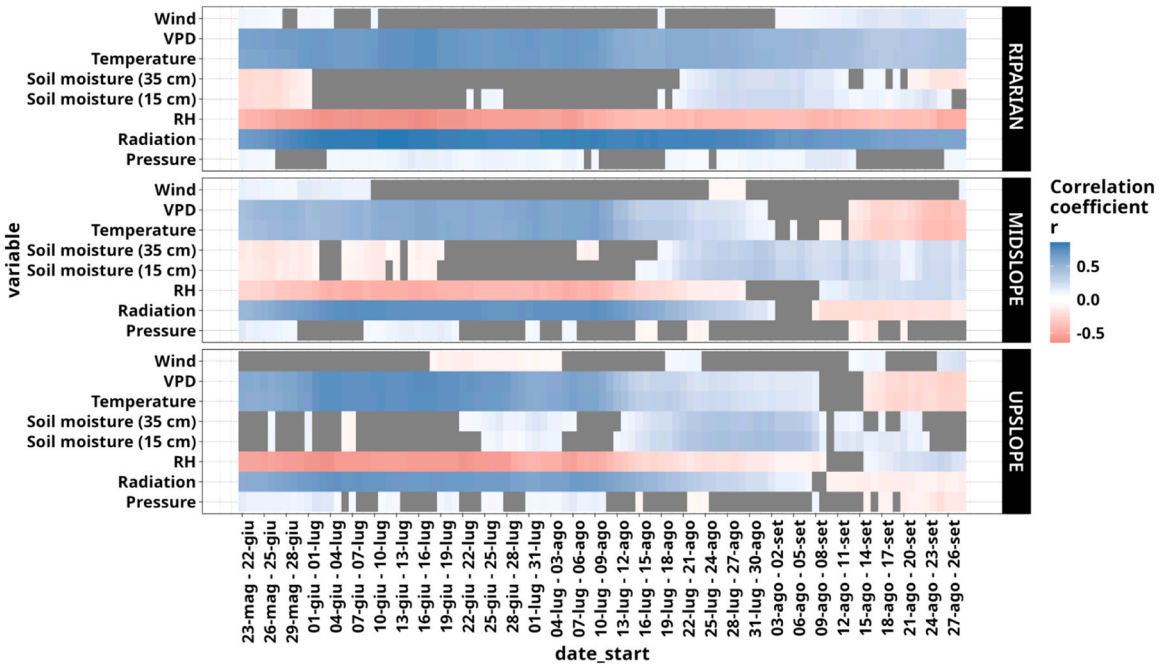

Fig. 5. Pearson correlations between sap flux and the hydro-meteorological variables for each hillslope location, computed over 30-day long timeframes. In blue, the positive correlations, in red the negative ones, and in grey the non-significant ones. The intensity of the colour reflects the strength of the correlation.

radiation remained high and stable across all topographic positions, while the correlation with soil moisture was negligible or slightly negative. However, once soil moisture values became lower than this threshold, the meteorological drivers of sap flux highlighted a dramatic shift, particularly at the midslope (green squares) and upslope (orange squares) positions (Fig. 6). In these water-limited conditions, the correlation with radiation collapsed, dropping from roughly 0.70 toward zero, while the correlation with soil moisture increased sharply, peaking at correlation values between 0.20 and 0.45. In contrast, the riparian zone (blue squares) maintained a consistently high correlation with radiation even at lower soil moisture values, further confirming its decoupling from soil water deficit. The plots of these correlations against the other transpiration forcings (namely radiation and VPD) showed different patterns Fig. S4.

3.3. Regression tree analysis

The relative influence of hydro-meteorological drivers on sap flux was analyzed across the three topographic positions using regression trees and variable importance plots. This analysis revealed marked differences

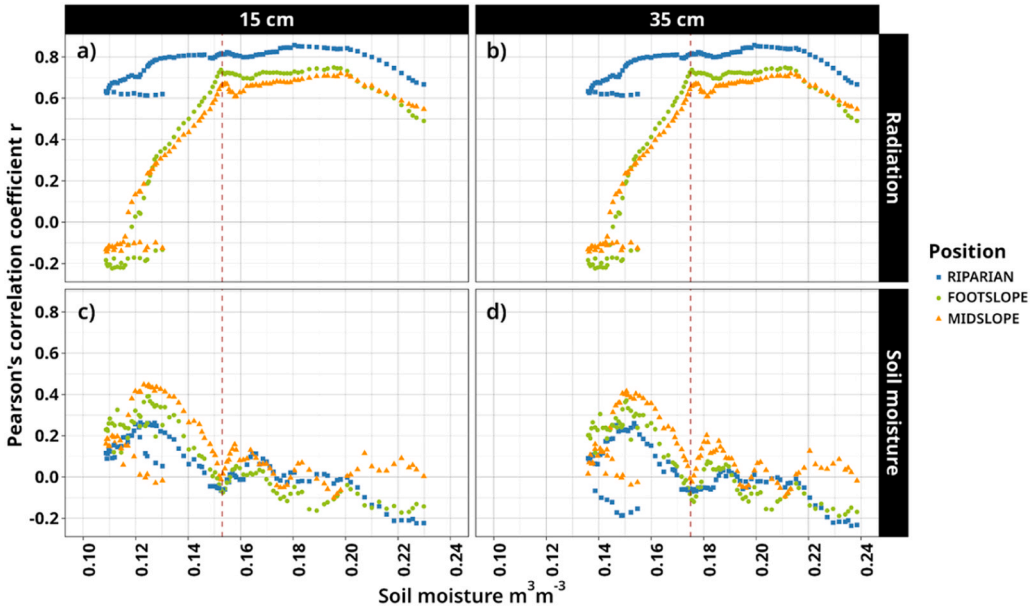

Fig. 6. Moving-windows correlation values plotted against the average soil moisture (m3m-3) during the corresponding time-period. a) Correlation between radiation and sap flux plotted against soil moisture measured at 15 cm of depth; b) correlation between radiation and sap flux plotted against the soil moisture measured at 35 cm depth; c) soil moisture-sap flux correlation plotted against soil moisture measured at 15 cm depth; d) soil moisture-sap flux correlation plotted against soil moisture measured at 35 cm depth. In each panel, the red line highlights the soil moisture threshold beyond which a trend change was visually identified; the colors identify the three different slope locations: blue = riparian, green = footslope, and orange = midslope.

in the hierarchy of predictors along the hillslope gradient.

At the upslope and midslope positions, soil moisture at both depths (15 and 35 cm) emerged as the key variable governing the model's accuracy in predicting sap flux(Fig. 7a and b), accounting for the largest share of predictive importance. The corresponding regression trees support this pattern, with early branching occurring on soil moisture thresholds (0.12 and 0.22 m^3 m^{-3} at 15 and 35 cm, respectively, at the upslope position; 0.13 m^3 m^{-3} at 15 cm at the midslope position), indicating that hillslope sap flux sensitivity is mainly governed by soil water availability. Solar radiation was also an important driver at the midslope position, with a score close to that of soil moisture. In contrast, in the riparian zone (Fig. 7c), solar radiation is the dominant driver, with an importance score nearly double that of the next most influential variables (temperature and VPD), and the root node split the entire dataset at a radiation threshold of 273 MJ m^{-2}.

Beyond these primary drivers, atmospheric variables, VPD and temperature served as consistent secondary predictors across all three

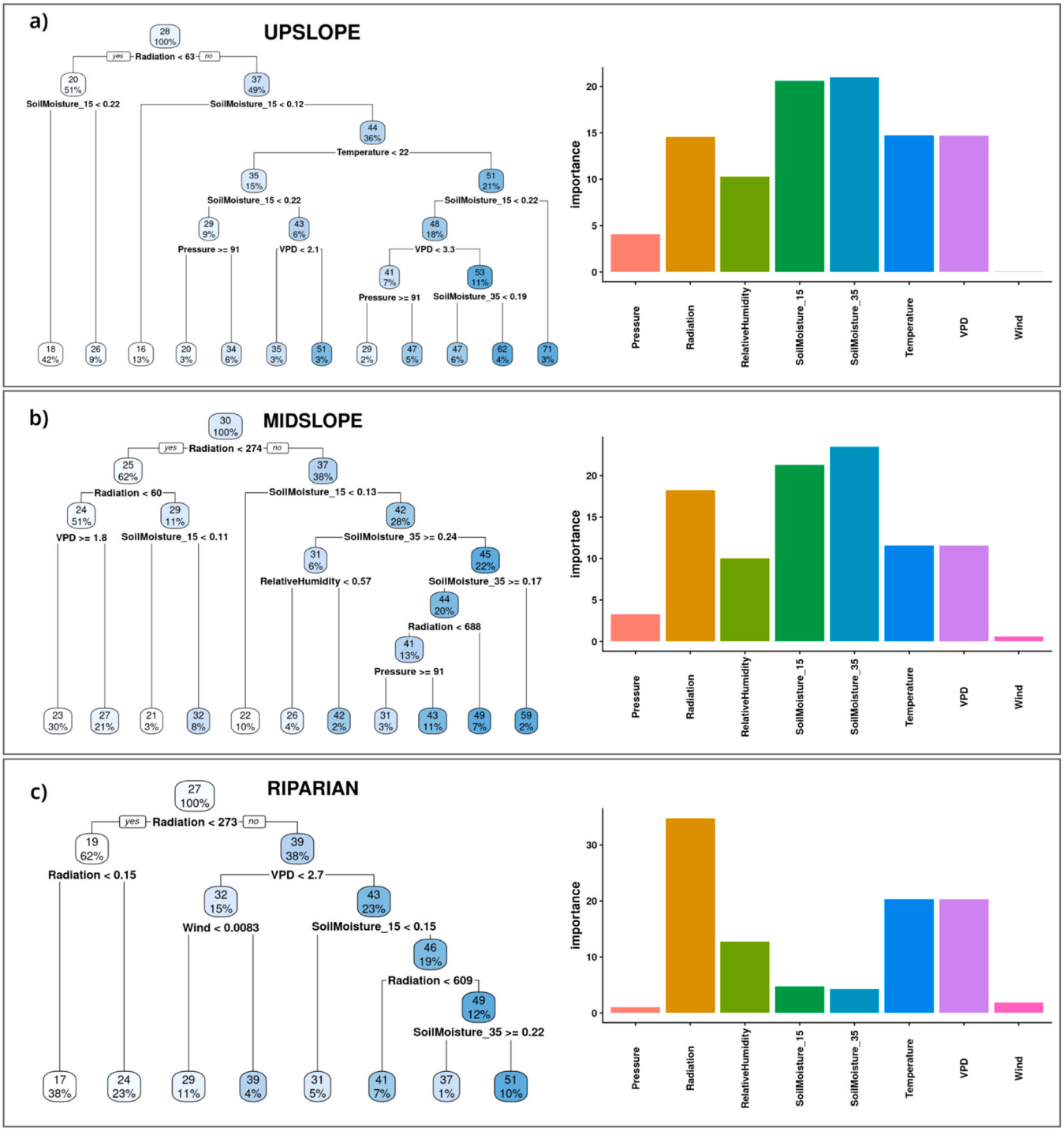

Fig. 7. Regression trees for the locations: a) upslope, b) midslope, c) riparian. In each node, the average value of sap flux for the observations belonging to that node, and the percentage (%) of observations included in that node, are reported. Below each node, the splitting rule is also reported: e.g., Radiation < 63 means that observations are split in that node according to their Radiation value, going to the left node if the value is less than 63, and to the right if the value is greater than 63, and so on, passing all the nodes of the regression tree until they reach the leaves. The nodes at the bottom do not lead to any further split. Below each regression tree, the relative importance (in %) of each variable is indicated. The nodes are colored according to the sap flux value from white (low values) to blue (high values).

topographic positions, though their relative importance increased markedly in the riparian zone, where they ranked immediately behind radiation. At the upslope and midslope positions, these atmospheric variables further partitioned the data only after soil moisture thresholds were met, reinforcing their subordinate role relative to water availability at these sites. Relative humidity exhibited a moderate, comparable contribution across all three positions, while wind and pressure consistently showed the lowest predictive power, with negligible importance scores and rarely appearing as significant nodes within the regression trees.

4. Discussion

4.1. Space- and time-variable controls on tree transpiration

This study examined how soil moisture variability along the hillslope influences the spatial and temporal dynamics of sap flux in beech trees, providing new field-based evidence on the spatially and temporally variable influence of different environmental factors on tree transpiration. The time series of sap flux recorded at the three hillslope locations showed different patterns and relationships with the hydro-meteorological variables, revealing a clear topographic gradient effect on xylem sap flux of beech trees. This indicates that the spatial variability of sap flux was influenced by a combination of local hydrometeorological controls that affected subsurface flow and soil water availability, as well as the timing of tree water demand across slope positions.

In agreement with other studies (Berry et al., 2016; Tromp-van Meerveld and McDonnell, 2006), hydro-meteorological conditions modulated the strength of coupling between transpiration and atmospheric demand. However, whereas Tromp-van Meerveld and McDonnell (2006) attributed late-summer transpiration differences to soil texture, our study site lacks spatial variability in soil texture modulated by topography (Kaffas et al., 2025). Therefore, soil texture cannot be considered the primary driver of the observed spatial variations in transpiration, which are instead modulated by topographic position and hillslope connectivity. Recent geophysical and infiltration experiments conducted at this study site by (Di Prima et al., 2026) showed that the soil exhibits dual-permeability: while rainfall slowly wets the shallow matrix, stemflow bypasses it entirely through highly conductive, root-associated macropores. Considering that a large portion of the soil water is channeled through these fast-flow pathways, plant-water availability along the hillslope is not merely governed by the soil depth, but is strongly mediated by the rate of this preferential drainage. For this reason, upper slope trees are constrained by rapid subsurface routing that drains water away, whereas the riparian trees benefit because these same fast-flow networks continuously deliver and accumulate lateral subsurface inputs downslope. The interaction between preferential flow and topographic position drives rapid water depletion upslope and sustains water accumulation in the riparian zone. This spatial divergence in water availability directly shaped the trees' physiological responses to climate across the topographic gradient.

When considering the growing season, the abundant water supply allowed the riparian SFR to be primarily controlled by incoming radiation and evaporative demand, behaving as a well-watered system in which energy availability, rather than soil water supply, dictated the transpiration rate (Zhang et al., 2017). Conversely, moving upslope, the importance of atmospheric variables was replaced by that of soil moisture (Fig. 4), marking a transition to a water-limited regime (Aranda et al., 2005; She et al., 2013). This can be regarded as an effect of topography, which influences the distribution of water in soil by affecting drainage dynamics and ultimately tree transpiration (Bronstert et al., 1998; Fabiani et al., 2022b). The higher and more temporally stable water content detected in the riparian area, compared to the higher locations (Fig. 2), suggests a better water supply for the riparian trees than for the other two locations. Similarly, an isotopic study conducted on the same hillslope reported location-specific water use, with beech trees at the riparian location accessing a more temporally stable water source than trees in the hillslope positions (Fabiani et al., 2024), enabling them to sustain a longer growing season. Such a reduction in water uptake, driven by soil-water limitation under dry conditions, has been reported several times in the literature (Aranda et al., 2005, 2000; Fabiani et al., 2022a, 2022b; Granier et al., 2000; Renner et al., 2016).

The temporal evolution of the correlations (Fig. 5) revealed a seasonal shift in hydrometeorological controls. During the early growing season (May–June), sap flux variability was primarily governed by atmospheric demand, specifically solar radiation, temperature, and VPD. During this period, upslope trees (SFU) exhibited higher initial sap flux rates than midslope and riparian trees, peaking early in the season before soil water deficits developed. This early-season dynamic coincided with ongoing canopy development. As documented at this site by Verdone et al. (2025a), canopy expansion in May exhibited a distinct topographic lag, progressing from lower-slope positions (~90% cover) to upper-slope positions (~70% cover). Despite this lag in canopy development, high early-season atmospheric demand and radiation exposure on the upper slope drove rapid transpiration in SFU trees before soil moisture limitations set in. As the season progressed, the depletion of soil moisture triggered a fundamental shift in the ecosystem's functional state. Similar to observations in other temperate broadleaf and Mediterranean systems (e.g., Poyatos et al., 2008; Fu et al., 2021), this transition marks the point where soil water supply, rather than atmospheric demand, becomes the primary bottleneck for transpiration. This process is widely recognized as the crossing of a critical soil moisture threshold, below which vegetation water use functionally decouples from atmospheric drivers (Fu et al., 2022).

Crucially, the timing of this shift proved to be a high-resolution indicator of topographic constraints. The onset of a positive correlation with soil moisture occurred notably earlier in the upslope position than in the riparian zone. This asynchrony suggests that topography acted as a temporal buffer, where the duration of water-limited conditions was dictated by a tree's position along the slope. Specifically, a related but distinct pattern concerns the timing between the two hillslope positions. As reported in Section 3.2, the shift in atmospheric coupling occurred slightly later at the upslope position than at the midslope one (Fig. 5), with the positive soil moisture–sap flux correlation likewise emerging later at SFU than at SFM. This pattern appears to contradict the expectation that the drier upslope position should reach water limitation earlier, but our methodology explains this apparent discrepancy. As already detailed in Section 2.4, the correlation analysis for the midslope (SFM) and upslope (SFU) sap flux series was computed against the same averaged soil moisture values of the footslope and midslope probes (SMF and SMM), because no dedicated soil moisture probe was installed at the upslope tree position. The observed asynchrony between SFM and SFU therefore cannot be attributed to a difference in the soil moisture input itself. This shared signal is nonetheless heterogeneous: an independent, probe-level analysis of these same sensors by Kaffas et al. (2025) showed that the SMF is dominated by decoupled, non-sequential (preferential-flow-driven) soil moisture dynamics during dry periods, whereas the SMM position exhibits more tightly coupled, sequential (matrix-flow-driven) behaviour, also consistent with the divergence between the 15 and 35 cm signals at SMF against their close tracking at SMM (Fig. 3a). Because the soil moisture input for the correlation with sap-flux at the hillslope trees was identical, the delayed emergence of a significant positive correlation at the upslope position more likely reflects differences on the tree side. For instance, the canopy closure at the upslope lags behind that at midslope, reaching only about 70% of full cover by early May (Section 2.1; Verdone et al., 2025a), so a stronger and more persistent radiation/VPD-driven sap flux signal would be expected to hide the emerging soil-moisture control for longer at this position. This is consistent with the comparatively small sapwood-to-basal-area fraction in upslope trees (8%, versus 14% at midslope; Section 2.3), which may indicate reduced hydraulic buffering capacity as atmospheric forcing decreases.

Beyond these seasonal patterns, the moving-window correlations (Fig. 6a–b) also highlight hysteresis patterns: for a given soil moisture value, the radiation–sap flux correlation coefficient differs depending on whether soil moisture is declining (drying phase) or recovering (re-

wetting phase) (Figs. S7–S8). This hysteresis reflects, at the diurnal scale, the same shift in physiological control documented above at the seasonal scale. The pronounced clockwise hysteresis observed in riparian trees (and in midslope trees early in the season) is consistent with nighttime stem-water refilling, when soil water availability in the riparian zone facilitates nocturnal replenishment of internal water storage. This allows higher morning sap flux than in the afternoon. As the summer season continues, midslope trees transition toward a figure-eight (crossing) hysteresis loop, reflecting a dual-regulation regime in which morning sap flux tracks early radiation and overnight refilling, while rising afternoon VPD combined with moderate water limitation triggers stomatal closure. Upslope trees in late summer instead display a flattened, counter-clockwise pattern consistent with a severe water deficit, reduced peak sap flux, and a substantial time lag in the hydraulic response, with peak sap flux delayed until late afternoon. Integrating these diurnal hysteresis dynamics with the seasonal framework above provides a multiscale explanation of trees' water-use strategies. In fact, while seasonal metrics indicate when water deficit occurs, diurnal hysteresis details the specific physiological behaviors that drive those trends hour by hour.

Consistent with findings across various species (Jiao et al., 2019; Meng et al., 2022), our data confirm a shift from radiation to soil moisture limitation with a non-linear response (Jiménez-Rodríguez et al., 2022). In our relatively uniform sandy loam hillslope, this threshold is marked by a value of soil moisture values between 0.15 and 0.17 m^3 /m^3 , which functionally corresponds to the critical physiological threshold of 40% of relative extractable water required to sustain plant transpiration (Granier et al., 2000; Vicca et al., 2012). This sharp functional pivot and relatively high threshold align with macro-scale assessments of European forests, which frequently exhibit conservative thresholds to safeguard hydraulic integrity at the onset of soil drying (Fu et al., 2022) .

Reaching this tipping point depends strictly on the tree's position along the slope. In fact, while the hillslope position experienced a severe drawdown below this limit during the peak drought in August, soil moisture in the riparian zone reached a stable minimum and remained there without further decrease, providing environmental stability for sap flow processes. Once this critical soil moisture level was breached, the stomatal regulation of beech appeared to decouple from atmospheric demand to prioritize hydraulic safety, a finding that underscores the importance of soil-water status in predicting forest-atmosphere exchange under future climatic scenarios. Within our hillslope, the correlation-based analysis identified a common critical soil moisture value shared across the three topographic positions (0.15 and 0.17 m^3/m^3 at 15 and 35 cm, respectively), with topography instead governing the timing at which each position reached this threshold rather than the threshold value itself. While the identified soil moisture thresholds effectively capture these critical shifts in transpiration, these numerical values must be contextualized within the local physical setting. These critical thresholds are strongly dictated by local edaphic characteristics, including soil texture, pore size distribution, and hydraulic conductivity, as well as root distribution (Fu et al., 2024) . Consequently, these specific values represent local ecohydrological tipping points rather than broad, universal constants. Although monitoring in this study was restricted to 35 cm of soil depth, this layer represents the species' primary physiological zone, containing over 70% of the fine roots responsible for water and nutrient uptake (Meier et al., 2018). Therefore, while the overarching eco-functional dynamics and methodological framework are broadly applicable, the specific quantitative thresholds remain site- and period-conditioned and require local calibration when applied across different soil-climate regimes.

It is evident that the soil moisture thresholds identified by the correlation-based analysis (0.15 and 0.17 m^3/m^3 at 15 and 35 cm) differ from those identified independently by the regression trees at each hillslope position (0.12–0.22 m^3/m^3, depending on position and depth; Fig. 7). We attribute this difference to the two methods answering different questions: the correlation-based threshold is a single, pooled estimate of when the coupling between sap flux and radiation breaks down across the entire hillslope, based on a 30-day moving window; the regression tree threshold is fitted independently at each position from the full hourly dataset together with five other predictors, and so is shaped by the local soil moisture range and by covarying atmospheric conditions at that specific position, not by a shared window. Despite this methodological divergence, both approaches place the transition within a narrow, physiologically plausible soil moisture range (0.12–0.22 m^3/m^3) that is consistent with the 40% relative-extractable-water threshold reported for temperate forests (Granier et al., 2000; Vicca et al., 2012) and with the method-dependent variation documented for continental-scale soil moisture thresholds by Fu et al., (2022). This convergence across independent analytical approaches strengthens confidence that soil moisture limitation in this system sets in within this range, rather than at a single precise value. This convergence across independent analytical approaches reinforces our interpretation that soil moisture limitation in this system emerges within this range rather than at a single precise value.

4.2. Ecohydrological and management implications

Our findings demonstrate that a forest stand does not operate as a uniform "ecohydrological unit". Instead, beech trees along a hillslope gradient can be governed by distinct environmental hierarchies and exhibit highly localized water-use patterns. Across all three topographic positions, solar radiation consistently emerged as the primary energy input governing sap flux at the daily/sub-daily scale. However, the variable that limited or modulated this radiation-driven response shifted along the hillslope: at the upslope and midslope positions, soil moisture (15 and 35 cm) acted as the dominant constraint, indicating water-limited conditions, whereas at the riparian position, where proximity to the water table kept soil moisture non-limiting, VPD and temperature, i.e., atmospheric demand, became the main limiting factor instead. This spatial partitioning supports the "opportunistic" plasticity of the species: trees in riparian zones maximize transpiration under favorable conditions, while those only meters away on the upslope shift to a survival-based, water-limited strategy (Puchi et al., 2024). Such fine-scale heterogeneity suggests that "one-size-fits-all" hydrological models may overlook the localized differences in environmental forcing and soil moisture availability created by topography.

This research adds novel high-resolution details to the debate on topographic influence. Previous studies at Lecciona established that topography modulates beech water-use strategies, and each identified soil moisture thresholds in different ways: through isotopic and growing-season evidence (Fabiani et al., 2024), through drought-severity classes (SWDI) associated with more negative VPD–sap flow time lags (Verdone et al., 2025a), and through wavelet coherence breakdown in the SM–VPD and SM–P couplings (Murgia et al., 2026). None of them derived the threshold directly from a continuous, cross-validated bivariate relationship between sap flux and soil moisture magnitude, nor identified it simultaneously against a competing driver (like radiation) to pinpoint the exact crossover point where control switches from energy-limited to water-limited transpiration. Our moving-window correlation analysis complements the wavelet-based approach of Murgia et al. (2026) by plotting the correlation coefficients of SF–radiation and SF–soil moisture directly against continuous soil moisture values themselves (rather than against time or frequency/scale), allowing us to identify the specific SM magnitude at which the two relationships invert, giving a threshold expressed directly in physical soil moisture units rather than inferred from the breakdown of a coherence pattern. Building on this, we introduce regression-tree analysis, a technique not used in any of the earlier Lecciona studies, which avoids pre-specifying linear or hysteretic relationships, ranks the relative importance of six candidate hydro-meteorological predictors simultaneously, and reveals the hierarchical structure of controls, i.e., that soil moisture only becomes a splitting variable once radiation-driven splits are exhausted at hillslope positions, and never at the riparian position. This hierarchical, threshold-based characterization (0.15 m^3 m^{-3} at 15 cm; 0.17 m^3 m^{-3} at 35 cm) refines and independently

corroborates, using a different sap flux network, the $\approx 0.15\ m^3\ m^{-3}$ threshold previously observed from drought-class analysis by Verdone et al. (2025a) and wavelet coherence by Murgia et al. (2026), while additionally resolving it for two soil depths and formally quantifying its relationship to a competing energy-driven predictor (like radiation) rather than to VPD or precipitation alone.

Unlike other studies that reported either highly correlated (Kume et al., 2016) or near-identical (Kumagai et al., 2007) sap flux patterns across slope position, we showed that these relationships evolve intra-seasonally. By identifying the timing of the shift in the limiting factor from soil moisture to atmospheric demand, we showed that topography-driven water redistribution generated a dynamic ecohydrological mosaic, rather than a static spatial pattern, layered on a radiation-driven baseline common across the entire hillslope. The observed asynchrony in responses to soil water deficit suggests that hillslope-scale processes, such as water redistribution and differential source availability (Fabiani et al., 2024), acted as a primary filter for atmospheric demand. Ultimately, the timing of this environmental switch was as critical to forest dynamics as the magnitude of the water flux itself.

Our focus was on the European beech (*F. sylvatica* L.), key to European forestry, especially in Mediterranean areas with severe summer drought. Water use by beech is well-known in Central Europe (Granier et al., 2000; Petrík et al., 2022), but data on its hydraulic behavior at the southern edge of its range are limited (Stojnić et al., 2018). This gap is worrying given the decline in Mediterranean beech growth linked to climate change (Calderaro et al., 2020; Serra-Maluquer et al., 2019). By analyzing transpiration during an anomalously hot summer, our study provides a high-resolution window into the intra-seasonal dynamics likely to become the "new normal" for these ecosystems. Unlike coarser regional studies (Klesse et al., 2024), our results demonstrated that topography serves as a primary driver of fine-scale spatial heterogeneity in transpiration. We observed a distinct physiological pivot: under high soil moisture, transpiration was governed by solar radiation; however, as the season progressed, topographic position dictated the onset of moisture-limited water use. This finding aligns with global concerns about shifts in gas-exchange regulators under climate change (Diao et al., 2020; Lu et al., 2024). From an ecohydrological perspective, our results challenge the assumption of uniform evaporative fluxes within forest stands. The "dynamic hydrological mosaic" created by hillslope gradients suggests that:

- Topography acts as a buffer or amplifier: local water availability determines whether transpiration remains governed by radiation and atmospheric demand (as in the riparian zone) or becomes constrained by soil moisture (as at the midslope and upslope positions).
- This mosaic is not restricted to the hillslope scale. We observed synchrony among neighboring trees, generally strongest within the same topographic position, but not uniform across individuals at a given position. This observation highlights that the ecohydrological mosaic is nested, expressed first at the scale of topographic position and then at the scale of individual root systems, consistent with the high intraspecific plasticity in water-regulation strategy documented for the isohydric–anisohydric continuum (Klein, 2014; Domec and Johnson, 2012).
- Management must be site-specific: decision-makers should move toward precision forestry practices that account for this fine-scale vulnerability to ensure forest health and carbon sequestration (Hartmann et al., 2022).

Ultimately, unraveling these localized patterns is essential for refining ecohydrological models. Future research should replicate these experiments across diverse species to confirm whether this topographic "filtering" of environmental constraints is a universal trait or a specific adaptation of Mediterranean beech populations.

5. Conclusions

This study, based on a network of low-cost, IoT-based TreeTalker sensors, showed that topography affected the water availability of beech trees across different sites along a steep Mediterranean hillslope. Across all three investigated hillslope positions, solar radiation consistently emerged as the primary driver of transpiration. However, topography modulated this baseline response: at the midslope and upslope positions, transpiration became increasingly constrained by soil moisture once a critical threshold was crossed, whereas in the riparian zone sustained water availability buffered trees from this limitation, allowing transpiration to remain governed primarily by radiation and atmospheric demand throughout the season. This shift from radiation-driven to soil-moisture-limited transpiration occurred once soil moisture fell below a critical threshold corresponding to about 40% relative extractable water, with timing varying across locations and reducing transpiration rates accordingly. While the eco-functional dynamics and methodological framework identified here are broadly applicable, this specific threshold value is likely site- and period-conditioned, requiring local calibration before being applied elsewhere. This study demonstrates that a spatially replicated, low-cost IoT sensor network can reliably capture these fine-scale ecohydrological dynamics, and provides new insight into the topography-driven soil moisture patterns underlying the spatial heterogeneity of tree transpiration at the hillslope scale, by defining this threshold from a continuous, cross-validated relationship between sap flux and a competing energy-driven predictor.

From a modeling perspective, this study confirms the importance of accounting for soil moisture effects on transpiration, especially under dry conditions in Mediterranean regions, with relevant implications for hydrological modeling and forest management. The fine-scale variability in soil moisture available to trees suggests that topographic effect should be taken into account when planning the acquisition of transpiration data to represent a broader context, like a whole catchment. From a management perspective, understanding the interaction between drought and topography may help identify forest areas where dry conditions have the most severe impact on trees and inform appropriate management strategies. However, further studies focused on plant functioning along steep hillslopes are necessary to better understand the role of trees in the hydrological cycle within forested catchments, and thus to support the sustainable management of forest and water resources in mountain areas.

CRediT authorship contribution statement

Jerzy Piotr Kabala: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Ilenia Murgia:** Writing – original draft, Formal analysis. **Matteo Verdone:** Writing – review & editing, Methodology, Data curation. **Ginevra Fabiani:** Writing – review & editing. **Ilaria Zorzi:** Data curation. **Alessio Giovannelli:** Writing – review & editing, Methodology, Data curation. **Giovanna Battipaglia:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Daniele Penna:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Claudia Cocozza:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124342.

Data availability

Data will be made available on request.

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