Resilience or decline? Insights from long-term sap flow and wood anatomy monitoring in fire-damaged *Pinus pinaster* Aiton forest

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Wildfires represent a major disturbance in Mediterranean forests, often triggering long-term functional decline in surviving trees. Understanding the hydraulic and eco-physiological trend of fire-affected stands is essential to assess whether trees are on a recovery path or progressing toward irreversible decline. In this study, we combined four years of continuous sap flow monitoring with wood anatomical analyses and satellite observations in a Mediterranean pine forest severely affected by fire. Continuous measurements in burned and control trees revealed contrasting transpiration strategies and progressive divergent pattern of hydraulic performance under recurrent drought conditions. Burned trees initially increased transpiration as a compensatory response but gradually exhibited signs of functional impairment, including reduced hydraulic efficiency, altered xylem traits, and limited canopy recovery. Further, remote sensing highlighted persistent canopy degradation and the spread of invasive vegetation, exacerbating water competition and accelerating decline. Control trees, by contrast, maintained a conservative water-use strategy and showed a greater capacity to exploit favorable climatic periods. These findings highlight the vulnerability of fire-damaged forest stands to eco-physiological decline, with potential implications for delayed mortality. The integration of long-term sap flow, wood anatomy, and satellite monitoring emerges as a powerful approach for detecting early-warning signals of resilience loss and informing post-fire forest management in drought-prone ecosystems.

KEYWORDS

sap flow monitoring, post-fire resilience, Mediterranean forests, wood anatomy, tree talker

1 Introduction

In recent decades, forest wildfires have increased exponentially worldwide as a consequence of climate change coupled with the intensification of human activities (Jones et al., 2024; Senf et al., 2020). Urban expansion near forests, rising temperatures and changes in precipitation regimes have increased the risk of wildfire ignition and spread, causing extensive environmental and ecological damage (Jolly et al., 2015). Although fire plays a positive ecological role in the renewal of forest ecosystems (Huntley, 2023), the increase in its frequency, severity and intensity are undermining the resistance and resilience of forests (Falk et al., 2022; Pausas and Fernández-Muñoz, 2012). Europe is one of the global hotspots for forest fires (Senf and Seidl, 2020). According to the annual fire report published by the Joint Research Centre (JRC), around 1.3 million hectares of vegetation burned on the European continent alone in 2017, a trend that has grown steadily in recent years. In fact, between 2022 and 2024, the total area affected by fires exceeded 1.9 million hectares (San-Miguel-Ayanz et al., 2025). Fire-induced tree mortality is closely linked to the intensity and duration of flame exposure, which determine different levels of damage to plant tissues (Hood et al., 2018).

In crown fires, high temperatures can reduce the photosynthetic surface area and affect the water balance, leading to physiological collapse (Bär et al., 2019; Varner et al., 2021). Flames can also damage the stem, cause cambium necrosis and disrupting xylem and phloem flow (Madrigal et al., 2023; Michaletz et al., 2012; Mundo et al., 2019). Finally, roots can also suffer irreversible damage, limiting water and nutrient uptake (Hood et al., 2018; Swezy and Agee, 1991). The combination of these effects can lead to immediate tree death in the most severe cases or trigger a progressive process of tree decline in the medium/long term, leading to delayed mortality (Bär et al., 2019). This is a well-documented phenomenon in the literature, where trees initially survive to fire, but undergo a slow decline that culminates in death several years later (Maringer et al., 2021). The immediate effects of fire are further influenced by post-fire stressors, including drought, elevated temperatures, intraspecific competition, alterations to soil biophysical properties, and increased susceptibility to insect or pathogen attack (Anderegg et al., 2015; Jeronimo et al., 2020; Kane et al., 2017; Niccoli et al., 2023a). The interaction of these factors leads to severe physiological imbalances that can progressively compromise the ability of trees to survive (van Mantgem et al., 2013).

In the Mediterranean context, post-fire tree survival is strongly influenced by frequent and prolonged droughts and heat waves, especially during summer (Camarero et al., 2024; Turco et al., 2018). In this region, even forests affected by low/medium intensity fires may show greater sensitivity to water stress, triggering widespread episodes of tree mortality (Blanco-Rodríguez et al., 2023; Rebollo et al., 2024). This phenomenon is particularly evident in countries such as Spain, Portugal and Italy, which are among the most affected by both climate stress and fires (San-Miguel-Ayanz et al., 2025). In these areas, numerous studies report episodes of post-fire tree mortality associated with exceptionally hot years (Calderisi et al., 2025; Niccoli et al., 2019; Rebollo et al., 2024).

The scientific literature on delayed mortality triggered by fire often presents heterogeneous results (Hood, 2021). Most studies agree that fire can severely compromise the hydraulic functionality of trees, causing embolism and structural damage to the xylem (Bär et al., 2019, 2018; Kavanagh et al., 2010; Michaletz et al., 2012; West et al., 2016). During a fire, high temperatures induce extreme vapor pressure deficits that can cause cavitation of xylem vessels, permanently reducing water transport capacity and, promoting tree mortality over time (Balfour and Midgley, 2006; Kavanagh et al., 2010; Thompson et al., 2017). In addition, the heat of the flames can cause irreversible deformations in the xylem tissue, further reducing the hydraulic conductivity of the cells. This process leads to decreased transpiration, accelerated depletion of carbon reserves, and disruption of hydraulic functioning, ultimately resulting in eco-physiological collapse of the affected trees (Bär et al., 2019; Hood, 2021; Michaletz et al., 2012). However, other studies have reported the ability of trees to recover over time, even in the presence of fire scar that reduced hydraulic conductivity and increased vulnerability to water stress in the post-fire period (Mundo et al., 2019). Other recent studies have not found significant changes in embolism vulnerability or xylem deformations in conifers, even after moderate intensity fires (Battipaglia et al., 2016; Niccoli et al., 2023c; Partelli-Feltrin et al., 2021, 2023). In some cases, increases in stomatal conductance and photosynthetic rates have been observed in the years following fire (Gričar et al., 2020; Salmon et al., 2015; Valor et al., 2018; Wallin et al., 2003). These contrasting results highlight the complexity of post-fire responses and suggest that factors such as species-specific traits and characteristics, disturbance intensity and subsequent environmental and climatic conditions are important determinants of tree survival, recovery and decline (Fernandes et al., 2008; Hood, 2021; Paula et al., 2009; Pellegrini et al., 2017).

In this context, dendro-anatomy studies have proven to be particularly effective in analyzing the response of trees to fire: these approaches allow to reconstruct the variation in growth dynamics between pre- and post-fire years (Battipaglia et al., 2016; Beghin et al., 2011; Camarero et al., 2024; De Micco et al., 2013; Niccoli et al., 2023c, 2023b; Valor et al., 2018, 2015) and to study in detail the structure and functionality of xylem cells over time, also in relation to climatic variables (Battipaglia et al., 2014; Castagneri et al., 2018; Kabala et al., 2024; Niccoli et al., 2024b; Olano et al., 2012; Pacheco et al., 2016; Piermattei et al., 2020). While these techniques allow the analysis of responses at seasonal and annual scales, the development of new technologies, such as sap flow measurement, allows the monitoring of hydraulic dynamics of trees under stress with higher temporal resolution (Čermák et al., 2004; Do et al., 2018). However, only a few studies have analyzed sap flow in Mediterranean burned trees. For example, Ferrat et al. (2021) in France observed that sap flow of *Pinus nigra* did not show significant differences between control and burned trees after a prescribed fire. On the contrary, other studies conducted in Spain and Italy found after a moderate intensity fires an increase in trees

transpiration in the years following the fire, which was interpreted as a strategy to increase carbon uptake despite significant defoliation (Niccoli et al., 2023c; Salmon et al., 2015). Unfortunately, sap flow monitoring of burned trees has often been limited to short periods, such as a few months or at most a year. Longer-term studies are lacking, while they are crucial for understanding tree recovery or irreversible decline dynamics and to eventually identify early warning signals of tree mortality.

Our study aims to fill this gap by monitoring long-term sap flow dynamics in a *Pinus pinaster* Aiton forest located in southern Italy, affected by a fire in July 2017 that caused significant defoliation.

The post-fire responses of this pine forest have been previously examined in both the short and medium term using dendrochronological and isotopic approaches (Niccoli et al., 2023b, 2023c, 2019), offering complementary insights into the early stages of recovery. Indeed, immediately following the fire, field observations at burned site documented an average trunk scorch height of approximately 3 m and minimal crown consumption (~10%), with very low tree mortality (<2%) (Niccoli et al., 2019). Nevertheless, extensive bud mortality was observed, resulting in progressive canopy defoliation over the subsequent years; visual assessments estimated an average foliage loss of about 60% (Niccoli et al., 2023b, 2023c). In this study, for the first time, sap flow in both burned and control trees was continuously monitored over a four-year period, with the goal of analyzing transpiration strategies and hydraulic dynamics following fire stress in a drought-prone area. The study focused on a species that is widely distributed across the Mediterranean basin, such as *Pinus pinaster* Aiton. Monitoring was integrated by remote sensing analyses of NDVI to monitor changes in forest canopy over time and by wood-anatomical measurements to assess potential structural and functional changes in xylem tissue over time, such as modifications in cell size and structure aimed at improving hydraulic efficiency or safety. Based on previous evidence that post-fire hydraulic adjustments and xylem trait plasticity can enhance cavitation resistance in Mediterranean species (Bär et al., 2018; Brodribb et al., 2010; Dickman, 2024), together with documented changes in water use following canopy scorch (Buckley et al., 2012; Dukat et al., 2024), we hypothesize that fire-defoliated trees exhibit distinct transpiration strategies relative to non-defoliated control trees.

Specifically, we expect that following canopy loss, burned trees will initially exhibit reduced sap flow as a result of decreased leaf area and partial hydraulic impairment, with transpiration progressively recovering over subsequent growing seasons. We, further, anticipate that xylem anatomical traits in burned trees (such as reduced vessel lumen area and increased cell wall thickness) will indicate a shift toward safer hydraulic architecture and enhanced resistance to cavitation. Finally, we expect that under recurrent drought and heat stress typical of Mediterranean climates, these post-fire differences in sap flow and wood anatomy between burned and control trees will persist, reflecting sustained adjustments in hydraulic function and carbon allocation. The results of this study aim to shed light on whether fire-damaged trees are on a path to recovery or decline, by identifying early signals that may indicate either resilience or delayed post-fire mortality.

2 Materials and methods

2.1 Study area

The study area is located in southern Italy, in Campania Region, within the Vesuvius National Park. This protected area extends over 8,000 hectares along the slopes of Vesuvius volcano and nearby Monte Somma (Figure 1A). Close to the city of Naples and the Tyrrhenian Sea coasts, the area is in the center of the Mediterranean basin and is characterized by a climate with hot and dry summers and mild winters (Figure 1B).

In recent decades, the study region has become increasingly exposed to prolonged dry spells and heatwaves, with 2017 classified among the hottest and driest years of the last quarter century according to the 12-month Standardized Precipitation Evapotranspiration Index (SPEI-12) (Figure 1C). During that summer, a wildfire burned approximately 3,000 ha of the park's vegetation, severely affecting Mediterranean maquis communities and forest stands dominated by *Quercus ilex* L., *Pinus nigra* Arnold, *Pinus halepensis* Mill. and *Pinus pinaster* Aiton (Battipaglia et al., 2017; Silvestro et al., 2021). For this study, two nearby *Pinus pinaster* stands were selected, one burned and one unburned, both of similar age (35 ± 10 years) and stand density, each covering about 1 hectare. The stands are located at ~ 650 m a.s.l. on a south-facing slope of the Vesuvius volcano within the integral reserve of the National Park (Figure 1A). The burned site (BS; 40° 48′43.0″ N, 14°24′44.6″ E) experienced a wildfire of moderate severity based on post-fire Sentinel-2 imagery (Silvestro et al., 2021). As the 2017 wildfire was accidental, detailed records of fire behaviour and flame temperature are not available. Nevertheless, Copernicus Sentinel-3 thermal data indicated a peak land-surface temperature of approximately 85 °C in the Vesuvius area on 11 July 2017 (around 09:00 UTC), suggesting a moderate heat release consistent with a medium-severity fire (Niccoli et al., 2023c). The control stand (CS; 40°48′35.8″ N, 14°24′52.7″ E) is located less than 1 km away and remained unaffected by the 2017 wildfire. Trees in this area showed no evidence of trunk charring, crown scorch, or root damage. Both stands grow on shallow volcanic soils with abundant surface outcrops (De Vivo and Costabile, 2004). Topographic features (including elevation, slope, and aspect) are comparable between the two sites, ensuring that the primary environmental distinction between them is the occurrence of fire.

2.2 NDVI time series and climate data processing

To assess vegetation dynamics over time, the Normalized Difference Vegetation Index (NDVI) was calculated for each site from 2015 to 2024, as it is commonly used to monitor changes in
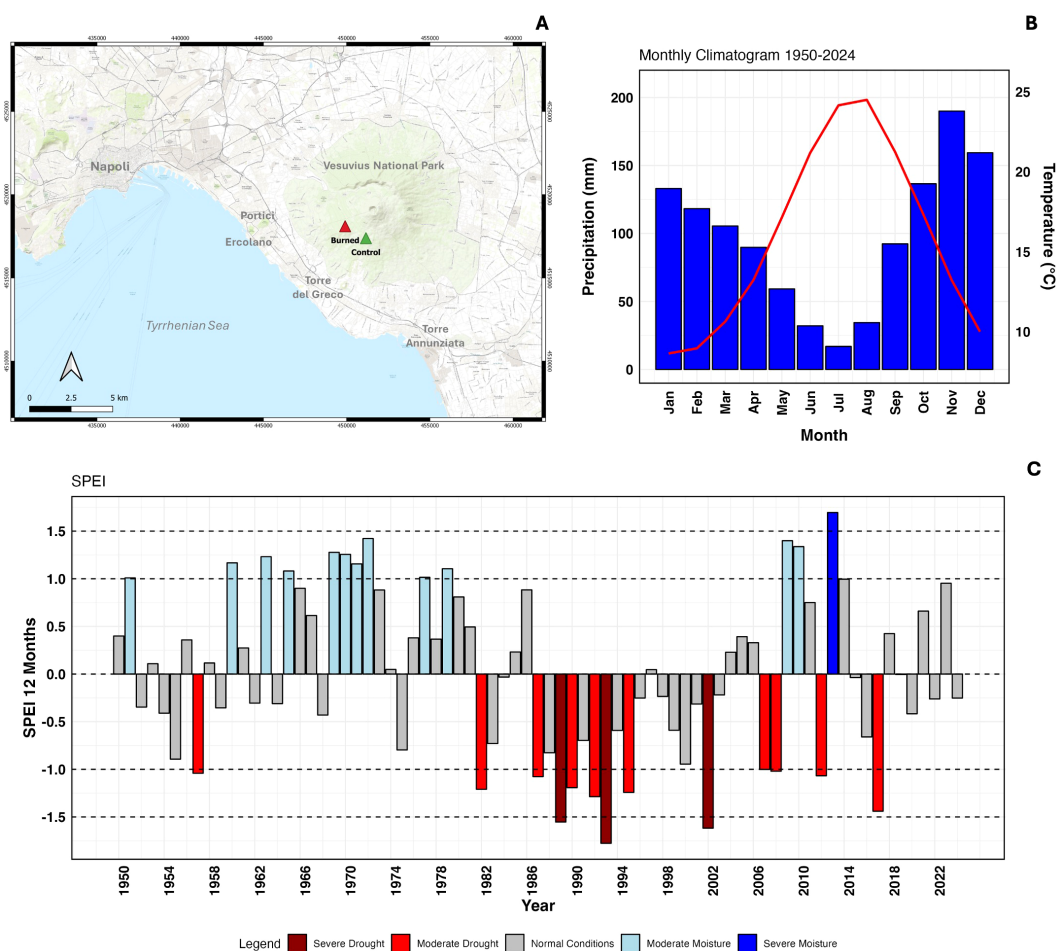
FIGURE 1
(A) Geographic location of the study area. **(B)** Monthly pluvio-thermal graph and **(C)** Standardized Precipitation Evapotranspiration Index computed on 12 months (SPEI-12) of the study area based on climate data extracted from the ERA-5 database from 1950 to 2024.

forest canopy over time (Huang et al., 2021; Sun et al., 2022; Wang et al., 2021). Data were extracted from the Landsat 8 Level 2A surface reflectance product using the Google Earth Engine platform, which allows access and processing of large amounts of geospatial data. The NDVI was calculated using a 100-meter buffer centered around the area of the forest where the sap flow sensors are installed. This distance was chosen to ensure that the analyzed area was representative of the forest environment immediately surrounding the monitored trees. All the satellite images were filtered to exclude those affected by cloud cover and to ensure that the calculation was not affected by atmospheric conditions (Niccoli et al., 2024a).

The NDVI was calculated using the near infrared (NIR, band 5) and RED (RED, band 4) spectral bands using the Equation 1:

$$NDVI = \frac{(NIR - RED)}{(NIR + RED)} \qquad (1)$$

The values obtained were then processed in R-Studio. The monthly mean of NDVI was calculated for each site. To highlight

seasonal trends and reduce short-term variability, a three-month moving average was applied using the *zoo* R package. Then, the long-term trends of the NDVI of the two sites were smoothed by a generalized additive model (GAM) line.

Finally, to characterize the climatic conditions of the study area during the analysis period, meteorological data were extracted from the ERA5-land dataset via the Google Earth Engine (Muñoz-Sabater et al., 2021). The following variables were considered: precipitation (Precip, mm), vapor pressure deficit (VPD, Kpa), air temperature (minimum, mean, and maximum, °C), relative humidity (RH, %), soil water content (SWC, %), and incoming radiation (J m^{-2} day^{-1}).

2.3 Long-term sap flow monitoring

In each of the two study sites, 10 dominant trees were selected (BS: DBH [mean diameter at breast height] 36.5 ± 3.5 cm, mean height 18 ± 0.1 m; CS: mean DBH 32.7 ± 3.6 cm, mean height 18 ±

0.2 m) on which Tree Talker Plus (TT+) devices were installed. This is an innovative high-frequency monitoring system capable of continuously recording various eco-physiological parameters of trees (Valentini et al., 2019).

The devices were installed on the trunk at a height of about 2 m above the ground and, thanks to their sensors, they can monitor several microenvironmental conditions and eco-physiological parameters, such as sap flow density (SFD). The latter is detected by a heating probe, inserted into sapwood at a depth of 2 cm under the bark, using the Transient Thermal Dissipation (TTD) technique, according to the methodology described by Do and Rocheteau (2002) and subsequently improved by Do et al. (2018, 2011).

The system measures the thermal change (ΔT) between a heating cycle (10 min) and a cooling cycle (50 min) on an hourly basis (Asgharinia et al., 2022). ΔT is calculated to minimize the effects of daily thermal gradients within the sapwood according to the Equation 2:

$$\Delta T \ (°C) = Theat1_t - \text{linear interpolation} \ (Theat0_t - Theat0_{t+1})$$

(2)

Where $Theat1_t$ is the temperature measured at the end of the heating cycle; $Theat0_t$ and $Theat0_{t+1}$ are the temperatures measured before heating and at the end of the cooling cycle.

The value of ΔT is then used to estimate the SFD (L m^{-2} h^{-1}) according to the Equation 3 proposed by Do and Rocheteau (2002):

$$SFD = 12.95 \times \left[\left(\frac{\Delta T_0}{\Delta T_U} \right) - 1 \right] \times 100$$

(3)

Where ΔT_0 is the thermal variation at zero flow, computed as the maximum temperature difference recorded during the night, when sap flow is assumed to cease and thermal equilibrium is reached within the sapwood, while ΔT_u represents the signal recorded under operating conditions, when sap flow is active (Do and Rocheteau, 2002; Do et al., 2018, 2011). This approach minimizes the influence of residual thermal gradients and provides a reliable reference value for the estimation of sap flow density.

Then the sap flow density was converted to total sap flow (SF, L h^{-1}) for each tree by multiplying the SFD value (L m^{-2} h^{-1}) by the corresponding sapwood conductive area (m²), estimated by Niccoli et al. (2023c) using the translucency method. This method consists of extracting wood cores near the sensor positions, moistening them, and exposing them to a light source to distinguish the lighter, translucent sapwood from the darker heartwood, allowing the determination of sapwood depth (Quiñonez-Piñón and Valeo, 2018).

The TT+ devices were installed in July 2020, exactly three years after the fire. After a short calibration period, monitoring started in January 2021. The installation was made possible thanks to the availability of specific research funding obtained in the following years. Therefore, the data reported in this study cover the period up to December 2024, but the devices are still active and collecting data useful for future research developments.

2.3.1 Management and processing of sap flow data

The sap flow data recorded on an hourly scale by each TT+ device between January 2021 and December 2024 were stored on internal memory and transmitted via radio to a data collection unit (TT-Cloud) installed in each study site. This unit allows data acquisition and their uploading to a remote web server, making it possible to consult the information in real time from our laboratory. Each TT+ device is identified by a unique serial code, which allows direct association between the collected measurements and the monitored tree. The raw data were subjected to a cleaning process to eliminate outliers using the dedicated R package *ttprocessing* (Kabala et al., 2024). The process involves a first selection of valid days for each tree, including only those for which complete recordings (24 hours) are available. Subsequently, to reduce the influence of potential outliers, the median sap flow value for each hour of the day was calculated across all trees within the same site. Finally, it was possible to determine the daily mean of sap flow at site level, aggregating the daily median values of all monitored individuals (Niccoli et al., 2023c).

2.4 Wood anatomy analysis

To investigate the morphological and functional characteristics of xylem cells in the monitoring years, in January 2025 wood cores were collected for each tree equipped with TT +. The samples were collected using a 5 mm incremental borer (Haglöf, Sweden) at breast height (about 1.30 m from the ground). Each core, containing at least the four most recent tree rings, was labeled and transported to the dendrochronology laboratories of the University of Campania "Luigi Vanvitelli", where the treatments necessary for the wood anatomy analyses were performed.

In a first phase, the wood cores were immersed in distilled water and boiled to soften the tissue and remove resins and impurities. Then, the samples were fixed on supports to facilitate their cut in histological sections of about 10–12 µm thickness, performed with a rotary microtome (Jinhua Yidi-315). The sections obtained were stained with a 1% safranin solution, rinsed with distilled water and subjected to a progressive dehydration process using 50% and 95% ethanol. The thin sections were then permanently mounted on glass slides using Eukitt gel (Bioptica, Milan, Italy).

High-resolution color images of the sections were acquired with a digital camera (OPTIKA C-P20CC) mounted on an optical microscope (OPTIKA B-510FL) at 100x magnification. The images were analyzed with ROXAS v3.0.31 software (Prendin et al., 2017; von Arx and Carrer, 2014), which allowed the automated measurement of several parameters related to the anatomical structure and functionality of xylem cells for each year between 2021 and 2024.

In particular, the following parameters were quantified: lumen area (LA, µm²), cell wall thickness (CWTall, µm), theoretical hydraulic conductivity (Kh, m³ MPa^{-1} s^{-1}), embolism resistance index (Bend), and mean ring width (MRW, mm). Cell wall thickness (CWTall) was determined following the approach

described by Almeras and Gril (2007). Theoretical hydraulic conductivity (Kh) was calculated according to Tyree and Zimmermann (2002), while the embolism resistance index (Bend) was computed following Hacke et al. (2001). Furthermore, the Mork index was calculated for each cell to distinguish earlywood (EW) cells, characterized by wider tracheids, from latewood (LW) cells, which have narrower tracheids. Following the criterion described by Denne (1989), Mork index values <1 indicate EW cells and those >1 LW cells. The use of this index allowed the identification of Intra-Annual Density Fluctuations (IADFs), as described by De Micco et al. (2014), contributing to the interpretation of anatomical dynamics within the tree rings.

2.5 Statistical analysis

Statistical correlation analysis and mathematical models were conducted to evaluate the influence of climatic conditions on sap flow dynamics. For these analyses, in addition to meteorological data extracted from the ERA5 dataset, sapwood temperature measured by TT+ devices was also used. The average daily sap flow of each site was correlated with the climatic variables through a monthly correlation analysis, considering a threshold of p< 0.05 as significant. The results were represented through heat maps generated in R-studio using the *dplyr*, *tidyr* and *ggplot2* packages, allowing the hydraulic response of the tree to be studied on a monthly scale.

In addition, to investigate the specific contribution of both climatic drivers and canopy dynamics to sap flow patterns, a multiple linear regression model was computed. The model included as dependent variable the mean daily sap flow measured by TT+ at each site and as independent variables NDVI, VPD, RH, SWC, incoming radiation, precipitation and a synthetic index of maximum, mean and minimum temperatures (obtained by principal component analysis – PCA - in order to reduce multicollinearity). Climatic variables were extracted from the ERA5 dataset, which provides spatially representative estimates for the entire study area.

The model was implemented in R-studio, using the packages *dplyr*, *broom*, *ggplot2* and stats for data preparation, analysis and visualization of results. The results were analyzed in terms of coefficient significance (P< 0.05), direction of effect (positive/ negative) and statistical strength (t value). The estimated coefficients were then plotted graphically using an oriented bar chart (with standard error), to facilitate visual interpretation. Finally, in order to compare the wood anatomy parameters in the control and burned sites a radar plot was used to display the median values of each variable measured for each year of analysis (2021–2024). The median was preferred because it represents a robust measure of central tendency: it is less sensitive to extreme values, thus ensuring a more reliable representation of the monitored data (Kabala et al., 2024).

To enable a normalized comparison across sites, the median values of the anatomical variables measured in the burned site were expressed as a percentage variation relative to the corresponding

median value observed in the control site, which was used as a baseline and set to 100% (Marfella et al., 2024). The relative variation was quantified using the following formula (Equation 4):

$$Relative \ Difference \ (\%) = \left(\frac{Median_{Burned}}{Median_{Control}} \right) \times 100 \qquad (4)$$

where Median$_{Burned}$ refers to the median value of the anatomical parameter in the burned site, and Median$_{control}$ is the corresponding median value in the control site. Finally, a Student's *t*-test was conducted on the non-normalized values for each year to assess the statistical significance of the differences visualized in the radar plots.

3 Results

3.1 Vegetation cover dynamics and climate trends

NDVI analyses (Figure 2A) revealed similar vegetation cover at both sites until 2016. Following the 2017 fire, the burned stand showed a marked NDVI decline (approximately of 50%), confirming the canopy loss previously reported by Niccoli et al. (2023c). The lowest NDVI values were recorded in 2021, mainly due to the removal of dead trees during management operations (Figure 2B). From 2023 onwards, NDVI progressively increased, reflecting the spread of *Robinia pseudoacacia* L., an invasive species already reported in the Vesuvius region (Silvestro et al., 2021). In contrast, NDVI values at the control site remained stable throughout the study period, indicating undisturbed conditions.

Daily meteorological data (2021–2024) characterized a typical Mediterranean climate (Figure 3). Precipitation was concentrated in spring and autumn, with recurrent summer droughts (Figure 3A). Vapor pressure deficit (VPD) frequently exceeded 2 kPa in summer, indicating high evaporative demand (Figure 3B). Minimum and maximum temperatures alternated between optimal spring conditions and hot summers (> 30 °C; Figure 3C). Relative humidity (RH) varied inversely with temperature (Figure 3D), while soil water content (SWC) dropped sharply each summer (Figure 3E). Incoming radiation peaked between April and September (Figure 3F).

3.2 Transpiration dynamics and environmental drivers of sap flow

Sap flow monitoring revealed distinct transpiration patterns between sites (Figure 4). Control trees showed stable seasonal dynamics, with spring sap flow rates generally below 7.5 L/h and reduced summer values, except in July 2023 when the values exceeded 10 L/h. The control site frequently displayed a bimodal transpiration pattern, with peaks in October and November, particularly in autumn 2022, when sap flow values were comparable to those observed in spring. In winter, transpiration levels were minimal. Burned trees exhibited higher transpiration rates than control during the first monitored years. In 2021, sap flow often exceeded 10 L/h and remained slightly higher than control
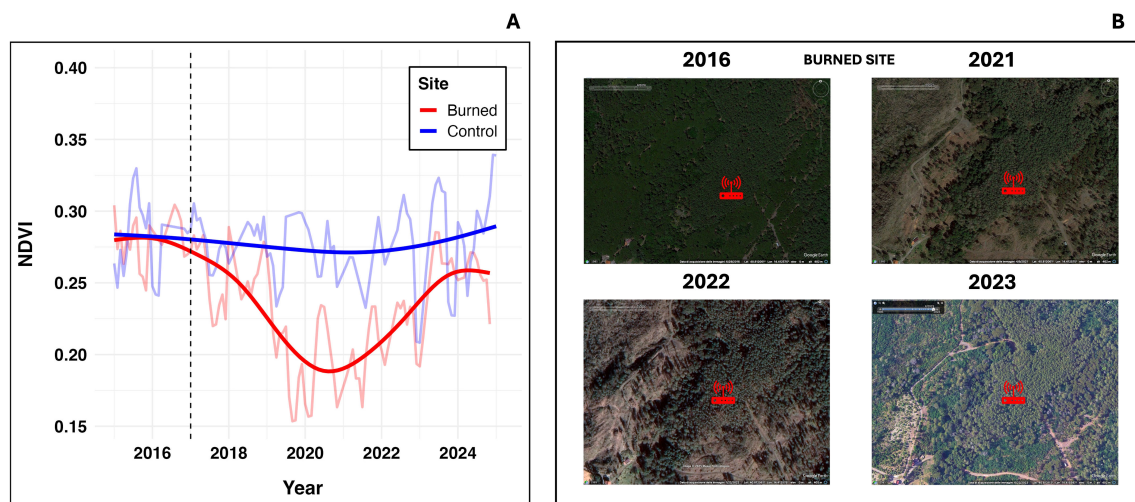
FIGURE 2
(A) NDVI trend of the burned (red) and control (blue) site from 2015 to 2024. **(B)** Sequence of satellite images of the burned site, the red symbol indicates the zone of the forest where Tree Talker devices are installed.

values also in 2022. From 2023 onwards, however, values began to decrease, becoming lower than those of the control stand.

Burned trees consistently recorded higher sap flow in summer, but the bimodal pattern was less evident, with few or no sap flow peaks in autumn. Seasonal comparison confirmed significant differences between sites (p< 0.05) in all cases, except for winter 2022. Statistical test results are reported in the Supplementary Material (Supplementary Table S1).

Correlation analyses of monthly sap flow data (2021 to 2024), with climatic variables, provided detailed insights into transpiration strategies of burned and control trees (Figure 5; for the corresponding correlation plots showing mean climatic values see Supplementary Figure 1). In the control site (Figure 5A), sap flow showed several significant correlations (p< 0.05): solar radiation consistently had a positive influence on sap flow throughout the year, except in summer months (July-September), with a similar trend for vapor pressure deficit (VPD). Positive correlations also emerged with mean and maximum air and sapwood temperatures, particularly in spring (April-May) and late autumn (October-November). Soil water content (SWC) was positively correlated in July and August, while relative humidity (RH) was negatively associated with sap flow for most of the year. Additional negative correlations were observed between SWC and precipitation in spring and autumn, and between mean and minimum temperatures in December. Overall, few significant correlations were detected during the warmest months (June-September).

In the burned site (Figure 5B), sap flow showed several negative correlations (p< 0.05): air and sapwood temperatures showed consistent negative influence throughout the year, as did precipitation in April and May. Solar radiation and VPD were the only variables with positive correlations over time. Occasional, positive correlations were found with SWC in February and December, and with air and sapwood temperatures in May and August.

The multiple regression model clarified the contribution of environmental variables to overall transpiration trend (Figure 6).

In the control site (Figure 6A), the model explained 71.19% of the variance, showing that incoming radiation had a strong positive effect on sap flow (p< 0.001), as well as air temperature (p< 0.05). In contrast, SWC and precipitation were negatively associated with transpiration, (p< 0.05 and p< 0.01, respectively). Other variables, including RH, NDVI, and VPD, showed no significant effects.

In the burned site (Figure 6B), the model explained 63.83% of the variance, confirming a strong positive impact of incoming radiation on sap flow (p< 0.001). However, both VPD (p< 0.01) and NDVI (p< 0.001) were negatively associated with transpiration, while no significant effects were observed for temperature, SWC, RH, and precipitation.

3.3 Wood anatomy traits in post-fire years

Wood anatomy analysis examined xylem characteristics of the two tree groups to evaluate the impact of fire on cell structure and hydraulic function (Figure 7). Significant differences were found between burned and control trees. In all years, mean ring width (MRW) was significantly lower in burned trees, showing a similar trend to lumen area (LA). Although hydraulic conductivity (Kh) was statistically comparable between groups in 2021, a significant decrease was observed in burned trees in subsequent years. In contrast, the embolism resistance index (Bend) was consistently higher in burned trees, while cell wall thickness (CWTall) was greater in all years except 2024.

The Mork index was used to analyze the formation dynamics of earlywood (EW) and latewood (LW) cells (Figure 8). In the control site (Figure 8A), about 70% of the tree rings length in 2021 and 2024 were composed of EW cells. Although the proportion of EW cells was lower in 2022 and 2023, a marked decline in Mork index values occurred in the second part of the rings, indicating the formation of earlywood-like cells and the occurrence of intra-annual density fluctuations (IADFs).
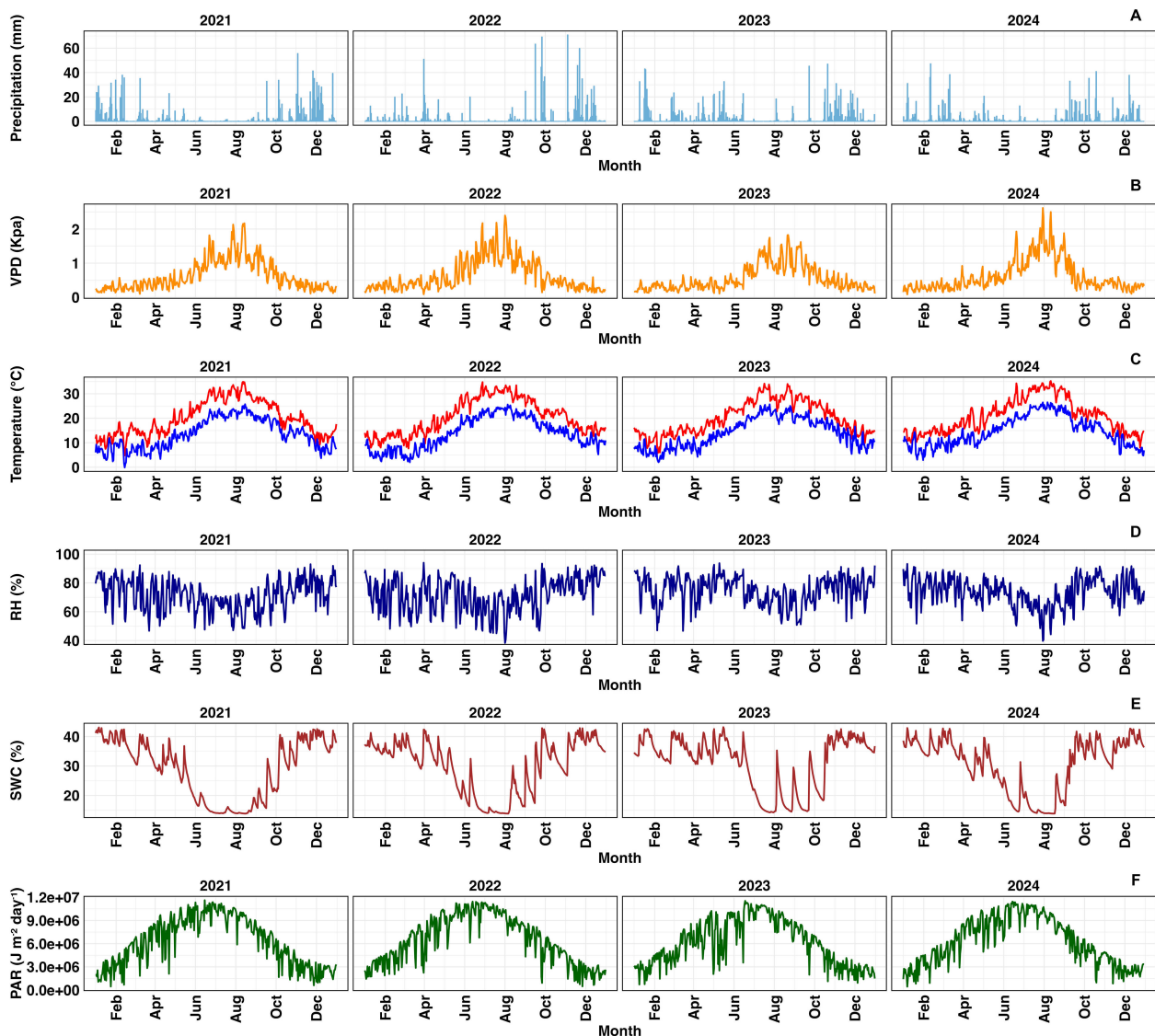
FIGURE 3
Daily meteorological variables recorded in the Vesuvius National Park between 2021 and 2024. **(A)** Precipitation, **(B)** vapor pressure deficit - VPD, **(C)** max (red) and minimum (blue) temperature, **(D)** air relative humidity, **(E)** soil water content, **(F)** incoming radiation.

In the burned site (Figure 8B), EW cells production was generally lower. In 2021, EW cells accounted for ~75% of the ring length, whereas in the other years, the proportion was smaller. For example, in 2022 EW cells accounted for only 40% of the ring length. Overall, declines in Mork index values in latewood were less evident, suggesting reduced formation of earlywood-like cells.

4 Discussion

For the first time, sap flow and xylem anatomical traits were continuously monitored over a four-year period in a fire-affected forest exposed to a climate regime characterized by hot and dry summers. Although sap flow monitoring began four years after the fire, representing a limitation of the present study, our findings complement previous research conducted in the same forest. Earlier studies reconstructed the progressive decline of the burned stand, quantified the relationship between fire severity and tree growth during the immediate post-fire period, and revealed a persistent impairment of carbon assimilation and hydraulic regulation in burned trees over the subsequent years (Niccoli et al., 2023b, 2023c, 2019). The present work provides novel, high-resolution insights into the long-term hydraulic and eco-physiological responses of surviving trees, elucidating the mechanisms underlying their post-fire adjustment.

4.1 Compensatory response of burned trees

The first year of monitoring (2021) represented the most critical phase, as sap flow in the burned site often exceeded 10 L/h, revealed
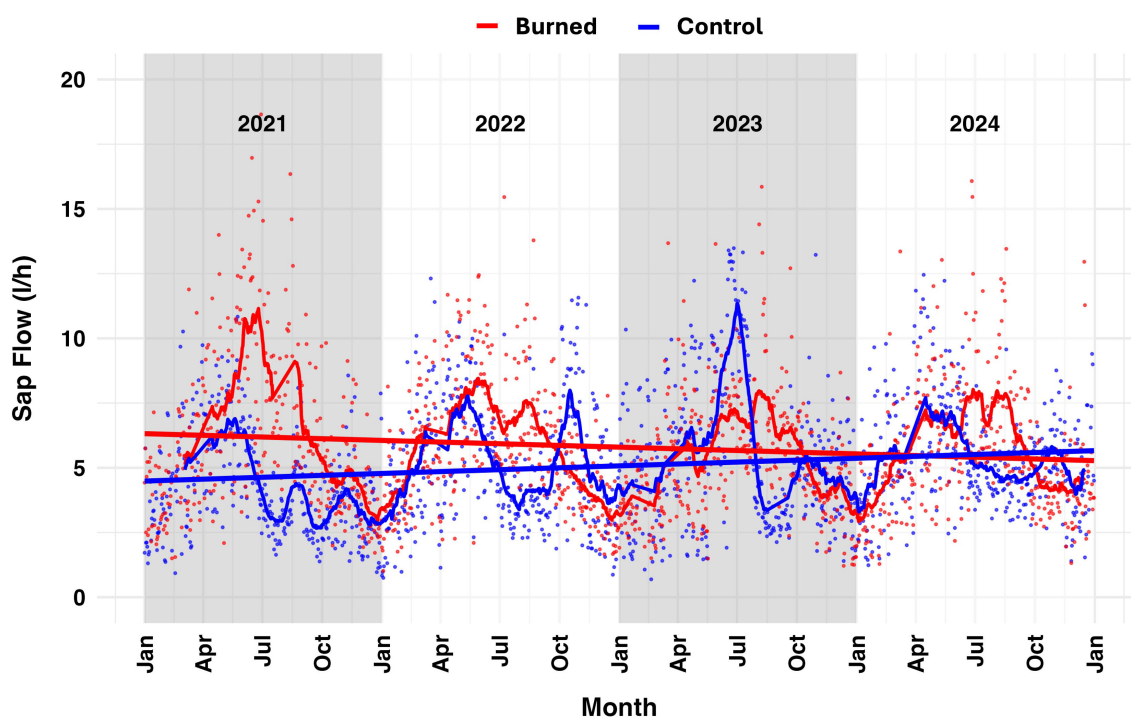
FIGURE 4
Average daily sap flow recorded by the 10 TT+ (points) of the control (blue) and burned (red) trees smoothed by a GAM line. Reference period January 2021 – December 2024.

unexpectedly high transpiration rates in burned trees compared to control trees, particularly during the summer. During this time, the Normalized Difference Vegetation Index (NDVI) reached its lowest values in the burned area. This agreed with the previous study conducted (Niccoli et al., 2023b) reported for this year a severe canopy loss, with an estimated defoliation of approximately 50%. This response was interpreted by Niccoli et al. (2023c) as a short-term compensatory strategy aimed at counteracting carbon depletion and maintaining vital functions despite the reduced leaf area, which ultimately proved ineffective in restoring carbon balance. Similar findings have been reported in other studies, where defoliated trees increased stomatal conductance, accepting a higher risk of xylem cavitation in an attempt to support carbon assimilation (Poyatos et al., 2013; Quentin et al., 2011; Salmon et al., 2015).

Our study confirms this trend in burned trees: the transient increases in transpiration of the first year were not sufficient to reverse the ongoing carbon deficit, as confirmed by the marked reduction in tree-ring width compared to control trees throughout the entire monitoring period. This consistent pattern suggests a progressive decline in overall photosynthetic capacity and a persistent imbalance between carbon supply and demand (Kagawa et al., 2006; Kuptz et al., 2011).

Nevertheless, wood anatomical analyses revealed that, despite severe canopy damage, xylem hydraulic function was largely preserved at least during the first year of monitoring, probably to support the increase in stomatal conductance. Indeed, in 2021,

burned trees exhibited hydraulic conductivity (Kh) values comparable to those of the control site. Although cell lumen area (LA) differed significantly between the two stands, the absolute values remained relatively close. Similar patterns of hydraulic resilience have been observed in experimental studies on poplars, where a significant loss of conductive sapwood was partially compensated by the functional redundancy of the xylem system, allowing the maintenance of sap flow and water supply to the canopy (Hillabrand et al., 2023).

An additional factor that may have contributed to the increased sap flow observed in 2021 was the removal of surrounding trees (Sohn et al., 2016). This thinning may have reduced competition and rainfall interception, potentially improving water availability and favoring higher soil moisture during the driest months (Mazza et al., 2011), although no direct measurements were available to confirm this hypothesis.

4.2 Contrasting functional responses in burned and control stands

From 2022, a slight increase in NDVI was recorded in the burned area. This was likely due by the spread of *Robinia pseudoacacia*, an alien and pioneer species already reported in the Vesuvius National Park (Silvestro et al., 2021), and well known for its ability to rapidly colonize disturbed sites (Kato-Noguchi and Kato, 2025). Robinia is characterized by traits such as fast growth, high photosynthetic

FIGURE 5
Correlation tables on a monthly scale between the daily average sap flow values and the corresponding climatic variables for **(A)** control and **(B)** burned sites. The blue boxes indicate positive correlation while coral boxes negative correlation. The cells that displaying the correlation coefficient (r) are statistically significant for p< 0.05. Reference period January 2021 - December 2024.

efficiency, and atmospheric nitrogen fixation, which confer strong competitive advantages in ecologically fragile environments (Kato-Noguchi and Kato, 2025). Thus, the observed increase in NDVI does not indicate a recovery of *Pinus pinaster* canopy (which was not observed), but rather a shift in species composition within the burned area (Sun et al., 2022). This interpretation was supported by forest survey data (Supplementary Figure S2), which showed that Robinia represented about 45% of the structural composition in the burned area, while in the control site its contribution was limited to approximately 8%. These results confirm that the post-fire environment favored the establishment and expansion of this invasive species. This shift could have triggered significant

implications for the ecosystem's water balance. Robinia, with its extensive root system, is capable of intense competition for water, directly affecting the hydraulic performance of surviving pines (Zhou et al., 2022). Indeed, from the second year onward, wood anatomical analyses revealed a significant decline in both Kh and LA of burned trees compared to control, indicating progressive structural and functional changes of xylem hydraulic efficiency (Farooq et al., 2023). Nonetheless, in 2022, although sap flow in the burned stand declined compared to 2021, it remained slightly higher than in control trees, particularly during the summer. This suggested the persistence of the stomatal strategy observed in the first year of monitoring.
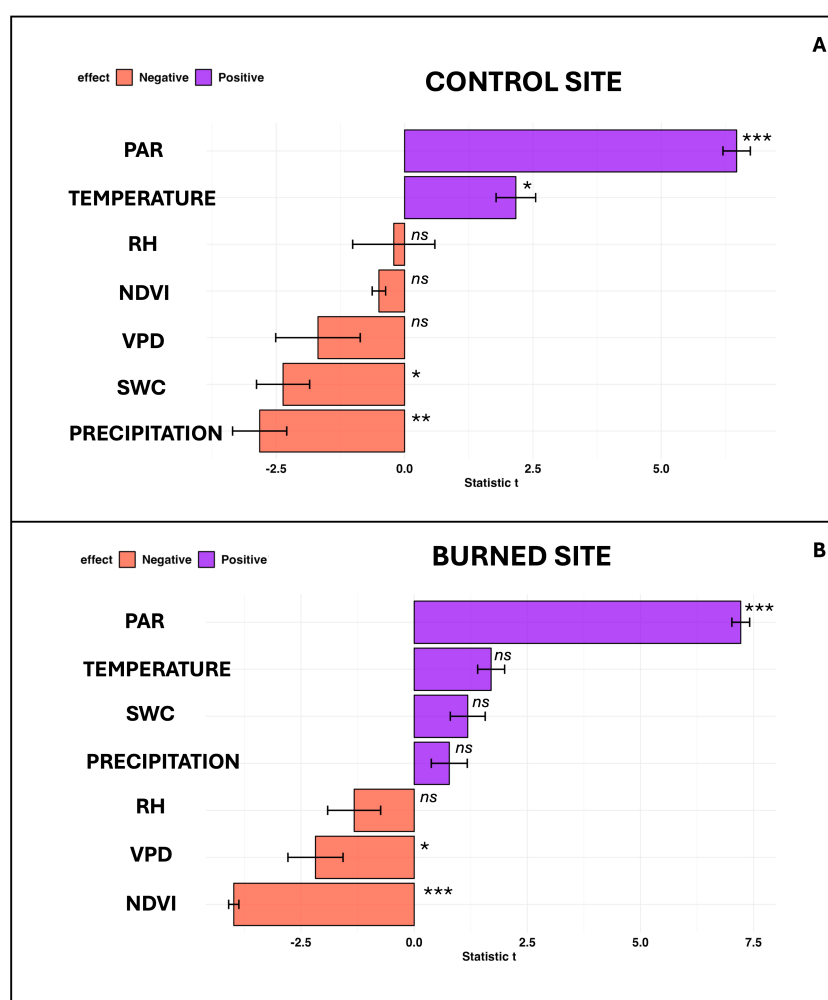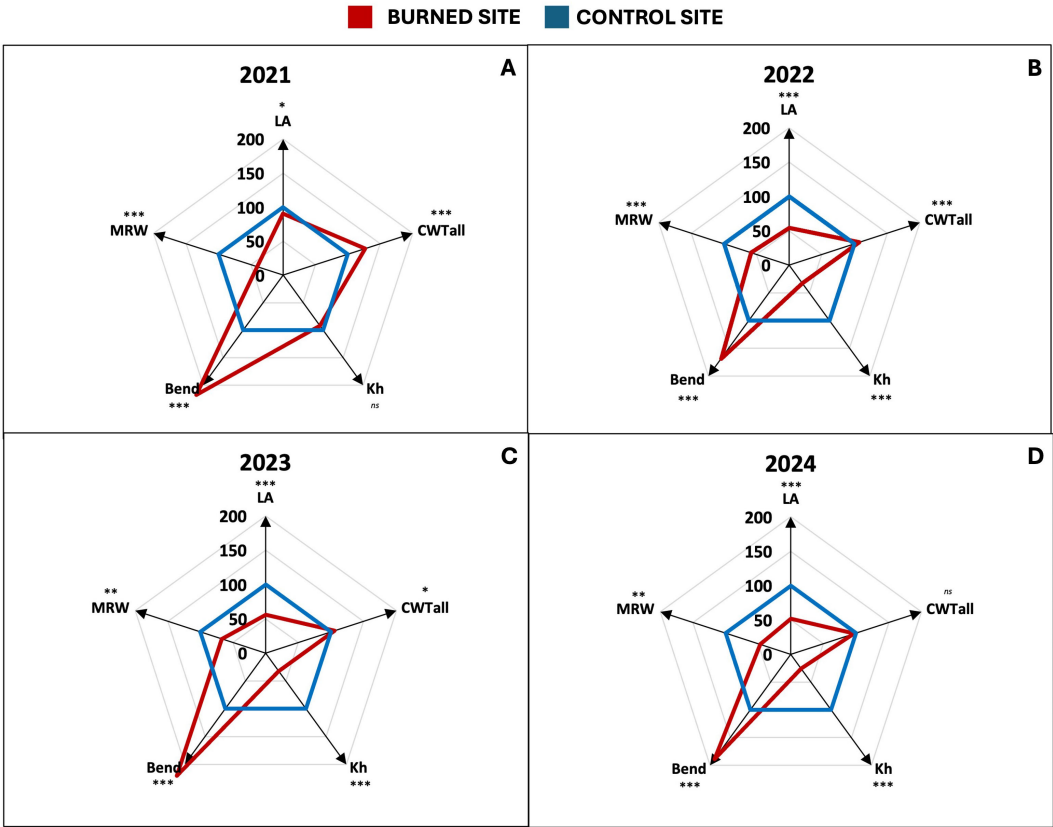
FIGURE 6
Multiple regression model between sap flow and the main climatic variables for the control **(A)** and burned **(B)** sites. Purple and coral bars indicate positive and negative trends of statistic t - value, respectively. Black lines represent standard errors. Symbols indicate significance levels (* p < 0.05; ** p < 0.01; *** p < 0.001), while "ns" denotes non-significant values.

In contrast, control trees showed moderate transpiration rates throughout the entire monitoring period and a conservative hydraulic behavior in the summer. During spring and autumn months, strong correlations between sap flow, incoming radiation, and vapor pressure deficit (VPD) indicated a stomatal activity closely aligned with atmospheric evaporative demand (Buckley, 2005; Medlyn et al., 2012). However, in summer (June–September), these relationships weakened, reflecting a proactive stomatal closure aimed at minimizing water loss under drought stress conditions (Chen et al., 2022; Martin-StPaul et al., 2017). This behavior aligns with the isohydric strategy commonly observed in pine species, with a reduction in stomatal conductance during dry and hot periods to avoid xylem embolism and tissues desiccation (Roman et al., 2015; West et al., 2008; Yi et al., 2017). Multiple regression model outputs confirmed that solar radiation and temperature were strong positive drivers of sap flow in control trees. As is known, stomatal opening is mainly light regulated, as radiation activates photosynthesis, triggering CO_2 uptake and, consequently, evapotranspiration (Buckley, 2005; Farquhar and

Sharkey, 1982). At the same time, temperatures within a certain range not only promote stomatal opening but also enhance photosynthesis by increasing the enzymatic activity of Rubisco and accelerating CO_2 fixation, if soil water availability is not limiting (Medlyn et al., 2002; Urban et al., 2017). The negative correlations observed between sap flow and precipitation or soil water content can be attributed to the seasonal dynamics of these variables. Periods of elevated rainfall and soil moisture typically coincide with cooler, cloudier conditions that are characterized by reduced temperature, solar radiation, and atmospheric evaporative demand. Under such conditions, partial stomatal closure commonly occurs, leading to decreased transpiration rates (Aparecido et al., 2016). Thus, these negative relationships do not indicate a physiological anomaly; rather, they reflect the dominant influence of meteorological conditions on tree water use during cold periods.

Furthermore, control trees demonstrated a higher capacity to exploit favorable climatic windows compared to burned stand. This was particularly evident in 2022, when optimal autumn conditions

FIGURE 7
Radar plot showing the percentage variation for 2021 **(A)**, 2022 **(B)**, 2023 **(C)**, and 2024 **(D)** between control (blue) and burned (red) trees for each monitoring year, for lumen area (LA), cell wall thickness (CWTall), cell hydraulic conductivity (Kh), embolism resistance index (Bend), and mean ring width (MRW). Symbols indicate significance levels (* p < 0.05; ** p < 0.01; *** p < 0.001), while "ns" denotes non-significant values.
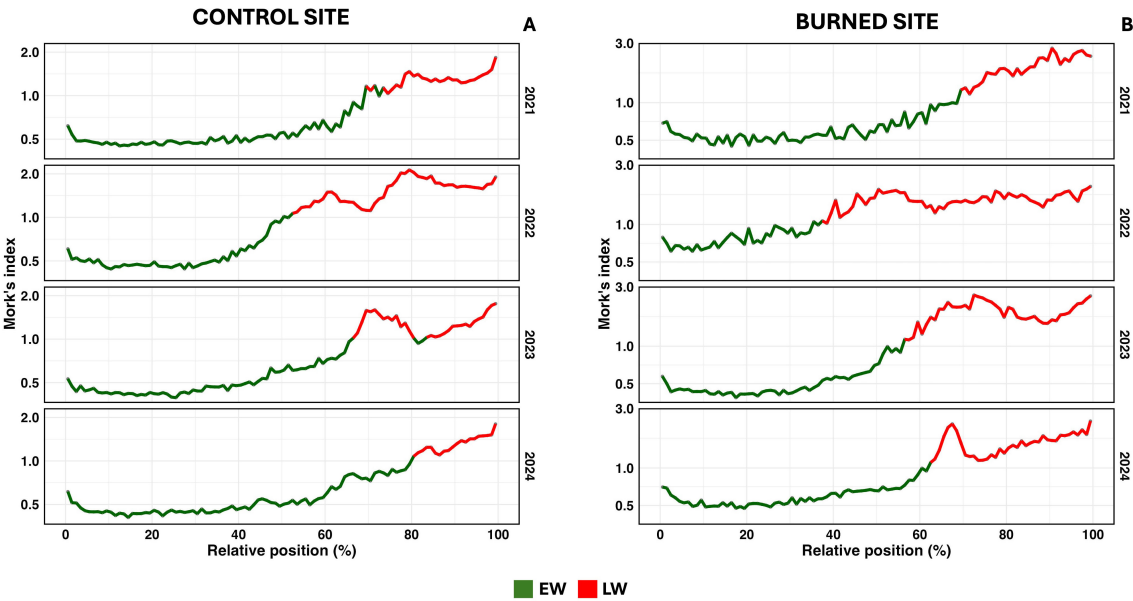
FIGURE 8
Average trend of the Mork index of **(A)** control and **(B)** burned trees for each monitoring year (2021-2024). The green lines indicated the earlywood (EW) cells, the red lines indicated the latewood (LW) cells.

(abundant rainfall, moist soil, and mild temperatures) triggered a second transpiration peak between October and November (Niccoli et al., 2024b). This highlights the good eco-physiological plasticity of control trees, which allowed them an extension of the growing season (Battipaglia et al., 2023; Camarero et al., 2010; Campelo et al., 2007; De Luis et al., 2011).

Anatomical data supports this interpretation. In control trees, the Mork index often showed an inflection during the second half of the tree rings, indicating the formation of Intra-Annual Density Fluctuations (IADFs), a functional trait, well documented in Mediterranean trees, and commonly formed by cambial reactivation following late-season rainfall (Camarero et al., 2021; Campelo et al., 2018; Garcia-Forner et al., 2019). In contrast, burned trees showed no signs of autumn activity. Their tree rings were narrower and composed of latewood cells accounting for more than 60% of their length, which clearly indicated an early cessation of cambial activity (Vieira et al., 2014). Indeed, the absence of significant correlations between sap flow and key climatic variables in October and November confirmed a lack of eco-physiological responses of burned stand to autumn conditions.

4.3 Long-term tree functional decline

In 2023 and 2024, in sharp contrast to the patterns observed during the first two years of monitoring, sap flow of burned trees showed a reversal trend: during spring and autumn, values were consistently lower than in the control site, indicating a progressive decline in transpiration and hydraulic functioning (Johnson et al., 2022). For this period NDVI values of burned area increased significantly, reaching those observed in the control site, confirming the strong presence of the alien species. Results from the multiple regression model suggested that while incoming radiation continued to have a positive effect on sap flow, NDVI had an overall negative influence on transpiration of burned trees. This supports the dual role of NDVI as an indicator of both post-fire defoliation (Varner et al., 2021) and increasing water competition from *Robinia pseudoacacia* (Kato-Noguchi and Kato, 2025; Zhou et al., 2022).

On the other hand, the negative correlation observed between sap flow and VPD suggested a lowered threshold of tolerance to atmospheric evaporative demand, often resulting in reduced transpiration even in climatic conditions that have been found to be favorable for control trees, such as autumn (Klein, 2014). Multiple negative correlations between sap flow, temperatures, and relative humidity on a monthly scale further confirmed that even moderate climatic fluctuations may act as limiting factors, interfering with stomatal control (Lapa et al., 2017). Trees affected by extreme events such as wildfire, while able to survive initially, may enter a trend of long-term functional decline, characterized by reduced eco-physiological efficiency and lower tolerance thresholds to abiotic stressors (Hood, 2021). Recent studies (Reed et al., 2025) confirmed that fire can deeply alter the carbon balance and

hydraulic function of trees, leading to delayed effects that can manifest over time.

Although weak positive correlations on a monthly scale between sap flow, solar radiation, and VPD were still observed, these likely reflect residual responses to atmospheric drivers. Further, during the summer months burned stand still show higher transpiration rates than control, suggesting a persistent difficulty in stomatal regulation, which exposes trees to a greater risk of hydraulic failure (Niccoli et al., 2023c). The evidence of increase in xylem cavitation risk was supported also by wood anatomy data: a progressive thickening of cell walls (CWTall) and a higher cavitation resistance index (Bend) were observed compared to control. These xylem traits adjustments indicate that burned trees have gradually modified their conductive tissue as a defensive response to mitigate embolism risk, reflecting an adaptive reaction to an increasingly stressful environment (Hacke et al., 2001).

Overall, the collected data revealed a state of eco-physiological decline in the burned pines. Although the initial compensatory transpiration strategy may have provided a short-term advantage by supporting carbon metabolism and ensuring immediate post-disturbance survival, this response does not appear to have led to functional recovery over the medium to long term. The lack of canopy regrowth has limited the trees' photosynthetic capacity, progressively compromising their carbon balance. In addition, increasing water competition from Robinia further intensified drought stress in the surviving pines. In this weakened state, trees are likely to become increasingly sensitive to climatic extremes, with a heightened risk of delayed mortality driven by carbon starvation and hydraulic failure (Kono et al., 2019; McDowell, 2011; Nardini et al., 2016; Petrucco et al., 2017; Savi et al., 2016; Tomasella et al., 2017).

5 Conclusions

The results of this study partially confirm our hypothesis regarding the post-fire hydraulic and functional adjustments of *Pinus pinaster*. Contrary to the expectation of a short-term suppression of sap flow following canopy loss, burned trees showed unexpectedly high transpiration rates during the first monitoring year (2021). These responses indicated a compensatory stomatal strategy aimed at maintaining carbon assimilation despite severe defoliation. Wood anatomy traits supported this interpretation, showing preserved hydraulic functionality.

However, the hypothesis that transpiration rates would gradually recover in subsequent seasons was not supported. From 2022 onward, the lack of canopy regrowth, coupled with the spread of *Robinia pseudoacacia* led to increasing hydraulic limitation and reduced sap flow. This phase was marked by a divergence in functional strategies: control trees maintained a conservative and climate-responsive water-use behavior, whereas burned trees

exhibited progressive hydraulic decoupling and reduced eco-physiological plasticity. Finally, the expected long-term adjustments toward safer water transport were only partially realized. By 2023–2024, burned trees exhibited increased cell wall thickness and a higher cavitation resistance index, indicating a defensive anatomical response. However, this shift was accompanied by reduced hydraulic efficiency and declining transpiration, suggesting that those acclimation traits were outweighed by the cumulative impacts of canopy loss, competition, and recurrent drought. Although monitoring data from the immediate post-fire years are unavailable, our findings indicate that seven years after the fire, burned trees are undergoing carbon imbalance and increasing vulnerability to hydraulic failure, potentially leading to delayed mortality. For this reason, the continuation of monitoring will be essential to track the evolution of these dynamics and to investigate the subsequent stages of potential post-fire mortality. This scenario highlights the need for active post-fire management in Mediterranean forests, including control of invasive species, selective thinning of weakened individuals, and the promotion of native, drought- and fire-resistant species to enhance long-term ecosystem resilience.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

FN: Methodology, Investigation, Formal Analysis, Data curation, Writing – original draft. JK: Investigation, Formal Analysis, Methodology, Data curation, Writing – review & editing. LF: Writing – review & editing, Methodology, Investigation. GB: Writing – review & editing, Supervision, Methodology, Conceptualization, Investigation, Funding acquisition, Resources, Data curation, Validation, Project administration.

Funding

Acknowledgments

Conflict of interest

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