

Heat wave impacts on tree growth and recovery in temperate forests depend on leaf phenology

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ABSTRACT

Climate change is leading to more frequent and severe extreme climate events, such as hot spells. However, we lack information on how trees recover after heat waves in terms of wood anatomy, radial growth (basal area increment, BAI), and wood $\delta^{13}\text{C}$, a proxy of intrinsic water-use efficiency (iWUE). This lack of information on recovery is notable in temperate forests, where heat waves reduce productivity and trigger canopy dieback. We filled this research gap by assessing the impacts of the 2022 heat wave on two temperate forests located at high (Cernobbio) and low elevation (Monza) sites in northern Italy. Eight winter-deciduous tree species were sampled with different leaf phenology (early leafing species, *Betula pendula*, *Quercus robur*; intermediate leafing species, *Fagus sylvatica*, *Acer pseudoplatanus*; and late leafing species, *Tilia cordata*, *Castanea sativa*, *Fraxinus excelsior*, *Quercus pubescens*). Some species experienced a severe BAI reduction during 2022 (*B. pendula*, -58%; *Q. robur*, -48 %), others showed a moderate drop (*A. pseudoplatanus*, -5 %; *F. excelsior*, -5 to -34 %; *T. cordata*, -29 %; *C. sativa*, -25 %; *Q. pubescens*, -18 %), whereas *F. sylvatica* showed a slight increase (+3 %). Negative growth legacies were detected in *F. excelsior* at the low-elevation site. *F. excelsior*, *A. pseudoplatanus* and *Q. pubescens* were the most sensitive species to summer maximum temperatures and drought severity. In the case of *A. pseudoplatanus*, the ray parenchyma fraction declined in 2022, indicating lower C storage. *A. pseudoplatanus* (-26.1‰) and *F. excelsior* (-25.6‰) showed the highest wood $\delta^{13}\text{C}$ values. Radial growth data indicate that the two early leafing species were the most negatively impacted by heat stress.

1. Introduction

A major component of climate warming is the increase in year-to-year climate variability leading to more frequent and severe climate extremes (IPCC, 2023). These extremes include heat waves and dry spells, which reduce forest productivity and rise tree mortality rates (Allen et al., 2015). Extreme events such as the 2003 European heatwave reduced ecosystem gross primary production by -30 % (Ciais et al., 2005), whereas the 2018 heat wave led to widespread stem dehydration due to depletion of water reserves (Salomón et al., 2022). In many cases, trees recover after such negative climate impacts, but their recovery capacity depends on multiple factors including: the severity and frequency of climate extremes (e.g., maximum temperatures reached

during a heat wave), post-event weather conditions, site variables (topography, soil depth and texture), stand structure and composition, and functional traits enhancing resilience (Anderegg et al., 2015; Rita et al., 2020). For instance, either too frequent drought or heat waves and carryover effects (legacies) constrain recovery trajectories, affecting growth resilience (Ingrisch and Bahn, 2018; Kannenberg et al., 2020; Schwarz et al., 2020; Serra-Maluquer et al., 2021). A high shoot-to-root ratio in trees due to previous favorable weather conditions, the so-called structural overshoot (Jump et al., 2017), may exacerbate die-off damage because overbuilt stands may be susceptible to subsequent dry and stressful conditions (Italiano et al., 2024). In contrast, favorable conditions after an extreme event, such as a wet period after a severe drought, can offset growth losses (Jiang et al., 2019). Such varied responses

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indicate that the drivers of the pace of recovery must be understood when assessing the return of tree functionality after extreme climate events (Ruehr et al., 2019).

Temperate forests are very vulnerable to heat and drought stress, that cause growth decline and die-off (Bréda et al., 2006; Nardini et al., 2013; Martín-Benito and Pederson, 2015; Rubio-Cuadrado et al., 2018). For instance, a record drought caused die-off in temperate mesic forests of Eastern North America, and the main mechanism involved was hydraulic failure, i.e. plant desiccation due to cavitation-induced loss of water transport exceeding a lethal species-specific threshold (Hoffmann et al., 2011). The timing of the extreme climate event with respect to major tree phenological phases (bud burst, leaf flushing, tree-ring formation) is a critical factor determining damage. For example, in North American temperate forests, drought-induced growth decline was more intense due to early-season droughts coinciding with peaks in radial growth, particularly for early-growing trees located in the warmest regions (D'Orangeville et al., 2018). Moreover, legacy effects were very important in response to late-season droughts (Kannenbergh et al., 2019). Overall, these findings indicate that leaf and wood phenology, the timing of heat waves or droughts, and site conditions contribute to explaining the recovery after such extreme climate events.

Leaves avoid heat stress through enhanced stomatal conductance and cooling via transpiration (Drake et al., 2018). In addition, leaves also minimize heating by reducing size, increasing lobing, and changing orientation to improve convective cooling, among other morphological features (Sisó et al., 2001; Vogel, 2009). Leaf thermoregulation may show trade-offs with water use depending on how transpiration responds to rising air temperature and vapor pressure deficit (VPD) along the growing season (Fauset et al., 2018). Under heat stress transpiration continues but photosynthesis declines leading to water loss, leaf drop/scorching and reducing carbon uptake and growth as has been observed in temperate forests (Griebel et al., 2020). However, leaf phenology and timing of exposure are also critical factors as shown by the negative impacts of elevated spring temperatures on leaf expansion (Filewod and Thomas, 2014; Teskey et al., 2015). Therefore, leafing phenology may contribute to predict differential responses of tree species to spring-summer heat waves in terms of growth, wood anatomy, and water use. During spring-to-summer heat waves, early leafing species may have developed mature and lignified leaves, whereas late leafing species may be starting leaf-out and present soft, underdeveloped and vulnerable leaves. Here, eight tree species abundant in temperate forests and showing different leaf unfolding dates were compared: early leafing species, *Betula pendula*, *Quercus robur*, intermediate leafing species, *Fagus sylvatica*, *Acer pseudoplatanus*; and late leafing species, *Tilia cordata*, *Castanea sativa*, *Fraxinus excelsior*, and *Quercus pubescens* (cf. Vitasse et al., 2009; Sass-Klaassen et al., 2011; Michelot et al., 2012; Bigler and Bugmann, 2018).

Long-term field observations or reconstructions following extreme climate events may improve our understanding of tree recovery given the opportunistic nature of many die-off cases. In this regard, tree rings provide retrospective proxies of tree functioning which may be analyzed to disentangle the influences of antecedent, current and subsequent conditions on post-stress tree recovery (Camarero et al., 2018). Multi-proxy approaches combining several sources of information on tree functioning including tree-ring width or basal area increment data, wood anatomy and C isotope ratios ($\delta^{13}\text{C}$) provide relevant information on post-stress resilience (e.g., Colangelo et al., 2017, 2025; Italiano et al., 2023). The $\delta^{13}\text{C}$ of tree-ring wood is a proxy of intrinsic water-use efficiency (iWUE), i.e. the ratio between photosynthesis and stomatal conductance rates (Francey and Farquhar, 1982; McCarroll and Loader, 2004). Heat waves may enhance transpiration to keep effective leaf cooling, but reduce photosynthesis rates, thus decreasing wood $\delta^{13}\text{C}$ and iWUE (Griebel et al., 2020). In this study, we followed a multi-proxy framework to assess the impacts of a heat wave on different aspects of tree functioning (growth, gas-water exchange, theoretical hydraulic conductivity, carbon storage in xylem). We investigated temperate

forests in northern Italy, where an exceptional heat wave affected this region from May to September 2022, particularly impacting regions of the Po river basin, where crop losses, wildfires and excess mortality rates reached very high numbers (Ballester et al., 2023). Forests in the region were also affected, showing extensive canopy dieback. We selected two sites that presented this type of damage after the 2022 hot spell and sampled stands of eight winter-deciduous tree species along a 1080-m elevation gradient. Tree species forming both diffuse-porous (*A. pseudoplatanus*, *B. pendula*, *F. sylvatica*, *T. cordata*) and ring-porous (*C. sativa*, *F. excelsior*, *Q. pubescens*, *Q. robur*) wood types were selected to encompass a wide range of wood traits and leaf onset phenology. Our specific objectives were: (i) to reconstruct radial-growth patterns and relate them to climate variables, paying particular attention to impacts of summer heat waves on wood production, (ii) to quantify the resilience after the hot spell in terms of growth, wood anatomy and $\delta^{13}\text{C}$ records, and (iii) to highlight the main responses to the studied extreme climate event. Using such a retrospective approach allows us to pinpoint the impacts of a heat wave on tree functioning within a wide temporal framework. We expect that the species showing the earliest leaf unfolding will be the most exposed and negatively impacted by the hot spell in terms of growth reduction.

2. Materials and methods

2.1. Study sites

We selected two study sites (Cernobbio, Monza) located in Insubria, Lombardia region, northern Italy (Fig. 1). Selected sites showed extensive canopy dieback and damage, characterized by leaf browning and abundant shedding, which were observed after the 2022 heat wave. Each site showed different forest composition and climate conditions. In the mid-elevation Cernobbio site (9° 04' 14" - 9° 04' 55" E, 45° 51' 15" - 45° 52' 27" N, 539 - 1249 m a.s.l.), six species were sampled (from lowest to highest elevation: *C. sativa*, *Q. pubescens*, *F. excelsior*, *A. pseudoplatanus*, *B. petula*, and *F. sylvatica*; Table 1). In the piedmont, low-elevation Monza site (9° 16' 10" - 9° 17' 08" E, 45° 35' 41" - 45° 36' 11" N, 170 - 195 m a.s.l.), three species were sampled (*F. excelsior*, *Q. robur*, and *T. cordata*).

The study forests are dominated by broadleaf, winter-deciduous temperate tree species (e.g., *Q. robur*), but are subjected to sub-Mediterranean influence (Pignatti, 1998). The mean annual temperature ranges 12.0–13.0 °C and the total annual precipitation increases upwards and ranges 1162–1250 mm. The warmest month is July (maximum temperature between 26.2 and 28.1 °C), and the driest periods are the winter and July, with precipitation peaking in November.

In ring-porous species, stem radial growth may occur at least one month before buds were swollen, whereas in diffuse-porous species these two phenological events are more synchronous (Suzuki et al., 1996). According to 2022 phenological data taken at the nearby Sagno Swiss station (9° 02' E, 45° 52' N, 670 m a.s.l.), half of the crown leaves were formed by *F. sylvatica*, *B. pendula*, *T. cordata* and *C. sativa* on 16 April, 22 April, 25 April and 5 May, respectively (data available at https://app.phaenonet.ch/stations/2022_SGO).

Soils are acidic and poor in nutrients, particularly in the Cernobbio site. The study sites correspond to secondary, young forests not being managed since the 1960s (Table 1). In Monza, *T. cordata* trees were located in a semi-urban area (Fig. 1).

2.2. Climate data

Due to the lack of long-term, homogeneous climate datasets in the two study locations, we used 0.1°-gridded monthly climate data (mean maximum and minimum temperatures, total precipitation; period 1960–2024) corresponding to the E-OBS climate dataset version 28.0e (Cornes et al., 2018). Using these data, we calculated monthly values of the Standardized Precipitation Evapotranspiration Index (SPEI), a

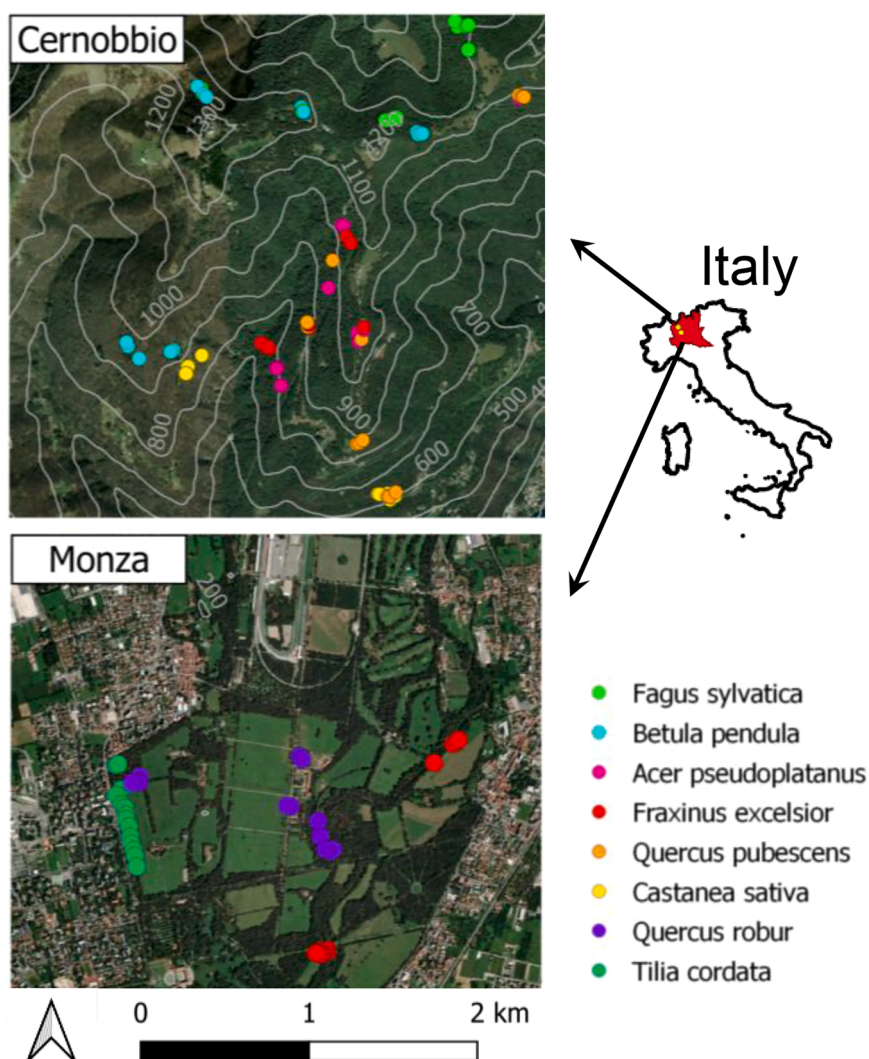


Fig. 1. Maps showing the location of the two study sites (Cernobbio, Monza) in northern Italy and the sampled trees of the eight species. Elevation curves were not plotted in the Monza map because of the short elevation range (25 m). See also [Table 1](#).

Table 1

Location and elevation of stands sampled in northern Italy. Leaf-out phenology classes: EL, early leafing species; IL, intermediate leafing species; and, LL, late leafing species. The last three columns show data on tree diameter at breast height (dbh), height and age (estimated at 1.3 m). Values are means $\pm$ SD.

Site	Tree species	Latitude N	Longitude E	Elevation (m a.s.l.)	Leaf-out phenology	Dbh (cm)	Height (m)	Age (years)
Cernobbio	<i>Castanea sativa</i>	45° 51' 15"	9° 04' 47"	591–876	LL	40.8 $\pm$ 12.5	14.0 $\pm$ 3.4	43 $\pm$ 16
	<i>Quercus pubescens</i>	45° 51' 44"	9° 04' 40"	539–1088	LL	38.5 $\pm$ 9.6	17.6 $\pm$ 4.8	55 $\pm$ 9
	<i>Fraxinus excelsior</i>	45° 51' 43"	9° 04' 14"	730–1050	LL	48.9 $\pm$ 10.2	20.5 $\pm$ 3.0	52 $\pm$ 9
	<i>Acer pseudoplatanus</i>	45° 51' 46"	9° 04' 39"	791–1088	IL	48.9 $\pm$ 11.1	23.7 $\pm$ 4.3	41 $\pm$ 8
	<i>Betula pendula</i>	45° 52' 24"	9° 04' 55"	928–1261	EL	45.5 $\pm$ 13.4	17.7 $\pm$ 1.5	44 $\pm$ 14
	<i>Fagus sylvatica</i>	45° 52' 27"	9° 04' 49"	1061–1249	IL	40.1 $\pm$ 11.8	18.4 $\pm$ 4.1	64 $\pm$ 15
Monza	<i>Fraxinus excelsior</i>	45° 35' 41"	9° 17' 08"	170–177	LL	36.0 $\pm$ 12.8	27.8 $\pm$ 6.2	41 $\pm$ 14
	<i>Quercus robur</i>	45° 36' 11"	9° 16' 59"	173–195	EL	57.0 $\pm$ 11.2	27.6 $\pm$ 5.7	88 $\pm$ 30
	<i>Tilia cordata</i>	45° 36' 11"	9° 16' 10"	187–191	LL	46.3 $\pm$ 9.0	32.5 $\pm$ 8.4	53 $\pm$ 17

multi-scalar drought index, at scales from 1 to 24 months of cumulative water balance. The water balance calculation depends on temperature and precipitation and determines if climate conditions are wet or dry. The SPEI was calculated using the SPEI R package ([Beguería and Vicente-Serrano, 2023](#)). To assess changes in soil moisture availability, we also obtained 0.1°-gridded monthly soil moisture data at 0–10 cm depth for the period 1982–2018 based on land surface model simulations with precipitation-based forcing ([Rodell et al., 2004](#)). To illustrate the conditions impacting radial growth during the 2022 heat wave, we calculated the mean maximum temperatures during the growing season

(from May to October). We selected the period from May to October because: (i) mean maximum temperatures from May to August were +0.5 °C higher in 2003, a widely studied European heat wave, than in 2022, and (ii) the selected period includes the months when latewood is formed ([Michelot et al., 2012](#)).

2.3. Field sampling and tree-ring width data

In each site, we selected 15 dominant mature trees per species with visible canopy dieback after the 2022 hot spell. We measured the

diameter at breast height (dbh) at 1.3 m using tapes, and the total tree height using a laser rangefinder (Nikon Forestry Pro). We sampled and extracted three cores from each tree at 1.3 m. Two cores were used to obtain tree-ring width and wood-anatomy data, whereas the third core was used to measure $\delta^{13}\text{C}$. The cores were extracted using Pressler increment borers with a 5-mm diameter. The cores for ring-width and wood anatomy data were glued onto wood supports. Then, they were air dried and sanded with sandpapers of increasing finer grain until tree-ring boundaries were conspicuous. Cores were visually cross-dated under the binocular scope using dendrochronology (Fritts, 1976). Then, the wood cores were scanned at 1200 dpi (Epson Expression 10000XL). The tree-ring widths (RW) were measured with a 0.001 mm resolution along two cores per tree using the CDendro-CooRecorder software (Larsson and Larsson, 2018). The visual cross-dating was checked using the COFECHA software, which calculates moving correlations between individual series and the mean species series (Holmes, 1983). The tree age at 1.3 m was estimated by counting the number of rings along the oldest core of each tree whenever it reached the pith or presented curved, innermost rings.

2.4. Processing tree-ring width data

Tree-ring widths were converted into basal area increment (BAI) to analyze growth trends or into ring-width indices (RWI) to calculate climate-growth relationships. The BAI was calculated using the following formula:

$$\text{BAI} = \pi(R_t^2 - R_{t-1}^2), \quad (1)$$

where R_t and R_{t-1} are the radii measured in years t and $t-1$, respectively, corresponding to the cumulative sums of annual ring widths ($\sum_i^t \text{RW}$ and $\sum_i^{t-1} \text{RW}$, respectively).

Using the individual RWI series, we calculated several growth resilience indices for each species and site to quantify the impact of the 2022 heat wave and the subsequent recovery. We used simple indices to overcome some of the problems associated with widely used resilience indices (Schwarz et al., 2020). Specifically, we calculated the following ratios for RWIs of several years (subscripts): $\text{RWI}_{2022} / \text{RWI}_{2021}$, $\text{RWI}_{2023} / \text{RWI}_{2022}$, $\text{RWI}_{2024} / \text{RWI}_{2023}$, and $\text{RWI}_{2024-2023} / \text{RWI}_{2022}$. The $\text{RWI}_{2024-2023}$ is the mean RWI for the years 2023 and 2024.

To calculate climate-growth relationships, the individual ring-width series were converted into standardized series of ring-width indices through detrending (Fritts, 1976). This procedure allowed the removal of most size-related trends in ring-width data and emphasized high-frequency variability. We fitted negative linear or exponential functions to individual ring-width series and obtained ring-width indices by dividing observed values by fitted values. Then, autoregressive models were fitted to remove the first-order autocorrelation of the series of dimensionless indices. The resulting pre-whitened individual series were averaged using a bi-weight robust mean to obtain mean ring-width series for each species. The BAI and RWI series were obtained using the dplR package (Bunn, 2008, 2010; Bunn et al., 2025) in the R statistical software (R Core Team, 2024).

2.5. Wood anatomy

To analyze wood anatomy, we selected five trees per species showing a high correlation between their indexed ring-width series and the species' mean series of each site, except in *A. pseudoplatanus*, with four trees being analyzed. We focused on the period 2020–2024 to analyze responses before, during and after the 2022 heat wave. Wood cross-sections (thickness of 10–20 μm) of the core part, including the rings formed in 2020–2024 were obtained using a sledge microtome (Gärtner et al., 2015). Sections were stained with safranin (1 %) and Astra blue (2 %), and fixed with Eukitt®. The high-resolution images of the sections were then captured using an Olympus BH2 microscope equipped with an

Olympus DP73 camera. The images were stitched with the PT-Gui software (New House Internet Services BV, Rotterdam, NL) to create one composite image for each annual ring. Finally, the images were analyzed along a 4-mm tangential window using the image analysis software ImageJ version 1.54i (Schneider et al., 2012).

Wood-anatomical variables were selected and measured following Scholz et al. (2013) and Ziemińska et al. (2023). In total, 40,218 vessels were measured. For the diffuse porous species, the cut-off measurement value for vessel diameter was set at 35 μm , while 80 μm was used for the ring-porous species (cf. Granda et al., 2018).

In each annual ring of each tree, we measured: the xylem vessel fraction (VF, $\mu\text{m}^2 \mu\text{m}^{-2}$) corresponding to the portion of the transversal area occupied by vessels; the mean radial vessel diameter (MVD, μm); the vessel density (VD, number of vessels per mm^2); and the fraction of the transversal area occupied by ray parenchyma (RP, %). Based on the measurements of transversal area of all vessels in each ring, we calculated the theoretical (K_h) and total (TK_h) specific xylem hydraulic conductivity (both in $\text{Kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$).

2.6. Carbon isotope discrimination

To analyze $\delta^{13}\text{C}$, we selected the same five trees per species used for wood anatomy analyses. In this case, we focused on the period 2022–2024 to analyze tree responses during and after the heat wave. The individual rings were separated under the binocular using scalpels. Then, they were milled and homogenized using a ball mixer mill (Retsch MM301, Haan, Germany). We used whole wood instead of cellulose because previous studies on hardwood species showed that they lead to similar trends and results considering $\delta^{13}\text{C}$ (D'Alessandro et al., 2004). In total, 135 samples were analyzed. Lastly, wood aliquots (0.8–1.2 mg) were weighed on a microbalance (AX205 Mettler Toledo, OH, USA) into tin foil capsules.

Isotope analyses were carried out at the Stable Isotope Laboratory of the University of Almería (Almería, Spain). Encapsulated wood samples were combusted to CO_2 with a combustion module (CM) coupled to a cavity ring-down spectroscopy (CRDS) System (G2201-I Analyzer, Picarro), achieving a flash combustion at temperatures of 1700–1800 °C. The released CO_2 was transferred to a Picarro Liaison A0301 interface and entered into CRDS for analysis. The $\delta^{13}\text{C}$ values were referenced to the Vienna PeeDee Belemnite (V-PDB) scale. Sugarcane, acetanilide, and urea were used as working reference standards for consecutive $\delta^{13}\text{C}$ analyses of the wood samples, covering a wide calibration range from -11.9 ‰ to -44.3 ‰ . These working reference standards were initially calibrated against the USGS (USGS-40 L-Glutamic acid) and the IAEA standards (IAEA-603 and NBS-18 calcites). Based on analyses of these international standards, the precision ranged between 0.01 and 0.34 ‰ ($n = 9$) and, in terms of accuracy, the $\delta^{13}\text{C}$ error ranged from -0.03 ‰ to 0.88 ‰.

2.7. Statistical analyses

We selected different periods for different analyses, specifically 1962–2024, 2020–2024, and 2022–2024 for tree-ring, wood anatomy and $\delta^{13}\text{C}$ data. All periods included the 2022 heat wave, but differed depending on the available laboratory working hours since processing wood anatomy and $\delta^{13}\text{C}$ is highly time consuming. Despite the different considered periods, we are confident they did not affect comparability since we mainly focused on the 2022 heat wave and subsequent years.

Regarding statistical analyses, first, the normality of variables was checked using Shapiro-Wilk tests. Second, several variables, such as BAI, vessel density and hydraulic diameter, were log-transformed to fulfill normality. To assess the departure in BAI during 2022 (BAI_{2022}) with respect to a reference period, we selected 1997–2024 ($\text{BAI}_{1997-2024}$) when BAI curves were stable and used one-sample t tests to compare BAI_{2022} values with the $\text{BAI}_{1997-2024}$ mean. To compare resilience indices, $\delta^{13}\text{C}$ values (2022, 2023, and 2024) or wood-anatomical

variables of each species between years (2020, 2021, 2022, 2023, and 2024), we used ANOVAs and Bayesian t tests (Rouder et al., 2009). Bayes factor values larger than 3 or 10 indicate substantial or strong evidence, respectively, for unequal means. ANOVAs were then followed by Tukey's Q tests to compare means between species. To quantify the temperature and BAI trends, we used Mann-Kendall S tests.

To obtain climate-growth relationships, Pearson correlations were calculated between species' series of RWIs and monthly climate variables (mean maximum and minimum temperatures, precipitation, SPEI). The climate window of these analyses spanned from the prior (year $t-1$) to the current (year $t-1$) September. Correlations with the SPEI were calculated for 1- to 24-month long scales. Correlations were calculated for the common period 1962–2024, when all species were well replicated, using the treeclim R Package (Zang and Biondi, 2015). Correlations were also calculated between species' series of RWIs and the mean maximum temperatures from May to October during 1985–2024, when the warming rate was most intense. We also compared RWIs of the study species between hot, normal and cold summer (June to August) conditions. Hot, cold and normal summers were defined as those showing maximum summer temperatures above and below the highest and lowest 10th percentiles, respectively, and the rest of the years. Data analyses were carried out using the PAST version 5.2.2. software (Hammer et al., 2001) and the R statistical software (R Core Team, 2024).

3. Results

3.1. Maximum temperature, growth trends and wood anatomy

Maximum temperatures in the growing season showed significant ($p < 0.001$) positive trends in Cernobbio ($S = 1082$) and Monza ($S = 1156$; Fig. 2). In 2022, the maximum temperatures were $+1.45^\circ\text{C}$ and $+1.61^\circ\text{C}$ higher than the expected values, according to this trend, in Cernobbio and Monza, respectively. In addition, the 2022 hot spell occurred after two relatively cold years.

The rbar values indicated we built robust and well-replicated RWI chronologies, but differences in growth rate, AR1 and MS suggested diverse growth responses to climate variability (Table S1). *A. pseudoplatanus*, *F. excelsior*, and *B. pendula* showed the highest growth rates (2.94–4.02 mm), whereas *B. pendula* and *Q. robur* showed the highest (0.45) and lowest (0.25) MS values, respectively.

According to Mann-Kendall tests, all species showed significant BAI trends, except *B. pendula* in Cernobbio and *Q. robur* in Monza (Table 2, Fig. 3). Positive BAI trends were common and particularly strong in

some species (*T. cordata*, *F. sylvatica*, and *Q. pubescens*), except for *C. sativa*, which showed a negative BAI trend.

In 2022, BAI in Cernobbio was on average 85 % (–15 % loss) of the BAI measured in 2021, whereas in Monza it was 63 % (–37 % loss) (Figs. 3 and S1). However, there were great differences between species. In Cernobbio, the strongest and weakest BAI reductions corresponded to *B. pendula* (–58 %) and *A. pseudoplatanus* and *F. excelsior* (–5 %), respectively. Other species showed moderate BAI decreases (*C. sativa*, –25 %; *Q. pubescens*, –18 %). *F. sylvatica* showed a relative increase of BAI in 2022 (+3 %). According to one-sample t tests, BAI_{2022} was significantly lower than $\text{BAI}_{1997-2024}$ in *B. pendula* ($t = -12.48$, $p < 0.001$), *F. excelsior* ($t = -7.46$, $p < 0.001$), *A. pseudoplatanus* ($t = -6.52$, $p < 0.001$), *Q. pubescens* ($t = -2.71$, $p = 0.011$), but it was higher in *F. sylvatica* ($t = 2.96$, $p = 0.006$).

In Monza, *Q. robur* showed the strongest BAI reduction (–48 %), whereas the other two species showed moderate and similar losses in BAI (*F. excelsior*, –34 %; *T. cordata*, –29 %). Interestingly, the BAI reduction of *F. excelsior* during 2022 was significantly stronger at the low-elevation Monza site than at the high-elevation Cernobbio site ($F = 194$, $p < 0.001$; Bayes factor = 3.1). Moreover, BAI of *F. excelsior* in Monza showed another BAI reduction in 2023 (–17 %), when it reached a minimum value since 1995. The BAI_{2022} was significantly lower than $\text{BAI}_{1997-2024}$ in *Q. robur* ($t = -10.53$), *T. cordata* ($t = -9.91$) and *F. excelsior* ($t = -9.02$, $p < 0.001$ in the three cases).

In the period 2020–2024, *F. sylvatica* showed the highest BAI value (21.1 cm^2) and vessel density ($83\text{ vessels mm}^{-2}$) (Table 2). The highest ray parenchyma fraction (21.1 %) corresponded to *Q. pubescens*, whilst *Q. robur* presented the highest vessel area fraction (32 %), hydraulic diameter ($216\text{ }\mu\text{m}$), Kh ($1300\text{ Kg m}^{-1}\text{ MPa}^{-1}\text{ s}^{-1}$) and TKh ($1.18\text{ Kg m}^{-1}\text{ MPa}^{-1}\text{ s}^{-1}$).

The ray parenchyma fractions of *A. pseudoplatanus* in Cernobbio showed a significant reduction in 2022, whereas the hydraulic diameter increased (Table 3, Fig. 4). At this site, *F. excelsior* showed a reduction in vessel density during 2024.

3.2. Year-to-year growth variability

Regarding the series of ring-width indices, they again highlighted the severe growth reductions during 2022 of *B. pendula* and *Q. robur* in Cernobbio and Monza, respectively, and the negative legacy effects of *F. excelsior* in Monza (Fig. S2). In Cernobbio, the RWI series of all species showed significant ($p < 0.05$) and positive correlations (period 1962–2024), except for *F. sylvatica*. In Monza, the RWI series of the three species also showed significant and positive correlations, except for

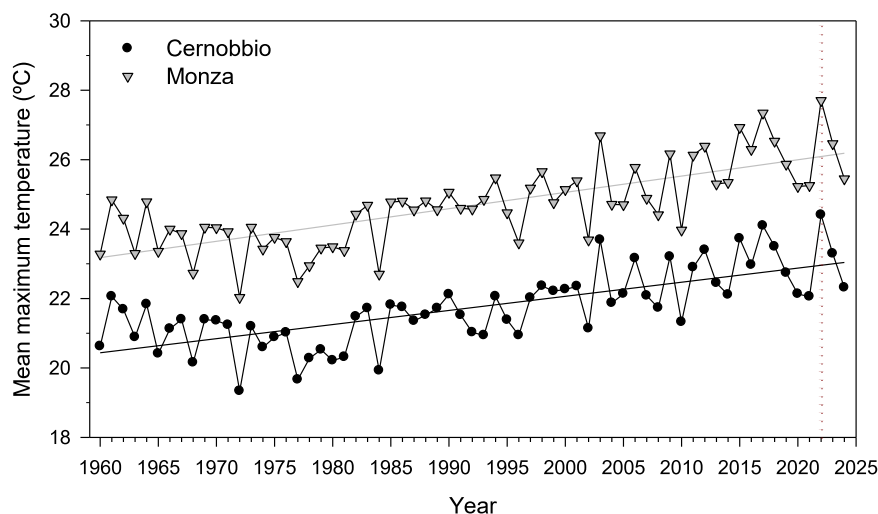


Fig. 2. Values and linear trends of mean maximum temperatures of the growing season (May to October) in the Cernobbio and Monza study sites. The dotted vertical line indicates the 2022 heat wave.

Table 2
Mean values ($\pm$ SD) of the growth and wood anatomical variables measured in the period 2020–2024. Abbreviations: BAI, basal area increment; K_h , theoretical specific xylem hydraulic conductivity; TK_h , total ring area hydraulic conductivity. The BAI trend was assessed using Mann-Kendall S tests. Underlined S values were not significant ($p > 0.05$). Different letters indicate significant ($p < 0.05$) differences between species within each site according to Tukey's Q tests.

Site	Tree species	Ring width (mm)	BAI (cm ²)	BAI trend, S	No. measured vessels	Vessel density (No. mm ⁻²)	Vessel area fraction (%)	Fraction of ray parenchyma (%)	Hydraulic diameter (μ m)	K_h (Kg m ⁻¹ MPa ⁻¹ s ⁻¹)	TK_h (Kg m ⁻¹ MPa ⁻¹ s ⁻¹)
Cernobbio	<i>C. sativa</i>	1.17 $\pm$ 0.37	6.6 $\pm$ 2.1a	−640	3702	34 $\pm$ 5ab	22.7 $\pm$ 3.2ab	9.5 $\pm$ 1.3a	169.3 $\pm$ 9.0c	310.9 $\pm$ 76.4c	0.19 $\pm$ 0.07b
	<i>Q. pubescens</i>	1.20 $\pm$ 0.32	7.9 $\pm$ 2.3a	1646	1939	38 $\pm$ 7ab	17.1 $\pm$ 4.2ab	21.1 $\pm$ 2.3b	207.2 $\pm$ 15.2c	305.4 $\pm$ 81.9c	0.19 $\pm$ 0.04b
	<i>F. excelsior</i>	1.40 $\pm$ 0.30	11.2 $\pm$ 2.5a	1002	1824	14 $\pm$ 2a	20.5 $\pm$ 3.5ab	11.8 $\pm$ 1.1a	198.7 $\pm$ 9.4c	243.3 $\pm$ 52.8c	0.21 $\pm$ 0.03b
	<i>A. pseudoplatanus</i>	1.75 $\pm$ 0.48	16.5 $\pm$ 5.0ab	981	2893	23 $\pm$ 4a	9.7 $\pm$ 1.8*	13.8 $\pm$ 2.2ab	74.5 $\pm$ 5.0a	17.7 $\pm$ 4.8a	0.02 $\pm$ 0.01a
	<i>B. pendula</i>	1.06 $\pm$ 0.49	8.6 $\pm$ 3.9a	<u>168</u>	2800	32 $\pm$ 4ab	15.1 $\pm$ 2.9ab	15.4 $\pm$ 3.9ab	86.4 $\pm$ 4.4b	36.9 $\pm$ 12.0b	0.03 $\pm$ 0.01a
	<i>F. sylvatica</i>	2.28 $\pm$ 0.71	21.1 $\pm$ 6.8b	1716	15,417	83 $\pm$ 9b	23.3 $\pm$ 2.8ab	13.3 $\pm$ 2.1a	62.7 $\pm$ 6.0a	32.7 $\pm$ 5.9b	0.06 $\pm$ 0.03a
Monza	<i>F. excelsior</i>	1.07 $\pm$ 0.34	10.5 $\pm$ 3.2a	1230	1747	19 $\pm$ 5a	21.2 $\pm$ 3.8ab	13.9 $\pm$ 1.7ab	192.4 $\pm$ 14.2c	242.3 $\pm$ 53.1c	0.27 $\pm$ 0.06b
	<i>Q. robur</i>	1.29 $\pm$ 0.49	13.1 $\pm$ 4.6ab	<u>2</u>	3646	41 $\pm$ 13ab	32.0 $\pm$ 1.5b	17.4 $\pm$ 1.6ab	216.3 $\pm$ 36.5c	1300.0 $\pm$ 1702.3d	1.18 $\pm$ 1.36c
	<i>T. cordata</i>	1.19 $\pm$ 0.74	11.6 $\pm$ 6.7a	2318	6250	66 $\pm$ 16ab	19.4 $\pm$ 3.7ab	14.5 $\pm$ 2.3ab	64.2 $\pm$ 5.0a	27.5 $\pm$ 6.5ab	0.03 $\pm$ 0.02a

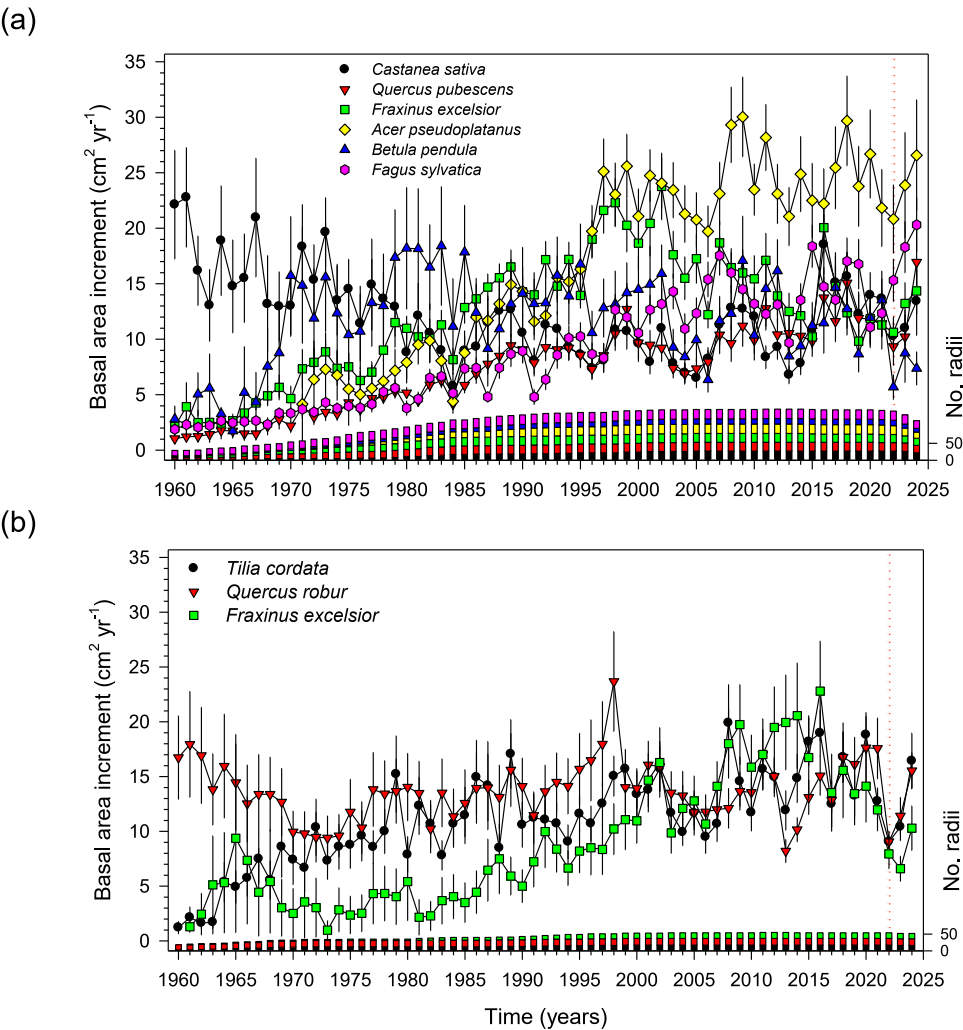


Fig. 3. Basal area increment measured in the tree species sampled in (a) Cernobbio and (b) Monza sites. The vertical dotted lines indicate the 2022 summer heat wave. Values are means $\pm$ SE. The annual number of measured radii is shown on the right y-axes (bars).

T. cordata and *F. excelsior*. The resilience indices of *B. pendula* showed a strong RWI reduction in

Table 3

Comparisons of growth and wood-anatomy data between years 2020, 2021, 2022 (heat wave), 2023, and 2024 based on ANOVAs. Data correspond to five trees per species, except in *A. pseudoplatanus* ($n = 4$ trees). The statistics show F values, and bold values indicate significant ($p < 0.05$) differences between years. Bold and underlined values indicate significant ($p < 0.05$) F values with strong evidence for unequal means (Bayes factor > 10). Upward and downward arrows indicate increases or decreases of the corresponding variable, respectively.

Site	Tree species	Ring width	BAI	Vessel density	Vessel fraction	Fraction of ray parenchyma	Hydraulic diameter	Kh
Cernobbio	<i>C. sativa</i>	1.479	0.904	0.657	1.122	1.537	0.167	0.426
	<i>Q. pubescens</i>	0.367	0.331	0.215	0.346	0.314	0.192	0.460
	<i>F. excelsior</i>	0.582	0.504	↓ 3.492	1.025	0.285	0.377	0.305
	<i>A. pseudoplatanus</i>	0.143	0.155	0.146	0.257	↓ 6.502	↑ 3.144	0.618
	<i>B. pendula</i>	0.977	1.007	0.019	0.633	0.393	0.110	0.647
	<i>F. sylvatica</i>	1.750	2.123	1.165	0.180	0.403	0.342	0.178
	<i>F. excelsior</i>	0.550	0.179	0.804	0.567	0.106	0.397	0.131
Monza	<i>Q. robur</i>	0.849	1.156	1.398	0.369	0.277	0.962	0.762
	<i>T. cordata</i>	2.131	1.662	1.059	0.991	0.279	0.091	0.219

Cernobbio during 2022, but also a strong relative recovery in 2023 and 2024 (Fig. S3). *F. excelsior* and *Q. pubescens* also showed remarkable RWI increases in 2023 and 2024, respectively. In Monza, we found the lowest recovery in *F. excelsior* (Fig. S4).

3.3. Comparing wood $\delta^{13}\text{C}$ values between years and species

Considering all species and years, the mean wood $\delta^{13}\text{C}$ values in Cernobbio (-26.9‰) and Monza (-26.5‰) were rather similar. During the period 2022–2024, we found no significant differences in wood $\delta^{13}\text{C}$ values between species neither in Cernobbio nor in Monza, except between *F. excelsior* and *Q. robur* from Monza in 2023 (-25.5 vs -26.9‰) and 2024 (-26.4 vs -27.6‰ ; Figs. S5 and S6). Taking into account the 2022–2024 data, *F. excelsior* showed higher $\delta^{13}\text{C}$ values (mean SD = $-25.6 \pm 1.0\text{‰}$) than *Q. robur* ($-27.0 \pm 0.9\text{‰}$) in Monza ($Q = 6.18$, $p = 0.0004$). In Cernobbio, *A. pseudoplatanus* showed significantly higher $\delta^{13}\text{C}$ values ($-26.1 \pm 1.2\text{‰}$) than *Q. pubescens* ($-27.6 \pm 1.0\text{‰}$; $Q = 5.52$, $p = 0.003$) and *F. sylvatica* ($-27.7 \pm 1.6\text{‰}$; $Q = 5.67$, $p = 0.002$).

3.4. Growth responses to climate variables and a drought index

Warm and dry June conditions constrained growth in Cernobbio (Fig. 4). The negative impact of maximum temperatures on growth indices extended until July in *F. excelsior*, *A. pseudoplatanus*, and *B. pendula*. High minimum temperatures in spring enhanced the growth of *Q. pubescens* and *F. sylvatica*, but elevated minimum temperatures in the previous autumn reduced the growth of *A. pseudoplatanus*. Wet spring conditions improved the growth of *Q. pubescens* and *A. pseudoplatanus*, but similar conditions in the previous November reduced the growth of *Q. pubescens*. This species and *C. sativa* were very sensitive to dry soil conditions from June to September, whereas *B. pendula* responded positively to wet soil conditions in the previous autumn Fig. 5.

In Monza, high maximum and minimum June temperatures reduced *F. excelsior* growth, whereas moist soil conditions in April and July improved it (Fig. 6). In contrast, elevated minimum temperatures in the previous November–December reduced growth. The growth of *T. cordata* decreased in response to elevated minimum temperatures of the previous autumn, but increased as soil moisture levels in August did. High minimum temperatures and precipitation in the prior winter enhanced *Q. robur* growth.

The highest RWI-SPEI correlations in Cernobbio corresponded to *F. excelsior* ($r = 0.64$, $p < 0.001$; July, 3-month long SPEI), *A. pseudoplatanus* ($r = 0.49$, $p < 0.01$; July, 9-month long SPEI), and *Q. pubescens* ($r = 0.47$, $p < 0.01$; June, 5-month long SPEI, Fig. S7). In Monza, the species most responsive to drought was again *F. excelsior* ($r = 0.45$, $p < 0.01$; October, 9-month long SPEI), followed by *T. cordata* ($r = 0.44$, $p < 0.01$; July, 6-month long SPEI) and *Q. robur* ($r = 0.42$, $p < 0.05$; October, 12-month long SPEI; Fig. S8).

3.5. Growth responses to maximum temperatures

We only found a significant correlation between the mean maximum temperatures from May to October and the ring-width indices in the case of *F. excelsior* from the low-elevation Monza site ($r = -0.439$, $p = 0.004$; Fig. 7b). Both variables started decoupling in the mid-2010s.

When comparing RWIs of *F. excelsior* from Monza for years with hot, normal and cold summer conditions, we found significantly lower values during hot summers ($F = 12.85$, $p = 0.005$, Bayes factor = 4.3; Fig. S9). In Cernobbio, differences in RWIs between summers of different thermal conditions were almost significant for *Q. pubescens* ($F = 4.75$, $p = 0.055$, Bayes factor = 1.1).

4. Discussion

We hypothesized that early leafing tree species would be the most negatively impacted by the 2022 heat wave in terms of growth loss. Early leafing species such as *B. pendula* and *Q. robur* showed the strongest growth reduction, whereas late leafing species (*T. cordata*, *C. sativa*, *F. excelsior*, *Q. pubescens*) showed moderate growth losses. Remarkably, *B. pendula* also presented a high recovery capacity. The growth of the intermediate leafing *F. sylvatica* was not negatively impacted by the hot spell, which is contradictory to its early flushing observed in 2022, but agrees with the limitation of its cambium activity by low temperatures at high elevation (Serra-Maluquer et al., 2019). Furthermore, warm and dry spring-summer conditions cause premature leaf discoloration, particularly in drought-sensitive species such as *F. sylvatica*, which should lead to growth reduction (Bigler and Vitasse, 2021). Beech showed a notable growth drop in 2020, when growing-season conditions were cool, and recovered afterwards, which could explain its elevated growth in 2022. Besides, it was growing at the highest-elevation site, near *B. pendula*, which could have buffered the impacts of the heat wave. The intermediate leafing *A. pseudoplatanus* showed a low growth reduction during 2022, despite its responsiveness to heat and drought stress. This is explained because it presented a prior BAI drop in 2021 (-18%), which could also be related to cool conditions, as in *F. sylvatica*. This idea is supported by the strong correlations found between the growth indices of *F. sylvatica* and *A. pseudoplatanus* and minimum temperatures in May. Our findings do not fully concur with the observation that late leafing, shade-tolerant species exhibit lower tolerance to high temperatures (Dreyer et al., 2001). The strong growth reduction found in early leafing, shade-intolerant species such as *B. pendula* and *Q. robur* could be explained by elevated temperatures early in the growing season impacting water-gas exchange and cambium dynamics and by the low drought tolerance of the birch species (Niinemets and Valladares, 2006).

Three species (*F. excelsior*, *A. pseudoplatanus* and *Q. pubescens*) were the most sensitive to summer maximum temperatures, low soil moisture levels and drought severity, and also showed high $\delta^{13}\text{C}$ values. In addition, the low-elevation warmer *F. excelsior* stand was the only one showing legacy effects (reduced growth in 2023, reduction in vessel

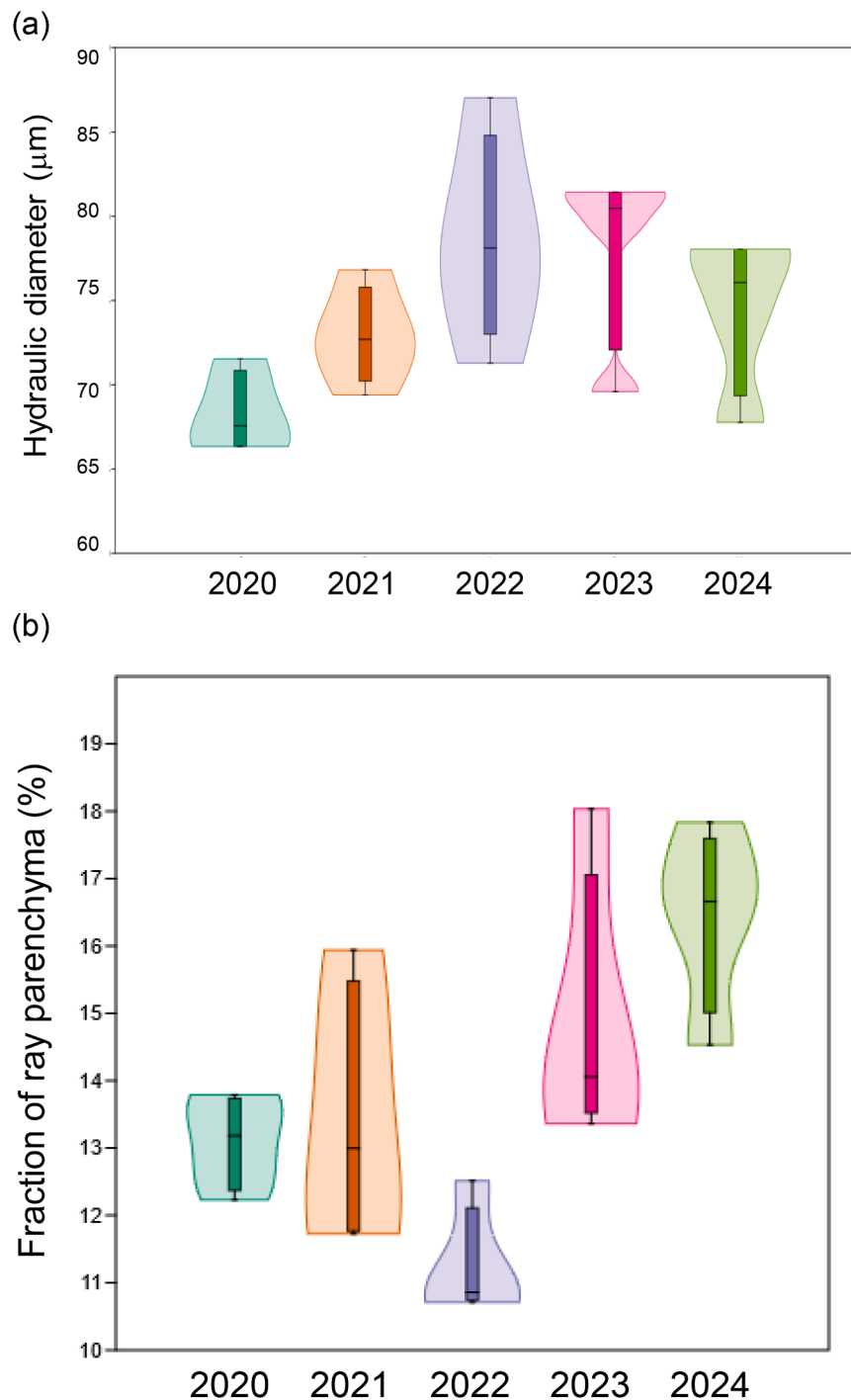


Fig. 4. (a) Hydraulic diameter and (b) ray parenchyma fractions measured in *A. pseudoplatanus* tree rings during the period 2020–2024 in Cernobbio.

density in 2024), and presented low resilience and a negative correlation between growth and maximum temperatures, whereas the vessel density increased during 2024 in the high-elevation cooler *F. excelsior* stand. At low elevation, *F. excelsior* growth was responsive to heat stress, whereas at high-elevation, under colder conditions, the same species responded more based on wood anatomy.

The presented findings do not agree with studies on drought impacts on temperate central European forests, who found marked growth and vessel-diameter reductions in diffuse-porous species such as *F. sylvatica* (Zimmermann et al., 2021; Bader et al., 2022). They ascribed the higher tolerance to drought of ring-porous species to a tighter regulation of sap flow. However, wood production does not only depend on sap flow

because elevated temperatures may damage foliage and reduce meristem turgor pressure that constrains cambial meristem activity (Peters et al., 2021). Under such C source and sink limitations, heat and drought stress may trigger the cessation of growth well before photosynthetic rates cease (Muller et al., 2011).

The most sensitive species (*F. excelsior*, *A. pseudoplatanus* and *Q. pubescens*) showed an improved iWUE after the heat wave, particularly at the low-elevation and drier site, which could be linked to changes in photosynthesis or stomatal conductance rates, but disentangling their roles would also require $\delta^{18}\text{O}$ data. It is plausible that *F. excelsior* and *A. pseudoplatanus* showed stomatal closure in response to heat stress and elevated VPD given their isohydric behavior (Battipaglia

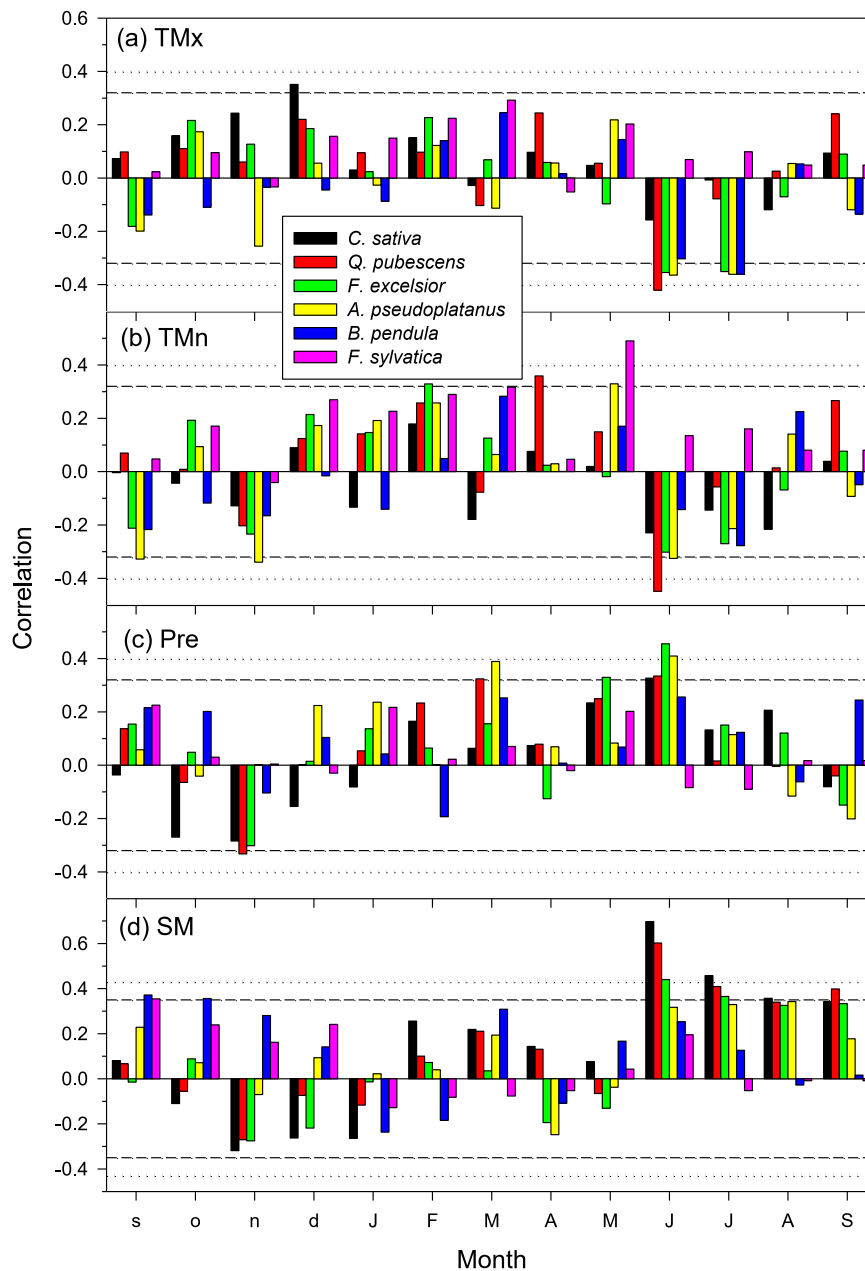


Fig. 5. Climate-growth relationships calculated for tree species sampled in Cernobbio. Climate variables include: mean maximum (TMx) and minimum (TMn) temperatures, precipitation (Pre), and soil moisture (SM). Bars are Pearson correlations and dashed and dotted horizontal lines show the 0.05 and 0.01 significance levels, respectively. The window of correlations goes from the previous (months abbreviated by lowercase letters) to current (months abbreviated by uppercase letters) years.

et al., 2008). In contrast, the anisohydric *Q. pubescens* could have responded by reducing its photosynthesis rate given its ability to uptake deep soil water sources and keep active leaf cooling through transpiration (Colangelo et al., 2025). Moreover, these three species showed moderate, but not strong, growth reductions, which evidenced the uncoupling between C sources and sinks, i.e. an enhanced iWUE does not necessarily translate into greater growth (Linares and Camarero, 2012).

We expected a decrease in wood $\delta^{13}\text{C}$ and iWUE due to enhanced leaf transpiration, but this was only observed in *Q. robur* two years after the heat wave. It is plausible that heat stress makes trees using stored carbohydrates from less stressful conditions to form wood (Kannenberg et al., 2022). Such response would explain the lack of $\delta^{13}\text{C}$ response, and could be explained by a decoupling between carbon sources (photosynthesis) and sinks (growth). In the case of *Q. robur*, the delayed

response could reflect legacy effects of elevated transpiration rates in this drought-intolerant species.

Other European ash species, such as *Fraxinus angustifolia*, were also very sensitive to summer drought under temperate conditions (Pericolo et al., 2023). Ash species can be considered semi-obligate phreatophytes (cf. Hultine et al., 2020) because their roots maintain continuous contact with the water table, but they may also extract water from the vadose zone. However, under severe heat stress, they can behave as obligate phreatophytes whose water requirements are derived exclusively from the water table to cool their leaves (Posch et al., 2024). Ash species form shallow and deep (bimodal) root systems, show isohydric behavior and are prone to xylem cavitation by drought. These traits could explain the vulnerability of *F. excelsior* to heat waves and soil drying that which would impair leaf cooling, damaging the photosynthetic apparatus. In the case of *A. pseudoplatanus*, its fast-growing, pioneer strategy would

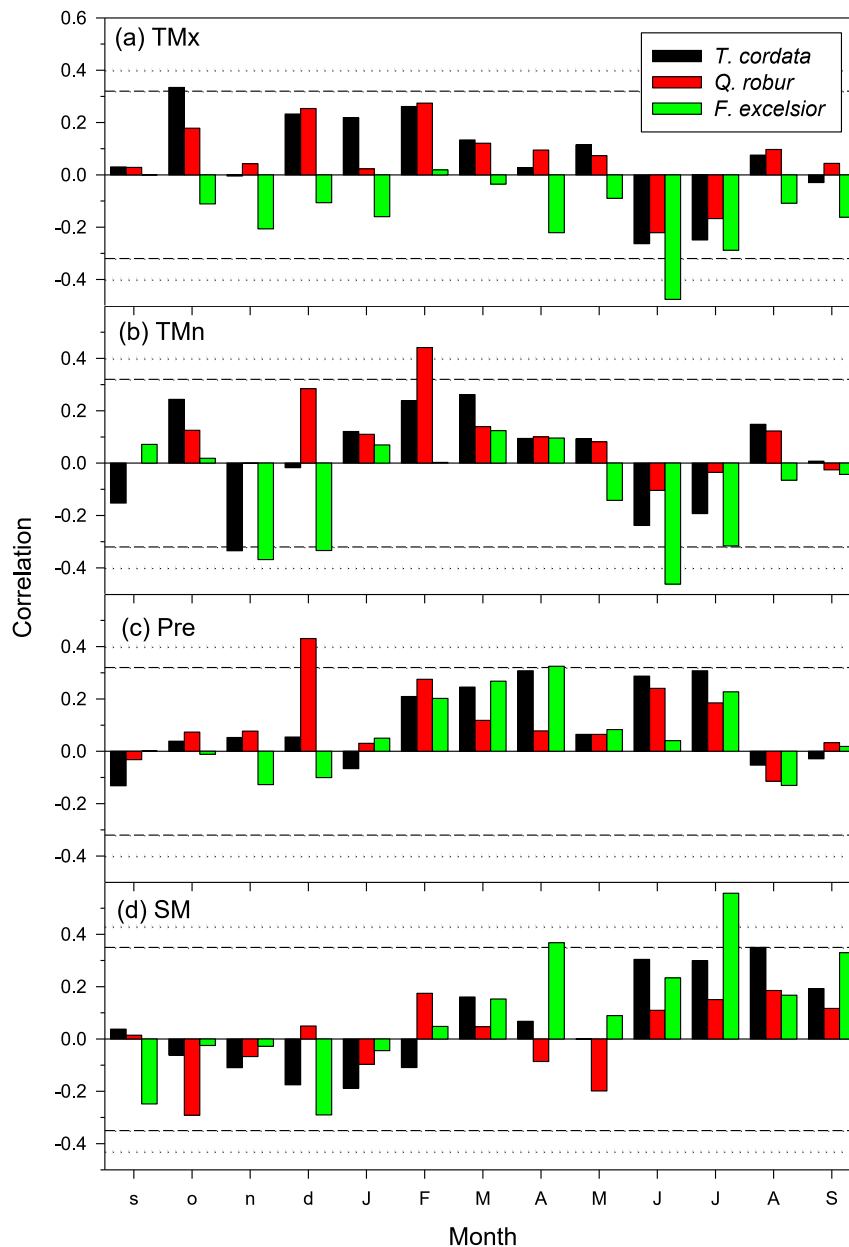


Fig. 6. Climate-growth relationships calculated for tree species sampled in Monza. Climate variables include: mean maximum (TMx) and minimum (TMn) temperatures, precipitation (Pre), and soil moisture (SM). Bars are Pearson correlations and dashed and dotted horizontal lines show the 0.05 and 0.01 significance levels, respectively. The window of correlations goes from the previous (months abbreviated by lowercase letters) to current (months abbreviated by uppercase letters) years.

explain its sensitivity to drought. This species shows rapid stomatal closure in response to a high VPD during the early growing season, exposing it to heat stress (Battipaglia et al., 2008). Lastly, oaks show a more anisohydric behavior, and the stronger growth reduction of *Q. robur* as compared to *Q. pubescens* could be due to the higher drought-tolerance of the second species (Rubio-Cuadrado et al., 2018; Bose et al., 2024; Colangelo et al., 2025).

Under drier conditions, plants form smaller xylem conduits, increased ray parenchyma, and higher vessel density to enhance resistance to drought-induced xylem embolism (Gleason et al., 2016; Hacke et al., 2022). However, we did not find any significant impact of the heat wave on the hydraulic diameter or theoretical hydraulic conductivity, except in *A. pseudoplatanus*. In this species, the hydraulic diameter increased in 2022, and the ray parenchyma decreased, two responses attributable to the hot spell which could indicate a decline in stored non-structural carbohydrates and a response to increase hydraulic

conductivity. Radial parenchyma mainly contributes to storage functions and radial conduction (Carlquist, 2013), and it increases with higher precipitation and lower temperature (Martínez-Cabrera et al., 2009; Plavcová and Jansen, 2015). A limitation of our study was that we could not measure the axial parenchyma, which is a relevant proxy of carbon storage in the xylem for species with wide vessels (Morris et al., 2018).

The carbon sink in European temperate forests declined by 12 % from the 2000s to the 2010s (Pan et al., 2024), but it is unclear how heat waves contributed to such decline. Predicting tree growth responses to heat stress is challenging because (i) species have developed several strategies to withstand thermal damage, and (ii) heat, VPD, and drought stress are strongly coupled (Evans et al., 2025). On one side, compound droughts characterized by low soil moisture levels and elevated VPD lead to sharp declines in ecosystem productivity, and trigger elevated defoliation and mortality rates (Gazol and Camarero, 2022; Gu et al.,

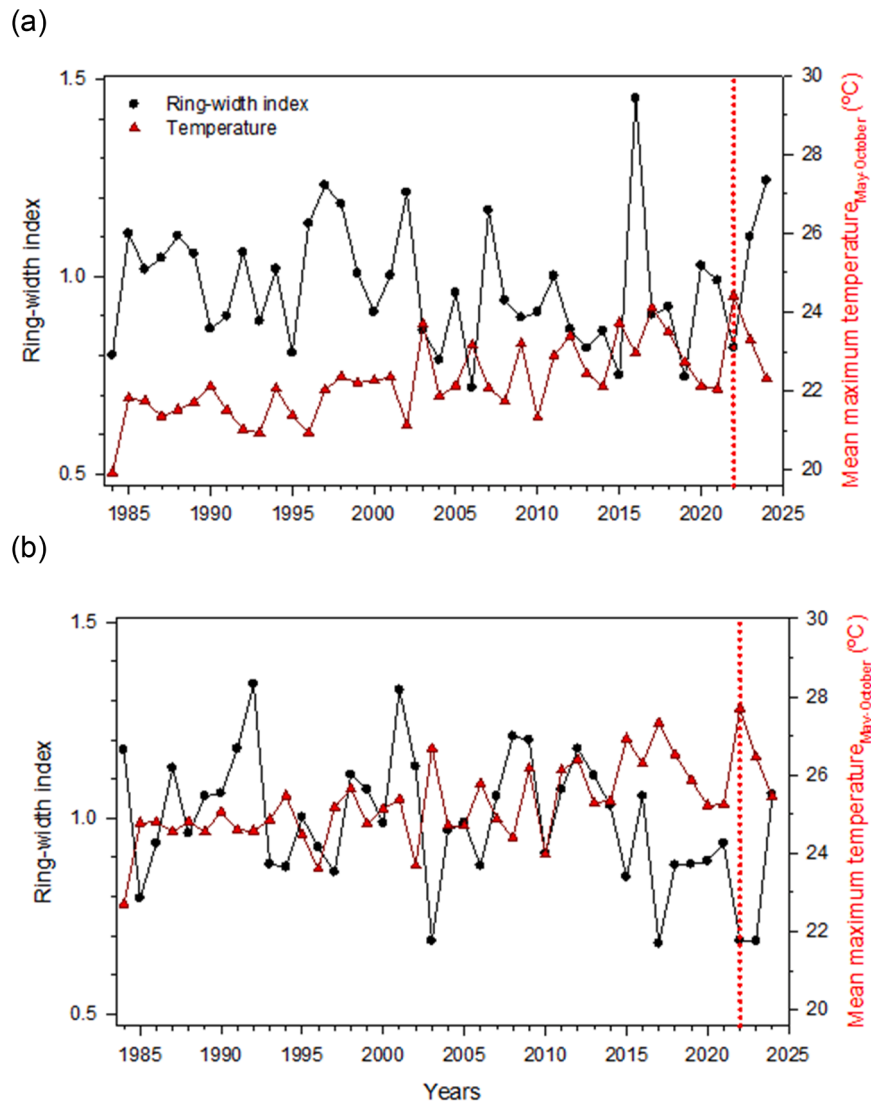


Fig. 7. Series of *F. excelsior* ring-width indices and the mean maximum temperatures from May to October (right y-axis) in the (a) high- (Cernobbio) and (b) low-elevation (Monza) sites. The vertical dotted line indicates the 2022 heat wave.

2025). In this sense, the 2022 heat wave was associated with flash droughts, characterized by a rapid increase in evapotranspiration, accelerating the drying of soil moisture over humid regions (Yuan et al., 2023). On the other side, high VPD and low soil moisture often occur during hot spells, but they can decouple during extreme heat waves leading to vegetation browning (Liu et al., 2023). For instance, *Populus fremontii* shows an efficient leaf cooling via transpiration in riparian forests of warm deserts, but small reductions in soil water availability during heat waves inhibit the cooling capacity, causing leaf necrosis and die-off (Moran et al., 2023; Posch et al., 2024). Our findings indicate that after disturbances such as heat waves, there may be few coordination between post-event growth rates and anatomical traits because wood production does not reflect the diverse aspects of tree growth, such as the formation of branches or roots (Hilty et al., 2021; Ziemińska et al., 2023). Lastly, we acknowledged the limitation derived from the unbalanced sampling between sites related to different forest composition and elevation, which constrained our ability to clearly differentiate phenological effects from site effects.

5. Conclusions

In two temperate forests, early leafing species such as *B. pendula* and

Q. robur showed the strongest growth reductions linked to the 2022 heat wave. Shade-intolerant pioneer species such as *F. excelsior* and *A. pseudoplatanus* were particularly vulnerable to the heat wave in terms of reduction in radial growth. Moreover, *F. excelsior* showed legacy effects after the heat wave, which affected growth and vessel density. Only *A. pseudoplatanus* presented a strong response in wood anatomy showing a lower ray parenchyma fraction which indicates a decline in xylem C storage. When assessing the impacts of heat waves on tree growth, the aboveground phenology should be considered. Growth reduction, recovery and legacy effects differ among coexisting species. Thus, winner (heat-tolerant) and loser (heat-intolerant) species will emerge after heat waves leading to shifts in forest composition.

CRediT authorship contribution statement

Ilaria Bonfanti: Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. Julio Camarero:** Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cristina Valeriano:** Writing – review & editing, Visualization, Software, Resources, Methodology, Investigation, Formal

analysis, Data curation. **Ángel Fernández-Cortés:** Writing – review & editing, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Nicoletta Cannone:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, 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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2026.111020](https://doi.org/10.1016/j.agrformet.2026.111020).

Data availability

Data will be made available on request.

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