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Quercus robur and *Q. petraea* responses to hydroclimatic changes and extremes in the Loire River valley, central France

Charlie Hureau^{a,b,c,*}, Sébastien Guillet^d, Valérie Daux^e, Emmanuèle Gautier^{a,b}, François Lebourgeois^e, Colombe Guerry^{a,b}

^a Université Paris 1 Panthéon-Sorbonne, Paris, France

^b Laboratoire de Géographie Physique (LGP), CNRS, UPI, UPEC, Thiais, France

^c Laboratoire des Sciences du Climat et de l'Environnement (LSCCE), CEA, CNRS, UVSQ, Université Paris-Saclay, Gif-sur-Yvette, France

^d Climate Change Impacts and Risks in the Anthropocene (C-CIA), Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland

^e Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France

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ABSTRACT

With more frequent and severe droughts under ongoing global warming impacting European forests, major components of French forest ecosystems, such as oak woodlands, are at increasing risk of decline. Tree-ring width (TRW) records provide valuable insights into both short- and long-term drought impacts on tree growth and have been widely used to improve our understanding of the spatial and temporal patterns of drought effects on forest ecosystems. However, such data are still lacking for oaks in central France over the past decade, and no high-resolution studies have yet explored oak responses to drought in French floodplain environments. Here, we investigated the climatic sensitivity, long-term growth response, and drought impact on TRW over the last century in two oak species from the Loire River basin in central France: riparian *Quercus robur* and non-riparian *Q. petraea*. Tree growth in both species was positively correlated with growing season SPEI and precipitation, and negatively with summer maximum temperature. Growth of riparian oaks was additionally influenced by summer river discharge and exhibited higher and more stable sensitivity to hydroclimatic variability than *Q. petraea*, reflecting species-specific traits and local site conditions. Despite these differences, both species showed consistent growth reductions during drought years, with full recovery to pre-drought growth levels not always achieved in the following year. Nevertheless, similar long-term growth patterns, with no overall decline over the last century, suggest a certain capacity of oaks to buffer drought impacts. These findings highlight the importance of continued monitoring of drought effects across contrasting ecological contexts and have direct management implications, particularly for Loire River riparian forests protected under the Natura 2000 network and encompassing national nature reserves.

1. Introduction

In 2024, global and European mean annual temperatures reached record highs, at +1.6 °C and +2.92 °C respectively, relative to the pre-industrial period (1850–1900) (Copernicus Climate Change Service, 2025). This marks the first year in which the global mean temperature exceeded +1.5 °C, a threshold beyond which extreme events are projected to become more frequent and more intense (IPCC, 2018). In France, 2024 ranked among the five warmest years on record, and the last decade (2015–2024) was, on average, 2.2 °C warmer than the pre-industrial period. This decade was also characterized by

increasingly severe and widespread droughts, affecting about 10% of the national territory (Météo-France, 2025). Under future climate scenarios, by the end of the 21st century and under a global warming level of +3 °C, summer precipitation in France is projected to decrease by about 20% (Soubeyrou et al., 2024), suggesting increases in drought frequency and severity during the growing season. This raises concerns about how forests will respond in the future, as drought have already caused widespread impacts on vegetation dynamics, including growth declines, dieback episodes, and increased mortality across many species (van Mantgem et al., 2009; Allen et al., 2010; Carnicer et al., 2011; Schuldt et al., 2020; Hammond et al., 2022).

* Correspondence to: Laboratoire de Géographie Physique, 2 Rue Henri Dunant, 94320 Thiais, France.
E-mail address: charliehureau@live.fr (C. Hureau).

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Pedunculate oak (*Quercus robur* L., hereafter *Q. robur*) and sessile oak (*Quercus petraea* (Matt.) Liebl., hereafter *Q. petraea*) are dominant deciduous trees of Europe's temperate lowlands, with *Q. robur* native to floodplains and wet lowlands and *Q. petraea* typically occurring in comparatively drier sites (Ducouso, Bordács, 2004; Rameau et al., 2018). In addition to regulating services such as carbon sequestration, water regulation, and soil fertility, oak forests provide cultural services through their high heritage value (Haneca et al., 2009). They also supply timber for construction, with France being the leading oak producer in Europe and accounting for 30–40% of continent's oak-growing area (Lebourgeois et al., 2015). However, the future of oaks under climate change remains uncertain. Some studies point to the high vulnerability of oaks to drought (Sohar et al., 2014a; Stojanović et al., 2015; Urli et al., 2015; Colangelo et al., 2018; Nechita and Camarero, 2025), particularly when droughts occur consecutively (Schnabel et al., 2022; Bose et al., 2024). Other studies, in contrast, emphasize their adaptive potential compared to co-occurring species (Zimmermann et al., 2015; Bert et al., 2022; Kasper et al., 2022; Gribbe et al., 2024; Nosenko et al., 2025). This adaptability is linked to deep rooting systems, hydraulically safe and efficient xylem water transport, and sustained stomatal conductance and transpiration, which enhances flexibility and resilience under drought conditions (Bréda et al., 1993a; Leuzinger et al., 2005; Gribbe et al., 2025). Even within the two main European oak species, differences in drought vulnerability remain unclear. *Q. robur*, which has higher water requirements and lower hydraulic safety is adapted to moist environments, exhibits lower resistance to xylem embolism, and is therefore more sensitive to drought than *Q. petraea* (Cocharde et al., 1992; Epron and Dreyer, 1993; Arend et al., 2011; Annighöfer et al., 2015). However, reduced post-drought recovery has been reported for *Q. petraea* (Bose et al., 2021, 2024), whereas broadly similar drought responses have also been observed in the two species (Bréda et al., 1993b; Cedro, 2007; Lebourgeois and Mérian, 2011).

In France, much of the current understanding of oak growth responses to climate comes from the extensive RENECOFOR monitoring network (Ulrich, 1995; Lebourgeois, 1997). However, the tree-ring chronologies developed within this network have not been updated since 2008, leaving a critical gap in assessing the impacts of the recent period marked by unprecedented warming and successive severe droughts. Furthermore, although oak responses to climate are now better understood in upland sites such as plateaus and alluvial terraces in France (Lebourgeois et al., 2004; Bergès et al., 2005; Mérian et al., 2011; Michelot et al., 2012; Barsoum et al., 2015), to our knowledge, no studies have investigated the sensitivity of riparian oaks to hydroclimatic variability, despite the ecological importance of these ecosystems (Ward et al., 1999; Piégay et al., 2003; Hupp and Rinaldi, 2007; Naiman et al., 2010). This is particularly concerning because climate models project a decline of up to 20% in the mean annual discharge of the Loire River by the end of the century (Dayon et al., 2018), potentially threatening the long-term sustainability of these riparian ecosystems (Villar et al., 2025), which are already among the most climate-sensitive and vulnerable worldwide (Tockner and Stanford, 2002; Perry et al., 2012; Capon et al., 2013; Rivaes et al., 2013).

Here, we focus on the Loire River basin, France's longest river (1000 km), which drains one-fifth of the metropolitan territory (117,000 km²) and represents an emblematic system due to its high conservation value and unique biodiversity (Cornier, 2002; Boudin et al., 2007; Chevalier et al., 2021). The alluvial hardwood forests of this watershed, notably dominated by *Q. robur*, are designated as Priority Habitat of Community Interest under the EU Habitats Directive (Council Directive 92/43/EEC, Natura 2000 code: 91F0). Given current and future challenges, this study presents a case study aimed at assessing whether, at a broader scale, management and conservation strategies should be grounded in a more detailed understanding of oak climate–growth relationships within the Loire River basin. Specifically, we address the following questions: (1) Which climatic variables and seasons most strongly control oak growth, and are these climate–growth

relationships stable over time? (2) How have recent changes in temperature and hydroclimatic conditions affected radial tree growth? (3) What is the impact of drought on riparian and non-riparian oak growth, and how effectively do these trees recover afterward? To address these questions, we developed two new tree-ring chronologies, updating and extending the existing RENECOFOR dataset through 2023. This provides a unique opportunity to evaluate oak growth responses to drought over the last century, and particularly during the last 15 years, a period of intensified climate change for which tree-ring data were previously lacking.

2. Material and methods

2.1. Study sites

In this study, three sites (HER, CUF and VLN) were sampled in the Loire River basin in central France (Fig. 1a). All three are located in the Middle Loire, within the “Island Loire River”, an anabranching section of the river between the Bec d'Allier and Briare, characterized by multiple channels enclosing wide sand and gravel bars, oxbow lakes, and large wooded islands (Gautier and Grivel, 2006). HER and CUF are within the alluvial forest at ~160 m above sea level (a.s.l.), with trees located between 5 and 160 m from the active river channel (mean distance = 60 m). CUF is located at the junction of the Allier and Loire rivers (46.96°N, 3.08°E), while HER is located 30 km downstream in the Val de Loire National Nature Reserve (47.25°N, 2.98°E). At these two sites, riparian vegetation naturally transitions from a softwood forest (*Salix alba*, *Populus nigra*) to a hardwood forest (*Q. robur*, *Fraxinus excelsior*, *Ulmus minor*, *Acer campestre*) as both the distance from the river channel and the elevation above it increase (Gautier et al., 2007; Cornier, 2002). Within the riparian zone investigated in this study, hardwood forests are dominated by *Q. robur*, while *Q. petraea* is absent (Fig. 1b). The two sites share similar geomorphological and sedimentological contexts, with sandy to gravelly alluvial soils. The VLN site is located on a plateau in the Bertranges forest at ~201 m a.s.l., outside the floodplain and about 5 km from the Loire River channel (47.19°N, 3.09°E) and 10 km from the HER site. The sampled site is dominated by *Q. petraea* on silty-clay soils, with *Q. robur* occurring only rarely (Fig. 1c).

At these sites, mean annual temperature and total precipitation over 1991–2020 average 11.2 °C and 720 mm, respectively. Precipitation is fairly consistent throughout the year, with a monthly average of 60 mm (Fig. 1e). May is the wettest month, with an average rainfall of 72 mm, followed by the period from October to December. June to September are the hottest and driest months. The mean annual discharge at Gien, the gauging station closest to the sites, is 328 m³/s, with high discharge from December to May and low discharge from June to November (Fig. 1d). Bankfull discharge, defined here as the mean of the 10 highest daily discharges for each year over the 1958–2023 study period ($Q = 1083 \text{ m}^3/\text{s}$), is exceeded on average 3.2% of days each year. Since 1901, annual hydroclimatic conditions have shifted toward warmer and drier states, with increasing maximum temperature (T_{max}), vapor pressure deficit (VPD), and climatic water deficit (CWD; since 1958), and decreasing annual Standardized Precipitation-Evapotranspiration Index (December SPEI12, i.e. calculated over a 12-month window) and mean discharge (Q ; since 1936), while mean precipitation (PRE) has remained unchanged (Fig. 1f). These changes reflect shifts in the magnitude and severity of hydroclimatic extremes. Over 1958–2023, significant linear trends ($p < 0.05$) were observed in T_{max} (+2.6 °C, i.e. +0.4 °C per decade), VPD (+1.78 hPa, i.e. +0.27 hPa per decade), SPEI12 (–1.39, i.e. –0.21 per decade), CWD (+131.7 mm, i.e. +20 mm per decade), and Q (–92.8 m³/s, i.e. –14.1 m³/s per decade) (Fig. 1f).

2.2. Tree-ring analysis

At HER, CUF and VLN sites, respectively 10, 12 and 31 trees, showing no visible sign of injury or disease, were sampled at breast height

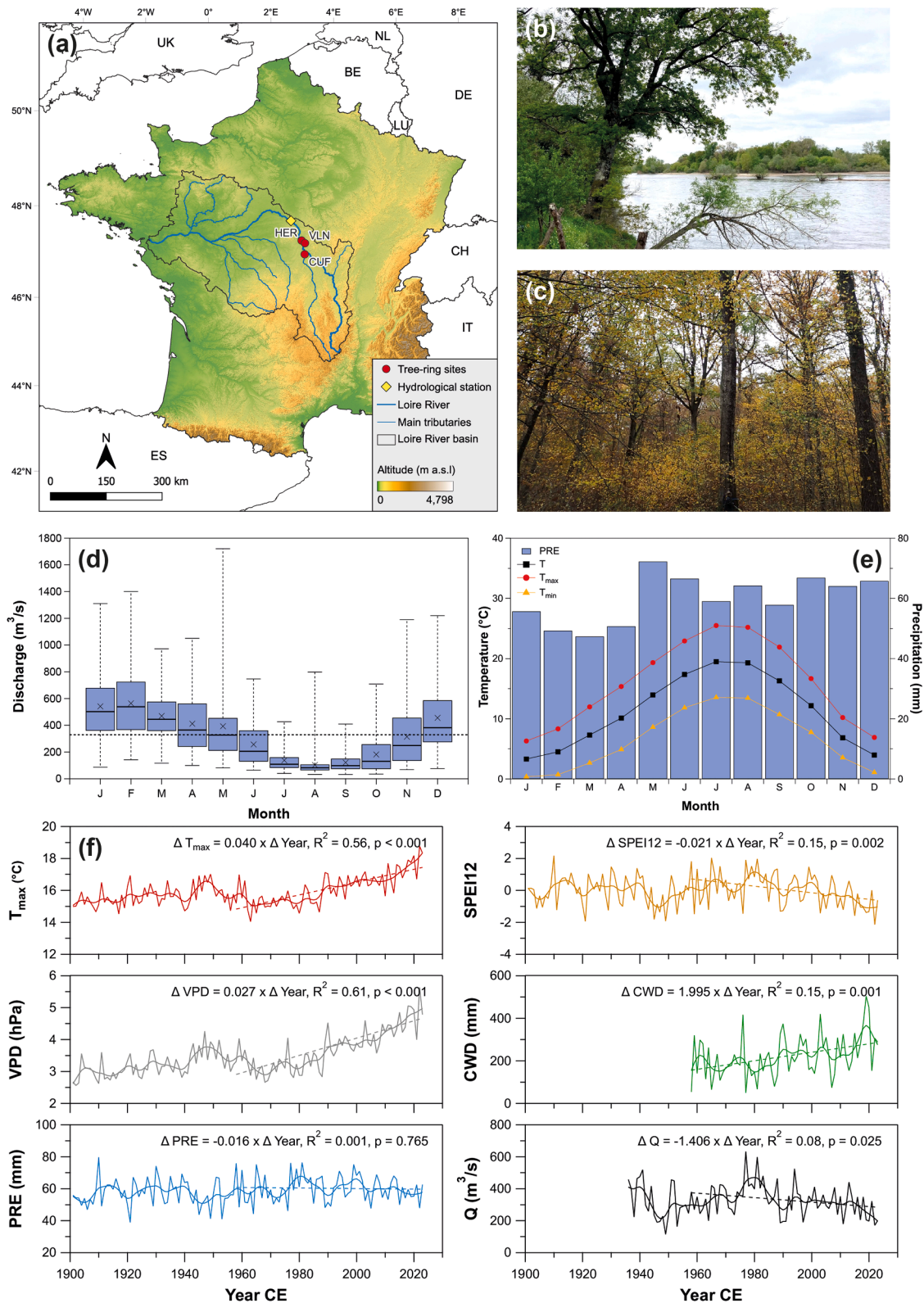


Fig. 1. (a) Location of the three sampled sites (HER, CUF, and VLN) and the Gien gauging station within the Loire River basin. (b) Pedunculate oak at the CUF site. (c) Sessile oaks in the Bertranges forest at the VLN site. (d) Loire River discharge over 1958–2023. Boxplots display minimum, first quartile (Q1), median (horizontal line), mean (cross), third quartile (Q3), and maximum monthly discharge, with the box representing the interquartile range (Q3–Q1). The dotted line indicates the mean annual discharge, marking the boundary between low and high flows. (e) Climograph between 1991 and 2020. (f) Interannual variations of maximum temperature (T_{max}), Standardized Precipitation-Evapotranspiration Index (December SPEI12), vapor pressure deficit (VPD), climatic water deficit (CWD), mean precipitation (PRE), and mean discharge (Q). The dotted lines represent linear trends over 1958–2023. Climate data were extracted from CRU TS4.08 (Harris et al., 2020), the Global SPEI database v2.10 (Begueria et al., 2014), and the TerraClimate reanalysis (Abatzoglou et al., 2018) at the grid points closest to HERCUF and VLN sites. Discharge data were obtained from the Gien gauging station.

(~120 cm), using a 4.3 mm diameter increment borer between winter 2023 and spring 2024. Two cores per tree were taken, successively sanded with 120- and 400-grit sandpaper, and scanned at 1200 DPI. Tree-ring widths (TRW) were measured and rings dated using Coorecorder and CDendro (Larsson, 2014; Maxwell and Larsson, 2021). The TRW series from each core were averaged per tree after visual and statistical crossdating.

Detrending, tree-ring chronology building and descriptive statistics were computed using the *dplR* package (Bunn, 2008, 2010) in R (R Core Team, 2024). The individual mean series were detrended using a cubic smoothing spline with a 50% cut-off at 67% of the series length (Cook and Peters, 1981), a method commonly applied to remove age-related growth trends in forest interior sites (e.g. Čufar et al., 2008; Kern et al., 2013; Mikac et al., 2018; Radaković and Stajčić, 2021). To reduce the biases associated with low replication and extend the length of the chronology (Fritts, 1976; Büntgen et al., 2012; Mérian et al., 2013), a single chronology (HERCUF) was constructed from the trees of the HER and CUF sites (Table 1). The final standardized chronologies were obtained by calculating the biweight robust mean of the individual series. The residual chronologies were derived in the same way, after pre-whitening the series using an autoregressive model. The running Expressed Population Signal (EPS) was used to estimate the number of individual series required for each chronology to be representative of a theoretical infinite population of trees (Wigley et al., 1984). It was calculated using 31-year running windows. The Subsample Signal Strength (SSS) was calculated to assess the decrease in climate signal linked to the decrease in the number of samples over time (Wigley et al., 1984; Buras, 2017). Finally, to ensure the consistency of individual series within our chronology, the running interseries correlation coefficient (running rbar) was calculated using a 31-year running window. Descriptive statistics of the raw tree-ring chronologies such as mean tree-ring series length (MSL), mean tree-ring series growth rate (MGR), mean sensitivity (MSI), mean tree-ring series intercorrelation (static rbar) and mean autocorrelation (MAC) are reported in Table 1. MSI quantifies the year-to-year variability in TRW series (Biondi and Qeadan, 2008). It ranges between 0 and 1, with complacent tree-ring series exhibiting values near 0, while values greater than 0.2 indicate sensitive series (Biondi and Qeadan, 2008; Speer, 2010). Static rbar is the mean value of all correlations between individual series. MAC, which measures the influence of the growth increment in the previous year on the increment of the current year, is the mean value of the first-order autocorrelation coefficients.

To identify possible long-term changes in growth related to recent climatic trends, temporal trends in the tree-ring chronologies were assessed using several methods. The Mann-Kendall test (Mann, 1945; Kendall, 1975) was applied to the standardized chronologies, which better preserve low-frequency signals, over windows of at least 30 years, considering all possible combinations of start and end years within the 1958–2023 period. The Pettitt test (Pettitt, 1979) was also used to detect potential shifts in individual tree-ring series and tree-ring chronologies (Table S1).

2.3. Climate and hydrological data

To investigate climate–growth relationships, we compiled hydrological and climatic variables describing water availability and atmospheric conditions in the Loire River basin. Daily discharge data for the

Loire River at the Gien gauging station (Fig. 1a) were retrieved from the HydroPortail database (<https://hydro.eaufrance.fr>), for the period 1936–2023. Two key hydrological parameters were retrieved. First, mean monthly discharge was calculated by averaging daily discharge values for each month. Second, a low-flow threshold was derived from the annual flow duration curve (FDC), which represents the percentage of time that a given discharge is equaled or exceeded. The FDC is a robust indicator of the combined influence of precipitation and groundwater contributions and is widely used to characterize hydrological variability in both gauged and ungauged basins (Blöschl et al., 2013; Lang-Delus et al., 2016; Ghotbi et al., 2020; Medici et al., 2023). At Gien, discharge exceeds 106 m³/s for 80% of the year (292 days). Discharges below this threshold correspond to very low flow conditions, which typically occur during summer.

Because meteorological stations in the Loire River basin are spatially dispersed and contain gaps in their records, monthly maximum temperature (T_{max}) and total precipitation (PRE), were extracted from the CRU TS4.08 gridded dataset (Harris et al., 2020). Standardized Precipitation-Evapotranspiration indices, calculated over accumulation periods ranging from 1 to 6-months (SPEI1–SPEI6 indices), were obtained from the Global SPEI database v2.10 (Beguería et al., 2014). Both datasets were extracted using the 46.5–47.5°N, 2.5–3.5°E grid box, which encompasses all three study sites.

We also extracted climatic water deficit (CWD) data from the TerraClimate reanalysis dataset (Abatzoglou et al., 2018). Together with SPEI, CWD provide information about agricultural drought by characterizing limitation in soil moisture availability. The SPEI integrates precipitation and potential evapotranspiration (PET), thereby accounting for atmospheric water demand and allowing drought characterization at multiple temporal scales (Vicente-Serrano et al., 2010). Climatic water deficit (CWD), defined as the difference between PET and actual evapotranspiration, represents the absolute magnitude of accumulated water deficit and provides a direct proxy for soil moisture limitation. Together, SPEI and CWD describe complementary aspects of drought related to atmospheric demand and soil water availability (Schwarz et al., 2020; Zang et al., 2020).

In addition, vapor pressure deficit (VPD) was used to characterize atmospheric drought, representing a distinct, atmosphere-driven constraint on tree growth not captured by soil moisture-based metrics (Gazol and Camarero, 2022). Monthly VPD was calculated as the difference between saturated vapor pressure (SVP) and actual vapor pressure (AVP) with AVP obtained from the CRU TS4.08 dataset. SVP was computed using the Tetens (1930) equation:

$$SVP = 6.108 \times \exp\left(17.27 \times \frac{T}{237.3 + T}\right) \quad (1)$$

Where T is the mean monthly temperature (°C).

2.4. Climate–growth relationships

Climate–growth relationships were assessed using bootstrapped correlations between climatic and hydrological variables and the residual tree-ring chronologies. Residual chronologies were used to retain high-frequency variability while minimizing temporal autocorrelation. Correlation analyses were computed using the *treeclim* package in R (Zang and Biondi, 2015) with 1000 replications following the classical

Table 1

General characteristics and descriptive statistics of the HERCUF and VLN tree-ring chronologies. EPS: expressed population signal; SSS: subsample signal strength; MSL: mean (min–max) tree-ring series length; MGR: mean growth rate (± 1 standard deviation); MSI: mean sensitivity index; rbar: mean series intercorrelation; MAC: mean autocorrelation.

Chronology name	Trees (cores)	Chronology length	Chronology with EPS and SSS > 0.85	MSL (yr)	MGR (mm/yr)	MSI	rbar	MAC
HERCUF	22 (44)	1950–2023	1958–2023	60 (43–74)	1.54 \pm 0.60	0.30	0.46	0.58
VLN	31 (62)	1878–2023	1901–2023	116 (69–146)	2.32 \pm 0.64	0.24	0.48	0.53

DENDROCLIM2002-style approach, in which individual years are resampled with replacement (Biondi and Waikul, 2004).

Analyses were performed over the period 1958–2023, during which both EPS and SSS consistently exceeded the 0.85 threshold (Buras, 2017). Monthly data from May of the previous year to October of the current year were included to capture lagged climate–growth responses. This temporal window accounts for the reliance of *Q. robur* and *Q. petraea* on carbohydrates stored from the previous season for vessel formation (Barbaroux and Bréda, 2002; Hoch et al., 2003). Additionally, twenty-one seasonal combinations, involving climate parameters averaged over 2- to 6-month periods from March to September, were analyzed.

The temporal stability of climate–growth relationships was evaluated using 31-year running correlation functions. All correlation coefficients presented in the result section are significant at $p < 0.05$.

All climate time series ($n = 225$) were detrended prior to analysis following the same procedure applied to the tree-ring data, as suggested by Ols et al. (2023). Autocorrelation in the detrended climate series was very low; only 6 out of 225 time series (2.7%) exhibited an absolute first-order autocorrelation (AR1) greater than 0.3, which is below the level expected by chance. Consequently, the detrended climate series were not prewhitened (Ols et al., 2023).

2.5. Growth response to drought events

Using SPEI and CWD, drought events were identified based on percentile thresholds calculated over the 1958–2023 period. Extreme droughts were defined as years in which SPEI values fell below the 10th percentile or CWD exceeded the 90th percentile, whereas moderate droughts corresponded to SPEI values below the 25th percentile or CWD above the 75th percentile. Droughts were calculated for the May–September period, which represents a compromise interval during which hydroclimatic conditions are most critical for tree growth at both sites. We also tested whether seasonal timing of droughts (winter: DJF; spring: MAM; summer: JJA) influenced the severity of tree growth responses (Table S2). VPD was additionally considered to identify drought events driven by atmospheric demand but is not emphasized further, as no significant reductions in tree growth were observed in response to VPD-based atmospheric drought (Fig. S1).

To evaluate growth response to drought, probability density functions (PDFs) of tree-ring indices were estimated for each chronology using kernel density estimation in R (R Core Team, 2024), and drought events were overlaid to evaluate their placement within the growth distribution.

Tree resilience to drought was quantified using the resistance (R_t), recovery (R_c), and resilience (R_s) indices of Lloret et al. (2011). R_t refers to the ability of trees to minimize the growth reduction during drought, and was calculated as the ratio between growth during the drought year and growth during the preceding years. R_c reflects the ability to regain growth following drought and was calculated as the ratio of post-drought growth to growth during the disturbance. R_s represents the ability of trees to recover their pre-drought growth levels and was calculated as the ratio between post-drought and pre-drought growth. Values of R_t and $R_s < 1$ indicate reduced growth during or after drought, whereas values > 1 indicate growth enhancement. R_c values < 1 indicate incomplete post-drought recovery, whereas values > 1 indicate post-drought growth exceeding drought-year growth. Indices were computed over reference periods ranging from one to five years, and since the results were consistent across periods, only the one-year results are presented. Although Basal Area Increment (BAI) was considered, analyses were restricted to tree-ring indices, due to the lack of pith offset data, as recommended by Klesse and Bigler (2025).

Overall tree-growth responses to drought were assessed using superposed epoch analysis (SEA), with drought years treated as key events and a five-year before and after each event (-5 to $+5$), using the dplR package (Bunn, 2008, 2010). Statistical significance was evaluated via

1000 resampling iterations to generate 95% confidence intervals.

3. Results

3.1. Tree-ring chronologies

A total of 106 cores from 53 trees were successfully crossdated, allowing us to develop two site chronologies extending to 2023 (Table 1). The HERCUF TRW chronology provides a robust record for investigating climate–growth relationships in riparian forests during the period 1958–2023. Its reliability is supported by relatively high mean series intercorrelation ($r_{bar} = 0.46$), high sensitivity ($MSI = 0.30$) (Table 1), and high running interseries correlation (running r_{bar}), running EPS, and running SSS values (Fig. 2a). Over 1958–2023, the mean 31-year EPS ranges between 0.86 and 0.94, with an average value of 0.91, the mean SSS ranges between 0.88 and 1, with an average value of 0.98 and the mean 31-year r_{bar} ranges between 0.32 and 0.63, with an average value of 0.44. The VLN TRW chronology, built from trees located outside the riparian zone, covers the period 1878–2023, with EPS and SSS consistently > 0.85 from 1901 onwards (Fig. 2b). Over 1958–2023, the mean 31-year running EPS varies from 0.97 to 0.98, with an average of 0.98. The SSS remains consistently at 1 throughout the period, and the mean 31-year r_{bar} is 0.60, ranging from 0.55 to 0.66. Mean growth rate is higher at VLN (2.32 mm/yr) than at HERCUF (1.54 mm/yr) (Table 1), and the same contrast holds over 1958–2023 (2.33 mm/yr at VLN vs. 1.50 mm/yr at HERCUF). Despite this difference in growth level, the two sites exhibit strong shared interannual variability ($r = 0.56$). These robustness statistics confirm that the two tree-ring chronologies are suitable for climate–growth analyses over the common 1958–2023 period.

3.2. Trends in tree growth

The multi-temporal trend analysis of tree-ring chronologies using the Mann-Kendall test revealed no significant trends at HERCUF, whereas at VLN one significant negative trend (1960–1992) and one significant positive trend (1972–2014) were detected (Fig. 3). The corresponding Mann-Kendall τ values ranged from -0.25 to -0.28 for 1960–1992 and 0.21 – 0.26 for 1972–2014, indicating weak trends. In addition, Pettitt's change-point tests supported these results, with no significant breaks detected at either the population or individual level, except for one tree at VLN showing a break in 1913, outside the study period (Table S1). We therefore conclude that no consistent upward or downward trends in tree growth have occurred at HERCUF or VLN since 1958.

3.3. Climate–growth relationships and temporal stability

At HERCUF and VLN, tree growth was predominantly influenced by hydroclimatic conditions from late spring through summer, with stronger correlations observed at HERCUF. The HERCUF tree-ring chronology was negatively correlated with maximum temperature in June and July (-0.53 , -0.33), with CWD in May (-0.42), June (-0.63), and July (-0.48), and with VPD in June (-0.56), July (-0.38) and August (-0.25). In contrast, it was positively correlated with precipitation and SPEI in May (0.44, 0.41), June (0.52, 0.58), July (0.37, 0.42), and over the May–July period (both 0.69) (Fig. 4a).

Tree-ring widths also showed positive correlations with monthly discharge from June to September (0.52, 0.61, 0.22, and 0.38, respectively), with the strongest association occurring during June–July (0.59). Similar relationships were observed between tree growth and discharge duration parameters. Tree growth was positively correlated with the number of days in June–July exceeding the low-water discharge threshold ($r = 0.61$), and with the number of days above the mean discharge, corresponding to the high-flow period associated with the submersion of unvegetated bars ($r = 0.48$) (Fig. 5b). More specifically, considering the low-water discharge threshold, 72% of years with

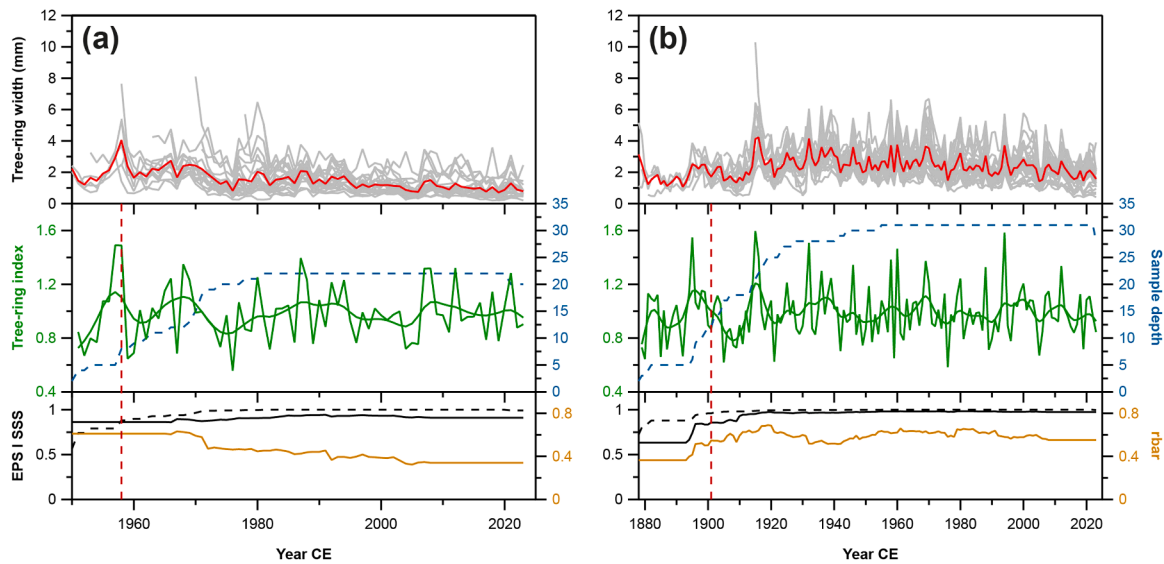


Fig. 2. HERCUF (a) and VLN (b) TRW chronologies. From top to bottom: raw individual tree-ring series (grey) and mean chronology (red); residual chronologies with 10-year cubic spline smoothing (green) and sample depth (dashed blue line); EPS (solid black line), SSS (dashed black line), and rbar (yellow). Red dashed vertical lines indicate years before which either EPS or SSS falls below 0.85.

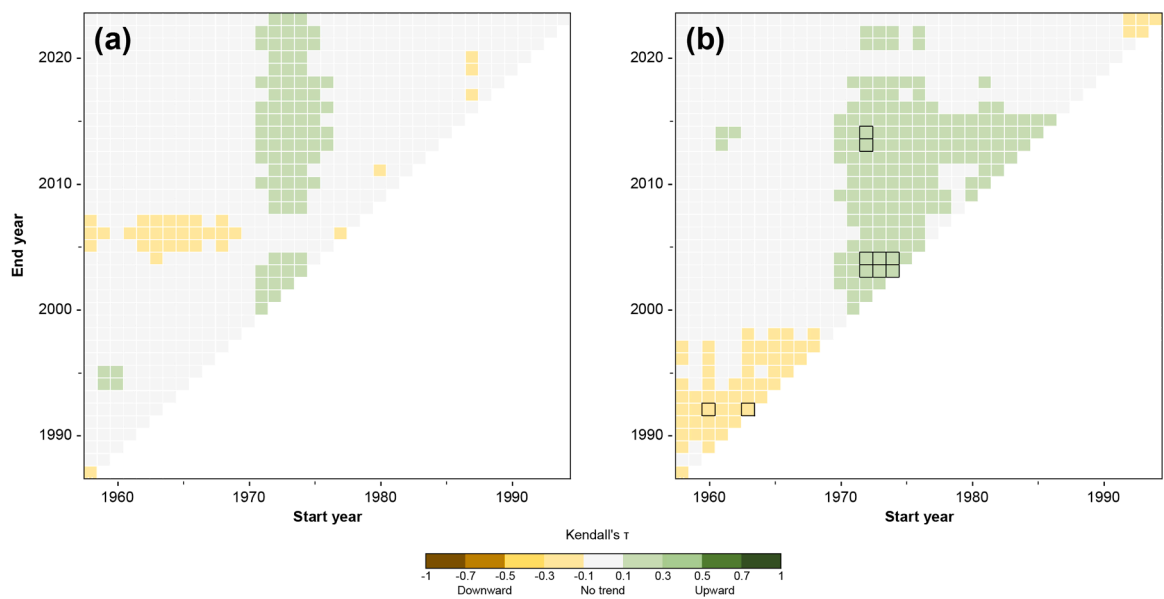


Fig. 3. Trends in HERCUF (a) and VLN (b) tree-ring chronologies using Mann-Kendall test. The tests were carried out over windows of at least 30 years, considering all possible start and end year combinations within the period 1958–2023. Significant windows ($p < 0.05$) are outlined in black.

above-median discharge coincided with years of above-median growth at HERCUF, while 65% of years with very high discharge (> 3rd quartile) coincided with years of very high growth (> 3rd quartile) (Fig. 5b). When using the mean discharge threshold, 69% of years with above-median discharge matched years of above-median growth, and 59% of years with very high discharge (> 3rd quartile) matched years of very high growth (> 3rd quartile) (Fig. 5b). The highest summer discharges (> 90th percentile), recorded in 1969, 1977, 1992, 2008, and 2016, also corresponded to some of the highest tree-growth values, which were consistently above the third quartile (Fig. 5a). The year 1981 represents an exception, as high summer discharges did not result in enhanced growth. Unusually cold spring and summer conditions during that year may have offset the positive effects of high-water levels on tree growth.

At HERCUF, climatic conditions during the previous winter, early spring, and autumn appeared to have little impact on oak growth.

However, weak but statistically significant correlations were observed with precipitation in the previous August and September (0.26, 0.28), as well as with the previous September SPEI1, CWD, and VPD (0.33, -0.28, -0.33), and with February river discharge (0.21).

At VLN, tree growth was positively correlated with precipitation from May to July (0.33, 0.29, 0.26) and with SPEI1 from May to August (0.27, 0.30, 0.30, 0.27). Positive correlations were also observed for both precipitation and SPEI over the May–September period (0.52 and 0.48, respectively) (Fig. 4a). In contrast, growth was negatively correlated with maximum temperature in July and over the June–July period (-0.28, -0.34), with CWD from May to September (-0.34, -0.40, -0.34, -0.31, -0.24), and with July VPD (-0.29). In addition, positive winter correlations were found for December precipitation and SPEI (both 0.30) and for February precipitation (0.26).

Hydroclimatic conditions from late spring through summer exert a

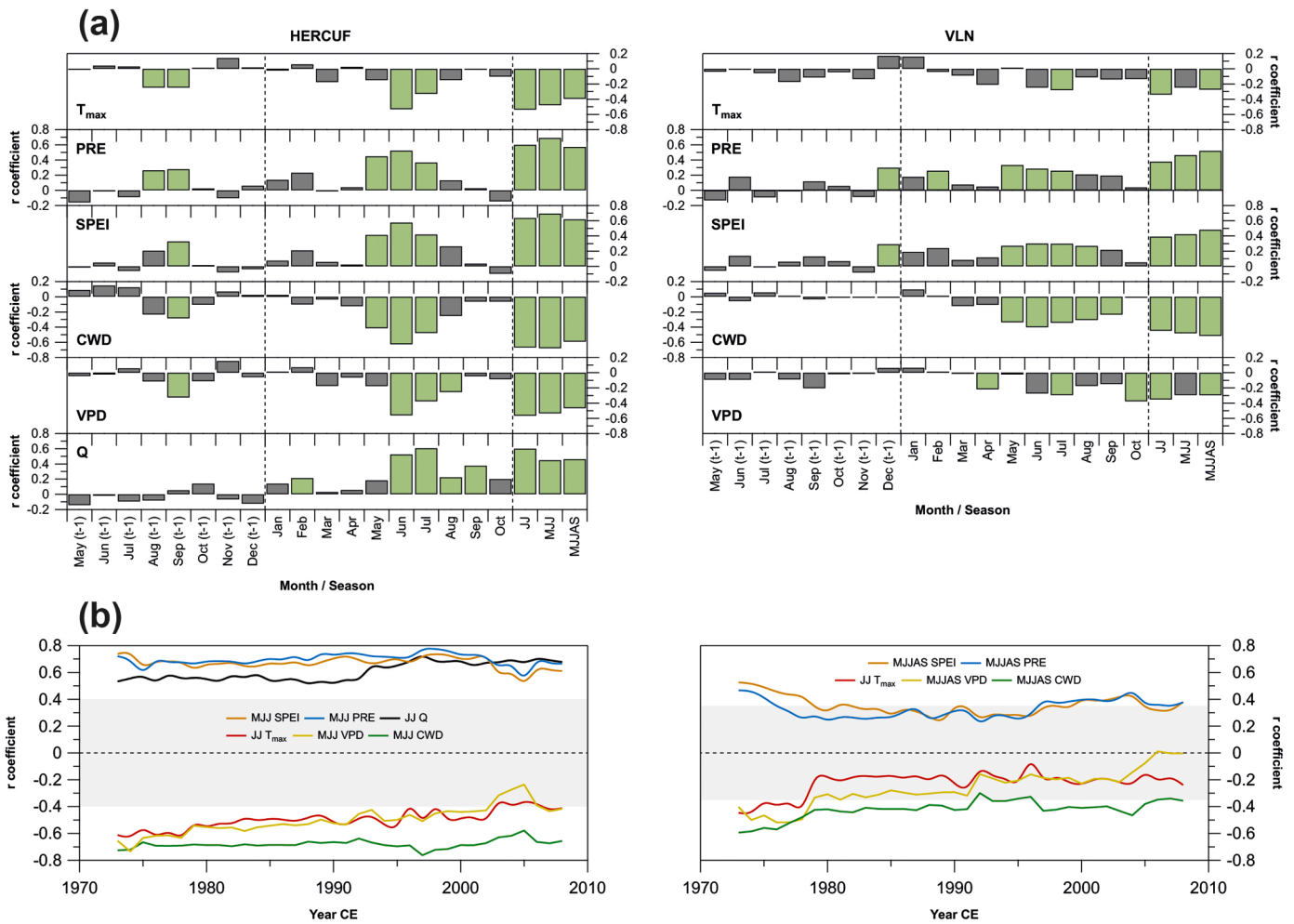


Fig. 4. (a) Static bootstrapped correlation functions between HERCUF, VLN, and climate variables from the previous May to the current October. T_{max} : maximum temperature; PRE: total precipitation; SPEI: SPEI1 (except for JJ, MJJ and MJJAS, which refer to July SPEI2, June SPEI3 and September SPEI5, respectively); CWD: climatic water deficit; VPD: vapor pressure deficit; Q: mean discharge. Green bars indicate significant correlations, while grey bars denote non-significant values ($p > 0.05$). (b) Running bootstrapped correlation functions (31-year window) between HERCUF, VLN, and key climatic parameters. The grey shaded areas indicate non-significant correlation values ($p > 0.05$). The correlation windows are centered, e.g. the value in 1973 corresponds to the correlation coefficient over the 31-year window 1958–1988.

strong and temporally persistent influence on oak growth throughout the study period at HERCUF. However, from 1992 onward we observe a strengthening of the statistical association with June–July discharge with an increase by 0.14 in 66 years, when considering the first (1958–1988, $r = 0.53$) and last (1993–2023, $r = 0.68$) 31-year correlation windows (Fig. 4b). In contrast, the associations with June–July maximum temperature and May–July VPD gradually weakened over the study period, decreasing by 0.20 and 0.24 over 66 years, from $r = -0.61$ and $r = -0.66$ in 1958–1988 to $r = -0.41$ and $r = -0.42$ in 1993–2023, respectively, and losing statistical significance between the 1988–2018 and 1991–2021 windows (Fig. 4b). At VLN, correlations with May–September precipitation and September SPEI5 slightly decreased over 66 years, by 0.09 and 0.15, respectively, when considering the first (1958–1988, $r = 0.47$ and $r = 0.53$) and last (1993–2023, $r = 0.38$ for both) 31-year correlation windows, while correlations with CWD weakened from -0.59 to -0.36 over the same period. Correlations with precipitation and SPEI were not significant between 1976 and 1996. Correlations with maximum temperature and VPD were non-significant since 1979 with r values fluctuating around -0.2 (Fig. 4b).

3.4. Impacts of severe droughts on tree growth

Based on the analysis of May–September SPEI and CWD data, we

identified 19 drought events between 1958 and 2023 (8 extreme and 11 moderate), of which 15 were common to both datasets. These droughts occurred in the years 1959, 1961, 1962, 1964, 1976, 1989, 1990, 1996, 1998, 2003, 2005, 2009, 2011, 2015, 2018, 2019, 2020, 2022, and 2023 (Fig. 6b, c). The extreme droughts recorded at our sites were not isolated anomalies but component of widespread drought episodes affecting northern France and, from the 1990s onwards, extending across all of France (Fig. 6a). We observed a marked increase in drought frequency since the 1990s, with nearly three times as many drought events in 1990–2023 as in 1958–1989 (Fig. 6b, c).

Probability density functions were used to position documented drought years within the distribution of annual growth indices at HERCUF and VLN. At HERCUF, 9 of the 19 identified droughts resulted in severe growth reductions and fell within the lower tail of the distribution (<25 th percentile) (Fig. 6d). Several of the narrowest rings occurred one year after drought events (1960, 2004, and 2006) (Fig. 6d), indicating delayed growth impacts. At VLN, a similar pattern was observed, although drought events more frequently translated into very low growth (<10 th percentile; 1959, 1962, 1976, 1990, 2005, and 2019) than at HERCUF (1976, 2005) (Fig. 6d, e). Notably, the 1976 drought, widely recognized as one of the most severe pan-European hydroclimatic events of the 20th century (e.g. Briffa et al., 2009; Parry et al., 2012), corresponds to the narrowest ring in both chronologies.

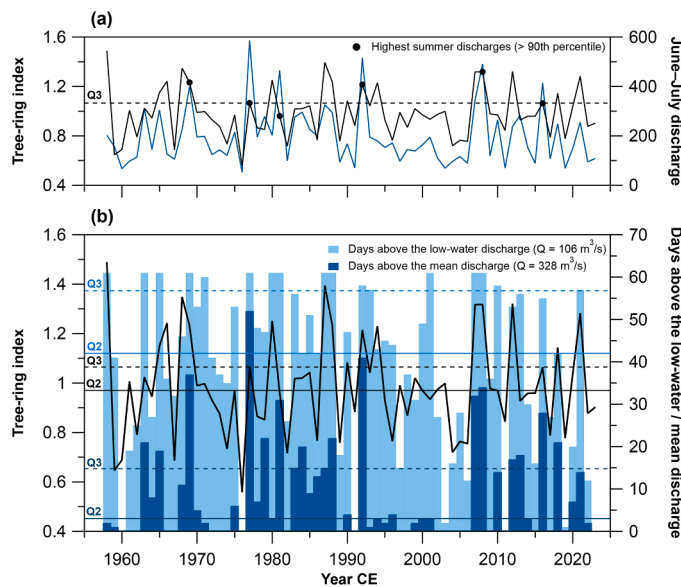


Fig. 5. (a) HERCUF tree-ring chronology (black line) and June–July mean discharge (blue line). Black dots indicate years with highest summer discharges (> 90th percentile), and horizontal line indicates the third quartile (Q3) of the HERCUF tree-ring chronology. (b) HERCUF tree-ring chronology (black line) and the number of days above the low-water threshold (light blue bars) and above the mean discharge (dark blue bars) in June–July. Solid and dotted horizontal lines indicate the median (Q2) and the third quartile (Q3) of each variable, respectively.

However, most other drought events coincided with growth values within the central portion of the distribution, particularly in recent extreme drought years (2015, 2018, 2020, 2022, and 2023), even though several of these years can be classified as extreme droughts (Fig. 6b, c). These results suggest a certain adaptive capacity of the oaks at HERCUF and VLN to both moderate and extreme droughts. This is particularly noteworthy given the marked increase in the intensity and frequency of such events since the 1990s (Fig. 6b, c), whereas overall tree growth has remained stable (Fig. 3, Table S1).

However, although these drought events do not always coincide with statistically defined low-growth years (Fig. 6d, e), they nonetheless exert a strong influence on radial growth, highlighting the sensitivity of both *Q. robur* and *Q. petraea* to drought stress. At both sites, Lloret resistance indices indicate that although drought years did not always correspond to exceptionally low TRW, they consistently exhibited reduced growth relative to the preceding year, reflecting a clear response to water deficit conditions (Fig. 7a). Recovery patterns were more variable across drought episodes, but in more than half of the cases, TRW in the year following drought were larger than during the drought year, indicating a capacity for post-drought growth compensation. In contrast, short-term resilience was generally low at both sites, as more than 50% of drought events were not followed in the next year by a full return to pre-drought growth levels.

The SEA results further support these findings, revealing a consistent negative growth anomaly during documented drought years for both species, with growth significantly below the long-term mean (Fig. 7b). This response was similar in *Q. robur* and *Q. petraea*. At HERCUF, trees exhibited a significant positive growth anomaly four years after drought events, suggesting a delayed compensatory response. A similar pattern was observed at VLN, although post-drought growth anomalies were not statistically significant there. This suggests that although immediate resilience is generally low at both sites, as shown by the resilience index, trees may still exhibit longer-term growth compensation several years after drought. SEA for drought events defined using VPD showed no significant growth reduction from $t-5$ to $t+5$ (Fig. S1), consistent with weaker and less stable correlations with tree-ring indices at both sites

(Fig. 4).

Overall, these results highlight, at both sites, a significant mean negative effect on tree growth during drought years (Fig. 7), although individual responses are nuanced, as not all droughts, even the most severe, correspond to low-growth years (Fig. 6d, e). Neither drought intensity nor the occurrence of successive droughts can fully explain these observations, since extreme drought periods (2018–2020, 1961–1962, and 1989–1990) did not lead to similar growth responses (Fig. 6d, e and Fig. 7a).

4. Discussion

4.1. Main climatic drivers of tree growth

Growth in both riparian *Q. robur* (HERCUF) and non-riparian *Q. petraea* (VLN) is primarily driven by May–July precipitation and SPEI, correlations being weaker when the window is extended to May–September. This is coherent with the typical response of these species, for which spring and early-summer water availability is a key driver of radial growth, a pattern widely observed across European oceanic (Pilcher and Gray, 1982; Friedrichs et al., 2009a; Mérian et al., 2011; Michelot et al., 2012), continental (Kern et al., 2013; Sochová et al., 2024), and Mediterranean climates (Santini et al., 1994; Rozas, 2005). Variations in water availability during this period directly affect tree growth: reduced moisture limits photosynthetic activity by decreasing sap flow, stomatal conductance, and carbon assimilation whereas higher soil moisture tends to support greater radial increment (Bréda et al., 1993a, b; Rust and Roloff, 2002). The strongest hydroclimatic responses, observed in May and June at both sites, are also consistent with the pronounced impact of spring droughts on oak growth (Camarero et al., 2015; Vanhellefont et al., 2019; Bose et al., 2021). Spring droughts are particularly critical, as they can disrupt the phenological cycle and delay the onset of xylogenesis (Horáček et al., 2003; Fonti et al., 2010; Pérez-de-Lis et al., 2016).

Tree growth is negatively influenced by June–July maximum temperature and May–July VPD, but these effects are weaker and less consistent, suggesting that atmospheric water demand exerts less control on oak growth than soil moisture availability. This may be explained by the fact that maximum temperature and associated VPD primarily affect stomatal conductance, which is more directly reflected in oak tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ records (Daux et al., 2018; Treydte et al., 2024), whereas oak radial growth is mainly limited by soil moisture availability (Bose et al., 2021, 2024), making tree ring widths less sensitive to atmospheric drought alone.

At HERCUF, in a riparian context, our findings are consistent with previously reported positive correlations between *Q. robur* growth and river discharge in European temperate floodplains (Hafner et al., 2015; Tumajer and Treml, 2016; Okoński, 2017; Mikac et al., 2018; Netsvetov et al., 2019). Moreover, our results indicate a positive influence of the duration of moderate river discharge on oak growth, suggesting that prolonged periods of moderate flow increase water availability, thereby reducing hydric stress and supporting tree growth. Floodplain ring-porous species, including oaks, primarily rely on surface water stored in the vadose zone, filled by precipitation and capillary rise from the groundwater (Sánchez-Pérez et al., 2008; Singer et al., 2013, 2014). To explain the effect of the Loire River discharge, we can hypothesize that higher and longer summer discharge promotes fine root development during this period (Ponti et al., 2004; Konópka et al., 2005). This, in turn, mitigates water stress in riparian oaks by enhancing capillary rise and increasing the water supply provided by the fine-root system (Skiadaresis et al., 2019; Mu et al., 2021; Šenfeldr et al., 2021; Leonova et al., 2022; Henkel et al., 2025). Conversely, during summer low-flow periods, the drop in the water table restricts water uptake by the shallow fine-root system, leading to ecophysiological dysfunctions that ultimately reduce growth (Bréda et al., 1995), an effect that is likely amplified in the sandy-gravelly alluvial soils of the Loire River where

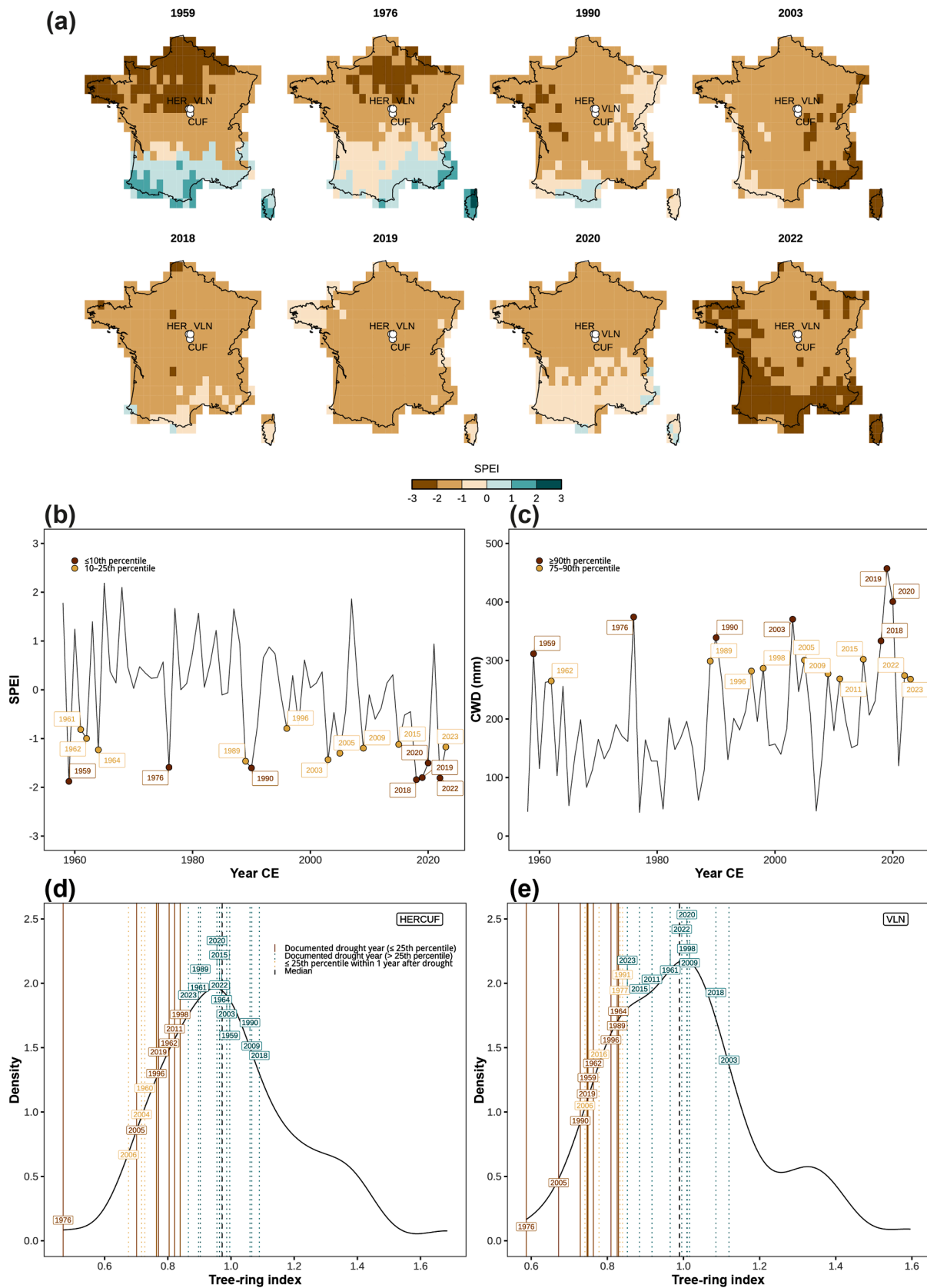


Fig. 6. (a) May–September SPEI conditions over France during the documented extreme droughts. (b) Time series of May–September SPEI and (c) CWD with associated drought events. (d) Probability density function showing the distribution of drought-year growth values within the HERCUF and (e) VLN chronologies. Years with documented droughts that coincide with low tree growth (<25th percentile) are shown in dark brown, droughts with no corresponding low growth in green, and low growth occurring within one year after a drought in light brown. The median of each distribution is indicated by a black dashed vertical line.

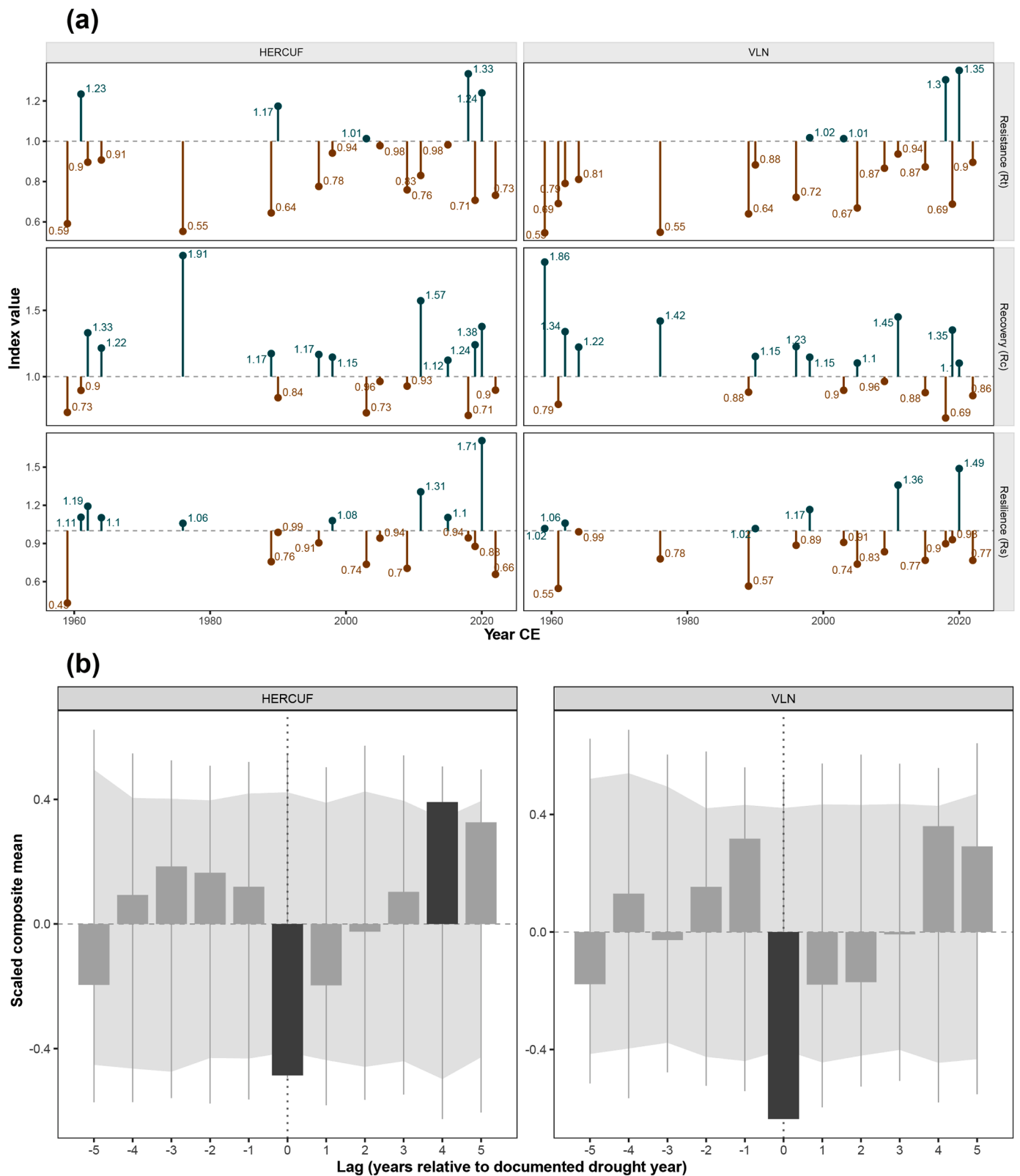


Fig. 7. (a) Resistance, recovery, and resilience indices of Lloret et al. (2011) computed for drought events using the HERCUF and VLN tree-ring standardized chronologies. (b) Mean tree growth responses to drought events at both sites based on superposed epoch analysis. The grey shaded area represents the 95% confidence interval, with epochal anomalies falling outside this interval (black) considered statistically significant ($p < 0.05$).

capillary rise is limited.

Riparian *Q. robur* growth at HERCUF shows a weak yet significant positive response to late-summer precipitation and SPEI from the previous year. This aligns with studies demonstrating that summer-to-autumn hydroclimatic conditions in the year before ring formation can influence current-year oak radial growth (Cedro, 2007; Cejková and Poláková, 2012; Matisons and Brūmelis, 2012; Bouwman et al., 2025). Some studies have also shown that hydroclimatic conditions spanning from the previous summer through the current summer best explains *Q. robur* growth (Friedrichs et al., 2009a; Stojanović et al., 2018). Positive correlations between earlywood width in the current year and latewood width from the previous year have also been reported in oaks (Lebourgeois et al., 2004; Radaković and Stajić, 2021), supporting a carryover effect between growing seasons. This delayed growth response likely results from the spring remobilization of carbohydrates (starch and sugars) stored during the late stages of the previous growing season (Lacointe, 2000; Barbaroux and Bréda, 2002; Hoch et al., 2003). Favorable late-summer hydroclimatic conditions can enhance these reserves, supporting increased growth in the following year. At HERCUF, *Q. robur* also shows a weak but significant relationship with the February discharge of the river. This sensitivity to winter conditions is even more pronounced in *Q. petraea* from VLN, whose growth is influenced by winter hydroclimatic conditions from December of the previous year and February of the current year. Numerous studies have likewise reported positive correlations between winter hydroclimatic conditions and *Q. robur* and *Q. petraea* growth (Cedro, 2007; Friedrichs et al., 2009a; Michelot et al., 2012; Mikac et al., 2018; Stojanović et al., 2018). Winter hydroclimatic conditions can favor oak growth by recharging soil and groundwater, maintaining the functionality of fine roots, and preventing early-season water deficit, thereby supporting earlywood vessel formation (Michelot et al., 2012). Winter flooding may also promote the deposition of nutrient-rich sediments, enhancing soil fertility and indirectly supporting tree growth (Kroes et al., 2015; Marchetti et al., 2020; Marks et al., 2020). However, overbank deposition at HERCUF is minimal due to the river's very low suspended sediment load (Gautier et al., 2007).

4.2. Riparian *Q. robur* and non-riparian *Q. petraea* climate sensitivity

Riparian *Q. robur* exhibited overall stronger and more stable sensitivity to hydroclimatic parameters compared to non-riparian *Q. petraea* (Fig. 4). Similar patterns have been documented in earlier studies, which describe *Q. petraea* as less sensitive to climate (Pilcher and Gray, 1982; Lebourgeois et al., 2004; Friedrichs et al., 2009b; Mérian et al., 2011; Michelot et al., 2012). The contrasted climate-growth relationships observed at HERCUF and VLN likely reflect differences in functional traits. *Q. petraea* has a more conservative water-use strategy, including higher intrinsic water-use efficiency that underpins its greater drought tolerance and buffers its growth against interannual hydroclimatic variability. In contrast, *Q. robur*, with lower hydraulic safety and higher vulnerability to xylem embolism, reacts more strongly to fluctuations in water availability (Cochard et al., 1992; Epron and Dreyer, 1993; Ponton et al., 2002; Arend et al., 2011; Annighöfer et al., 2015). Differences in hydraulic safety between species and genera remain debated, as many physiological processes contribute to xylem adjustment in trees (Choat et al., 2012; Cochard et al., 2021; Decarsin et al., 2024). The greater hydraulic safety of *Q. petraea* compared to *Q. robur* can be explained by differences in earlywood vessel anatomy, with *Q. robur* exhibiting a larger total earlywood vessel area than *Q. petraea*, due to a higher number of vessels (Feuillat et al., 1997; Hroš and Vavřík, 2014). In *Q. robur*, these anatomical traits maximize hydraulic conductivity but increase vulnerability to cavitation, consistent with the strong scaling between conduit diameter and cavitation risk in ring-porous species (Hacke et al., 2006; Sperry et al., 2006) and with the documented relationship between vessel size (length and diameter) and embolism vulnerability across *Quercus* species (Cochard and Tyree, 1990; Lobo

et al., 2018).

Site conditions likely contribute to the differences in climate sensitivities observed at VLN and HERCUF. At VLN, deep brown siliceous-clay soils provide relatively stable moisture conditions, whereas the sandy-gravelly soils at HERCUF impose stronger water limitations and variability (Jones et al., 2005), which likely amplify the sensitivity of riparian oaks. This interpretation is consistent with the lower growth rates at HERCUF, about 1.5 times lower than at VLN (Table 1). It aligns with previous studies showing that oaks on deep, drought-resistant soils respond weakly to summer precipitation, while those on soils with low water retention (shallow, sandy, dry environments) show stronger growth responses (Sohar et al., 2014b; Stojanović et al., 2018; Kostić et al., 2021; Bouwman et al., 2025).

4.3. Long-term responses of oak trees to drought

No significant decrease in radial growth was observed at either site over recent decades. This absence of a declining trend suggests that both *Q. robur* and *Q. petraea* have maintained relatively high long-term resilience to recent climatic changes, consistent with previous findings identifying these species among the most drought-tolerant temperate broadleaf species (e.g. Kunz et al., 2018; Fuchs et al., 2021; Enderle et al., 2024; Bouwman et al., 2025). Our results are in line with several recent studies reporting stable oak growth despite ongoing warming and increasing drought intensity and frequency across Europe (Zimmermann et al., 2015; Fuchs et al., 2021; Kasper et al., 2022; Enderle et al., 2024; Leuschner et al., 2024). *Q. petraea* has even shown increased growth under reduced precipitation in Germany, suggesting an acclimatization process (Gribbe et al., 2024), a pattern also observed for *Q. robur* in southern England and northern France (Barsoum et al., 2015), and in floodplains of the Czech Republic under rising temperatures (Tumajer and Tremel, 2016).

4.4. Oak responses to severe drought events

Despite the absence of long-term growth decline over the last decade, the Lloret indices, combined with the SEA results (Fig. 7a, b), indicate that oaks are nevertheless sensitive to short-term water deficits, with drought events causing growth reductions followed by variable recovery across years. Negative resistance values observed in 12 out of 18 drought years (Fig. 7a) are consistent with similar reductions in growth resistance reported for *Q. robur* and *Q. petraea* during major European droughts across various regions (Zang et al., 2012; Kunz et al., 2018; Heklau et al., 2019; Bose et al., 2021; Fuchs et al., 2021). These short-term growth reductions likely reflect physiological trade-offs. While *Q. robur* and *Q. petraea* can maintain transpiration and photosynthesis longer than more isohydric species due to their water-use strategy (Bréda et al., 1993a, b; Leuzinger et al., 2005), they are highly susceptible to embolism and cavitation (hydraulic failure) during severe droughts, leading to sharp reductions in cambial activity and cell production (Horáček et al., 2003; Fonti et al., 2010), canopy diebacks (Čater, 2015; Kermavnar and Kutnar, 2024) or even tree decline (Cochard et al., 1992; Percolla et al., 2021).

However, drought impacts were highly variable, with many drought years showing near-normal radial growth (Fig. 6d, e). This pattern is particularly evident for recent droughts (2003, 2015, 2018, 2020, 2022, and 2023), which rank among the driest on record (Fig. 6b, c). A similar trend has also been reported in previous studies. During the exceptional 2003 drought, *Q. robur* and *Q. petraea* were found to maintain radial growth (van der Werf et al., 2007), stable sap flow (Leuzinger et al., 2005), and full leaf cover (Bréda et al., 2006) despite severe water deficits across Europe, in contrast to many co-occurring species. Supporting evidence also comes from northern Germany, where *Q. robur* likewise maintained near-normal growth under the dry conditions of 2016, unlike *Fagus sylvatica* and *Carpinus betulus* (van der Maaten et al., 2018). In response to the 2018 extreme drought, *Q. robur* and *Q. petraea*

exhibited only limited growth reductions (Schnabel et al., 2022), no growth decline (Salomón et al., 2022), or even above-average annual growth (Neuwirth et al., 2021) and high gross primary productivity (Kowalska et al., 2020). These observations indicate that drought resilience of oaks is consistently reported across sites and years. This resilience is likely linked to phenological traits of ring-porous species, which initiate growth early in spring and rapidly form earlywood vessels before leaf-out, allowing them to sustain productivity even during drought, despite having a shorter overall growing season than diffuse-porous species (Pérez-de-Lis et al., 2017; van der Maaten et al., 2018; Kowalska et al., 2020; Schwarz et al., 2020). Another hypothesis is that the climate sensitivity observed at our sites, moderate at VLN and strong at HERCUF, has promoted physiological acclimation to drought, resulting in more efficient water use. This interpretation aligns with recent large-scale studies showing that, for *Q. robur* and *Q. petraea*, departures from pre-drought growth were smaller, recovery faster (Bose et al., 2021), and legacy effects shorter (Bose et al., 2024) at climate-sensitive compared to non-sensitive sites.

Overall, oak responses to drought are complex, as events of similar intensity can lead to markedly different growth outcomes, influenced notably by factors such as the occurrence of consecutive events (Lloret et al., 2004; Bréda et al., 2006; Schnabel et al., 2022) or their seasonality (Camarero et al., 2015; Vanhellefont et al., 2019; Bose et al., 2021). At our sites, we highlight that the influence of drought on oak growth is primarily linked to soil moisture conditions (i.e. agricultural drought) (Fig. 7) rather than atmospheric water demand (i.e. atmospheric drought) (Fig. S1). Nevertheless, no consistent seasonal pattern emerges, as both spring and summer droughts correspond to years of reduced growth (1962, 1976, 1996, 2005) as well as years of near-normal growth (1961, 2003, 2020, 2022), and consecutive droughts do not show a clear effect either (Table S2). This variability may reflect an inherent capacity of oaks to adjust to drought conditions, but further investigations, using, for example, intra-annual wood anatomical data (e.g. vessel traits) (Castagneri et al., 2017; Schwarz et al., 2020) or canopy observations (e.g. canopy dieback, early leaf shedding, or branch mortality) (Rybníček et al., 2015; Knutzen et al., 2025), are needed to clarify the timing, duration, and effects of drought on tree growth. In addition, age-related effects on drought resistance, resilience, and recovery deserve further study, as age-related patterns in tree responses to water stress remain poorly constrained (Rozas, 2005; Mikac et al., 2018; Au et al., 2022; Meeran et al., 2025). Finally, stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) could provide complementary insights, as they often carry stronger and more direct drought signals than tree-ring width data alone (Labuhn et al., 2016; Büntgen et al., 2021; Treydte et al., 2024; Arosio et al., 2025).

5. Conclusions

This study shows that annual radial growth of *Q. robur* and *Q. petraea* in the Loire River basin is mainly driven by late spring and early summer moisture availability and summer maximum temperature. The riparian site exhibits stronger and more consistent climate sensitivity than the non-riparian site, reflecting both species-specific traits and local hydrological conditions. The duration of discharge exceeding low-water level also plays a key role in controlling riparian tree growth, as relatively high summer discharge could help mitigate stress induced by extreme temperature. Despite these differences, both species display a dual response to drought: a high capacity to buffer long-term climatic stress, with no long-term decline in growth detected despite increasing severe droughts, alongside clear physiological limits that emerge during moderate to severe drought events, when growth often drops below pre-drought levels and full recovery is not always achieved.

As drought frequency and severity are expected to intensify in the coming decades, refining our understanding of the mechanisms underlying this dual form of resilience becomes essential. For riparian forests, our findings also have important management implications, as the Loire

River floodplain lies entirely within the Natura 2000 network and includes national nature reserves, where riparian vegetation is a critical component of floodplain biodiversity. Expanding tree-ring chronologies and integrating high-resolution anatomical data will be crucial for determining how, and for how-long, temperate oaks can withstand increasing climatic pressure, and for improving our understanding of their climate vulnerability.

CRedit authorship contribution statement

Charlie Hureau: Conceptualization, Methodology, Formal analysis, Investigation, Validation, Writing – Original draft, Writing – Review & Editing, Funding acquisition. **Sébastien Guillet:** Conceptualization, Methodology, Formal analysis, Validation, Writing – Review & Editing. **Valérie Daux:** Investigation, Validation, Writing – Review & Editing, Supervision. **Emmanuèle Gautier:** Conceptualization, Formal analysis, Investigation, Validation, Writing – Review & Editing, Supervision, Funding acquisition. **François Lebourgeois:** Validation, Writing – Review & Editing. **Colombe Guerry:** Investigation, Validation, Writing – Review & Editing.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2026.126511](https://doi.org/10.1016/j.dendro.2026.126511).

Data Availability

The raw tree-ring measurements from all sites sampled in this study are publicly available at: doi.org/10.5281/zenodo.18552014.

References

- Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A., Hegewisch, K.C., 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958 to 2015. *Sci. Data* 5, 170191. <https://doi.org/10.1038/sdata.2017.191>.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree

- mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Annighöfer, P., Beckschäfer, P., Vor, T., Ammer, C., 2015. Regeneration patterns of European Oak Species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLOS ONE* 10, e0134935. <https://doi.org/10.1371/journal.pone.0134935>.
- Arend, M., Kuster, T., Günthardt-Goerg, M.S., Dobbertin, M., 2011. Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiol.* 31, 287–297. <https://doi.org/10.1093/treephys/tpr004>.
- Arosio, T., Leuenberger, M., Nicolussi, K., Esper, J., Krusic, P.J., Bebhuk, T., Tegel, W., Hafner, A., Kirilyanov, A.V., Schlüchter, C., Reinig, F., Muschitiello, F., Büntgen, U., 2025. Tree-ring stable isotopes from the European Alps reveal long-term summer drying over the Holocene. *Sci. Adv.* 11, eadr4161. <https://doi.org/10.1126/sciadv.adr4161>.
- Au, T.F., Maxwell, J.T., Robeson, S.M., Li, J., Siani, S.M.O., Novick, K.A., Dannenberg, M. P., Phillips, R.P., Li, T., Chen, Z., Lenoir, J., 2022. Younger trees in the upper canopy are more sensitive but also more resilient to drought. *Nat. Clim. Chang* 12, 1168–1174. <https://doi.org/10.1038/s41558-022-01528-w>.
- Barbaroux, C., Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiol.* 22, 1201–1210. <https://doi.org/10.1093/treephys/22.17.1201>.
- Barsoum, N., Eaton, E.L., Levanić, T., Pargade, J., Bonnart, X., Morison, J.L.L., 2015. Climatic drivers of oak growth over the past one hundred years in mixed and monoculture stands in southern England and northern France. *Eur. J. For. Res.* 134, 33–51. <https://doi.org/10.1007/s10342-014-0831-5>.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Clim.* 34, 3001–3023. <https://doi.org/10.1002/joc.3887>.
- Bergès, L., Chevalier, R., Dumas, Y., Franc, A., Gilbert, J.-M., 2005. Sessile oak (*Quercus petraea* Liebl.) site index variations in relation to climate, topography and soil in even-aged high-forest stands in northern France. *Ann. For. Sci.* 62, 391–402. <https://doi.org/10.1051/forest:2005035>.
- Bert, D., Lebourgeois, F., Ouayjan, A., Ducouso, A., Ogée, J., Hampe, A., 2022. Past and future radial growth and water-use efficiency of *Fagus sylvatica* and *Quercus robur* in a long-term climate refugium. *Dendrochronologia* 72, 125939. <https://doi.org/10.1016/j.dendro.2022.125939>.
- Biondi, F., Qeadan, F., 2008. Inequality in Paleorecords. *Ecology* 89, 1056–1067. <https://doi.org/10.1890/07-0783.1>.
- Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* 30, 303–311. <https://doi.org/10.1016/j.cageo.2003.11.004>.
- Blöschl, G., Nester, T., Komma, J., Parajka, J., Perdigão, R.A., 2013. The June 2013 flood in the Upper Danube Basin, and comparisons with the 2002, 1954 and 1899 floods. *Hydrol. Earth Syst. Sci.* 17, 5197–5212. <https://doi.org/10.5194/hess-17-5197-2013>.
- Bose, A.K., Doležal, J., Scherrer, D., Altman, J., Ziche, D., Martínez-Sancho, E., Bigler, C., Bolte, A., Colangelo, M., Dorado-Liñán, I., Drobyshev, I., Etzold, S., Fonti, P., Gessler, A., Kolář, T., Koňasová, E., Korznikov, K.A., Lebourgeois, F., Lucas-Borja, M. E., Menzel, A., Neuwirth, B., Nicolas, M., Omelko, A.M., Pederson, N., Petritan, A.M., Rigling, A., Rybníček, M., Scharnweber, T., Schröder, J., Silla, F., Sochová, I., Sohar, K., Ukhvatkina, O.N., Vozmishcheva, A.S., Zweifel, R., Camarero, J.J., 2024. Revealing legacy effects of extreme droughts on tree growth of oaks across the Northern Hemisphere. *Sci. Total Environ.* 926, 172049. <https://doi.org/10.1016/j.scitotenv.2024.172049>.
- Bose, A.K., Scherrer, D., Camarero, J.J., Ziche, D., Babst, F., Bigler, C., Bolte, A., Dorado-Liñán, I., Etzold, S., Fonti, P., Forrester, D.I., Gavnin, J., Gazol, A., De Andrés, E.G., Karger, D.N., Lebourgeois, F., Lévesque, M., Martínez-Sancho, E., Menzel, A., Neuwirth, B., Nicolas, M., Sanders, T.G.M., Scharnweber, T., Schröder, J., Zweifel, R., Gessler, A., Rigling, A., 2021. Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. *Sci. Total Environ.* 784, 147222. <https://doi.org/10.1016/j.scitotenv.2021.147222>.
- Boudin, L., Cordier, J., Moret, J., 2007. Atlas de la flore remarquable du Val de Loire entre le bec d'Allier et le bec de Vienne. Muséum national d'Histoire naturelle, Paris, France.
- Bouwman, M., Akhmetzyanov, L., Mohren, F., den Ouden, J., Sass-Klaassen, U., Copini, P., 2025. Tree growth responses to severe droughts for assessment of forest growth potential under future climate. *For. Ecol. Manag.* 578, 122423. <https://doi.org/10.1016/j.foreco.2024.122423>.
- Bréda, N., Cochard, H., Dreyer, E., Granier, A., 1993a. Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Can. J. For. Res.* 23, 1136–1143. <https://doi.org/10.1139/x93-144>.
- Bréda, N., Cochard, H., Dreyer, E., Granier, A., 1993b. Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann. Sci. For.* 50, 571–582. <https://doi.org/10.1051/forest:19930606>.
- Bréda, N., Granier, A., Barataud, F., Moyné, C., 1995. Soil water dynamics in an oak stand. *Plant Soil* 172, 17–27. <https://doi.org/10.1007/BF00020856>.
- Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63, 625–644. <https://doi.org/10.1051/forest:2006042>.
- Briffa, K.R., van der Schrier, G., Jones, P.D., 2009. Wet and dry summers in Europe since 1750: evidence of increasing drought. *Int. J. Clim.* 29, 1894–1905. <https://doi.org/10.1002/joc.1836>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28, 251–258. <https://doi.org/10.1016/j.dendro.2009.12.001>.
- Büntgen, U., Tegel, W., Heussner, K.-U., Hofmann, J., Kontic, R., Kyncl, T., Cook, E.R., 2012. Effects of sample size in dendroclimatology. *Clim. Res.* 53, 263–269. <https://doi.org/10.3354/cr01107>.
- Büntgen, U., Urban, O., Krusic, P.J., Rybníček, M., Kolář, T., Kyncl, T., Ać, A., Koňasová, E., Čáslavský, J., Esper, J., Wagner, S., Saurer, M., Tegel, W., Dobrovolný, P., Cherubini, P., Reinig, F., Trnka, M., 2021. Recent European drought extremes beyond Common Era background variability. *Nat. Geosci.* 14, 190–196. <https://doi.org/10.1038/s41561-021-00698-0>.
- Buras, A., 2017. A comment on the expressed population signal. *Dendrochronologia* 44, 130–132. <https://doi.org/10.1016/j.dendro.2017.03.005>.
- Camarero, J.J., Franquesa, M., Sangüesa-Barreda, G., 2015. Timing of drought triggers distinct growth responses in Holm Oak: implications to predict warming-induced forest defoliation and growth decline. *Forests* 6, 1576–1597. <https://doi.org/10.3390/f6051576>.
- Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittcock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J., Parsons, M., Williams, S.E., 2013. Riparian Ecosystems in the 21st century: hotspots for climate change adaptation? *Ecosystems* 16, 359–381. <https://doi.org/10.1007/s10021-013-9656-1>.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci.* 108, 1474–1478. <https://doi.org/10.1073/pnas.1010070108>.
- Castagneri, D., Regev, L., Boaretto, E., Carrer, M., 2017. Xylem anatomical traits reveal different strategies of two Mediterranean oaks to cope with drought and warming. *Environ. Exp. Bot.* 133, 128–138. <https://doi.org/10.1016/j.enxpb.2016.10.009>.
- Čater, M., 2015. A 20-year overview of *Quercus robur* L. mortality and crown conditions in Slovenia. *Forests* 6, 581–593. <https://doi.org/10.3390/f6030581astagneri>.
- Cedro, A., 2007. Tree-Ring Chronologies of Downy Oak (*Quercus Pubescens*), Pedunculata Oak (*Q. Robur*) and Sessile Oak (*Q. Petraea*) in the Bielek Nature Reserve: Comparison of the Climatic Determinants of Tree-Ring Width. *Geochronometria* 26, 39–45. <https://doi.org/10.2478/v10003-007-0005-2>.
- Čejková, A., Poláková, S., 2012. Growth responses of sessile oak to climate and hydrological regime in the Zbytk Nature Reserve, Czech Republic. *Geochronometria* 39, 285–294. <https://doi.org/10.2478/s13386-012-0017-1>.
- Chevalier, R., Chantereau, M., Dupré, R., Evette, A., Greulich, S., Hémeray, D., Mârell, A., Martin, H., Villar, M., 2021. Comparaison de la biodiversité floristique entre berge et île de Loire. Étude de cas dans la réserve naturelle nationale de Saint-Mesmin (45). *Naturea* 1, 1–20. <https://doi.org/10.5852/naturea2021a1>.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755. <https://doi.org/10.1038/nature11688>.
- Cochard, H., Bréda, N., Granier, A., Aussenac, G., 1992. Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl., *Q. pubescens* Willd., *Q. robur* L.). *Ann. Sci. For.* 49, 225–233. <https://doi.org/10.1051/forest:19920302>.
- Cochard, H., Pimont, F., Ruffault, J., Martin-StPaul, N., 2021. SurEau: a mechanistic model of plant water relations under extreme drought. *Ann. For. Sci.* 78, 55. <https://doi.org/10.1007/s13595-021-01067-y>.
- Cochard, H., Tyree, M.T., 1990. Xylem dysfunction in Quercus: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* 6, 393–407. <https://doi.org/10.1093/treephys/6.4.393>.
- Colangelo, M., Camarero, J.J., Ripullone, F., Gazol, A., Sánchez-Salguero, R., Oliva, J., Redondo, M.A., 2018. Drought decreases growth and increases mortality of coexisting native and introduced tree species in a temperate floodplain forest. *Forests* 9, 205. <https://doi.org/10.3390/f9040205>.
- Cook, E.R., Peters, K., 1981. The Smoothing Spline: A New Approach to Standardizing Forest Inter-Tree-Ring Width Series for Dendroclimatic Studies. *Tree-Ring Bull.* 41, 45–53.
- Copernicus Climate Change Service, 2025. Global Climate Highlights 2024. (<https://climate.copernicus.eu/global-climate-highlights-2024>).
- Cornier, T., 2002. La végétation alluviale de la Loire entre le Charolais et l'Anjou: essai de modélisation de l'hydrosystème. Université François Rabelais, Tours, France.
- Čufar, K., De Luis, M., Eckstein, D., Kafjez-Bogataj, L., 2008. Reconstructing dry and wet summers in SE Slovenia from oak tree-ring series. *Int. J. Biometeorol.* 52, 607–615. <https://doi.org/10.1007/s00484-008-0153-8>.
- Daux, V., Michelot-Antalík, A., Laverge, A., Pierre, M., Stievenard, M., Bréda, N., Damesin, C., 2018. Comparisons of the performance of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of *Fagus sylvatica*, *Pinus sylvestris*, and *Quercus petraea* in the record of past climate variations. *J. Geophys. Res. Biogeosci.* 123, 1145–1160. <https://doi.org/10.1002/2017JG004203>.
- Dayon, G., Boé, J., Martin, E., Gailhard, J., 2018. Impacts of climate change on the hydrological cycle over France and associated uncertainties. *Comptes Rendus Géosci.* 350, 141–153. <https://doi.org/10.1016/j.crte.2018.03.001>.
- Decarsin, R., Guillemot, J., Le Maire, G., Blondeel, H., Meredieu, C., Achard, E., Bonal, D., Cochard, H., Corso, D., Delzon, S., Doucet, Z., Druel, A., Grossiord, C.,

- Torres-Ruiz, J.M., Bauhus, J., Godbold, D.L., Hajek, P., Jactel, H., Jensen, J., Mereu, S., Ponette, Q., Rewald, B., Ruffault, J., Sanden, H., Scherer-Lorenzen, M., Serrano-León, H., Simioni, G., Verheyen, K., Werner, R., Martin-StPaul, N., 2024. Tree drought-mortality risk depends more on intrinsic species resistance than on stand species diversity. *Glob. Change Biol.* 30, e17503. <https://doi.org/10.1111/gcb.17503>.
- Ducouso, A., Bordács, S., 2004. EUFORGEN Technical Guidelines for genetic conservation and use for Pedunculate and sessile oaks (*Quercus robur*) and (*Quercus petraea*). International Plant Genetic Resources Institute, Rome, Italy.
- Enderle, L., Gribbe, S., Muffler, L., Weigel, R., Hertel, D., Leuschner, C., 2024. A warmer climate impairs the growth performance of Central Europe's major timber species in lowland regions. *Sci. Total Environ.* 941, 173665. <https://doi.org/10.1016/j.scitotenv.2024.173665>.
- Epron, D., Dreyer, E., 1993. Photosynthesis of oak leaves under water stress: maintenance of high photochemical efficiency of photosystem II and occurrence of non-uniform CO₂ assimilation. *Tree Physiol.* 13, 107–117. <https://doi.org/10.1093/treephys/13.2.107>.
- Feuillat, F., Dupouey, J.-L., Sciamia, D., Keller, R., 1997. A new attempt at discrimination between *Quercus petraea* and *Quercus robur* based on wood anatomy. *Can. J. For. Res.* 27, 343–351. <https://doi.org/10.1139/x96-174>.
- Fonti, P., von Arx, G., García-González, I., Eilmann, B., Sass-Klaassen, U., Gärtner, H., Eckstein, D., 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *N. Phytol.* 185, 42–53. <https://doi.org/10.1111/j.1469-8137.2009.03030.x>.
- Friedrichs, D.A., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009a. Complex climate controls on 20th century oak growth in Central-West Germany. *Tree Physiol.* 29, 39–51. <https://doi.org/10.1093/treephys/tpn003>.
- Friedrichs, D.A., Trouet, V., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009b. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees* 23, 729–739. <https://doi.org/10.1007/s00468-009-0315-2>.
- Fritts, H.C., 1976. *Tree rings and climate*. Academic Press, London, UK.
- Fuchs, S., Schuldt, B., Leuschner, C., 2021. Identification of drought-tolerant tree species through climate sensitivity analysis of radial growth in Central European mixed broadleaf forests. *For. Ecol. Manag.* 494, 119287. <https://doi.org/10.1016/j.foreco.2021.119287>.
- Gautier, E., Burnouf, J., Carcaud, N., Chambaud, F., Garcin, M., 2007. Les interrelations entre les sociétés et le fleuve Loire depuis le Moyen Âge. In Trémolières, M., Schnitzler, A. (eds.), *Protéger, restaurer et gérer les zones alluviales, pourquoi et comment*. Tec Doc, 83–97.
- Gautier, E., Grivel, S., 2006. Multi-scale analysis of island formation and development in the Middle Loire River, France. In Rowan, J.S., Duck, R.W., Werrity, A. (eds.), *Sediment dynamics and the hydromorphology of fluvial systems*. International Association of Hydrologic Science Publ. 306, 179–187.
- Gazol, A., Camarero, J.J., 2022. Compound climate events increase tree drought mortality across European forests. *Int. Sci. Total Environ.* 816, 151604. <https://doi.org/10.1016/j.scitotenv.2021.151604>.
- Ghotbi, S., Wang, D., Singh, A., Mayo, T., Sivapalan, M., 2020. Climate and landscape controls of regional patterns of flow duration curves across the continental United States: Statistical approach. *Water Resour. Res.* 56, e2020WR028041. <https://doi.org/10.1029/2020WR028041>.
- Gribbe, S., Enderle, L., Coners, H., Hertel, D., Leuschner, C., 2025. Fine root morphological traits and root dynamics of beech, oak, pine and Douglas fir along a climatic aridity gradient. *Plant Soil*. <https://doi.org/10.1007/s11104-025-07706-x>.
- Gribbe, S., Enderle, L., Weigel, R., Hertel, D., Leuschner, C., Muffler, L., 2024. Recent growth decline and shifts in climatic growth constraints suggest climate vulnerability of beech, Douglas fir, pine and oak in Northern Germany. *For. Ecol. Manag.* 566, 122022. <https://doi.org/10.1016/j.foreco.2024.122022>.
- Hacke, U.G., Sperry, J.S., Wheeler, J.K., Castro, L., 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiol.* 26, 689–701. <https://doi.org/10.1093/treephys/26.6.689>.
- Hafner, P., Gričar, J., Skudnik, M., Levanič, T., 2015. Variations in environmental signals in tree-ring indices in trees with different growth potential. *PLoS One* 10, e0143918. <https://doi.org/10.1371/journal.pone.0143918>.
- Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nat. Commun.* 13, 1761. <https://doi.org/10.1038/s41467-022-29289-2>.
- Haneca, K., Katarina Čufar, Beeckman, H., 2009. Oaks, tree-rings and wooden cultural heritage: a review of the main characteristics and applications of oak dendrochronology in Europe. *J. Archaeol. Sci.* 36, 1–11. <https://doi.org/10.1016/j.jas.2008.07.005>.
- Harris, I., Osborn, T.J., Jones, P., Lister, D., 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci. Data* 7, 109. <https://doi.org/10.1038/s41597-020-0453-3>.
- Heklau, H., Jetschke, G., Bruehlheide, H., Seidler, G., Haider, S., 2019. Species-specific responses of wood growth to flooding and climate in floodplain forests in Central Germany. *IForest - Biogeosci.* 12, 226. <https://doi.org/10.3832/ifer245-012>.
- Henkel, S., Richter, R., Andrzejek, K., Mundry, R., Dotschev, M., Engelmann, R.A., Hartmann, T., Hecht, C., Kasperidus, H.D., Rieland, G., Scholz, M., Seele-Dilbat, C., Vieweg, M., Wirth, C., 2025. Ash dieback and hydrology affect tree growth patterns under climate change in European floodplain forests. *Sci. Rep.* 15, 10117. <https://doi.org/10.1038/s41598-025-92079-5>.
- Hoch, G., Richter, A., Körner, Ch., 2003. Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ.* 26, 1067–1081. <https://doi.org/10.1046/j.0016-8025.2003.01032.x>.
- Horáček, P., Šlezingerová, J., Gandelová, L., 2003. Analysis of cambial activity and formation of wood in *Quercus robur* L. under conditions of a floodplain forest. *J. For. Sci.* 49, 412–418. <https://doi.org/10.17221/4714-JFS>.
- Hroš, M., Vavřík, H., 2014. Comparison of earlywood vessel variables in the wood of *Quercus robur* L. and *Quercus petraea* (Mattuschka) Liebl. growing at the same site. *Dendrochronologia* 32, 284–289. <https://doi.org/10.1016/j.dendro.2014.07.007>.
- Hupp, C.R., Rinaldi, M., 2007. Riparian vegetation patterns in relation to fluvial landforms and channel evolution along selected rivers of Tuscany (Central Italy). *Ann. Assoc. Am. Geogr.* 97, 12–30. <https://doi.org/10.1111/j.1467-8306.2007.00521.x>.
- IPCC, 2018. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)].
- Jones, A., Montanarella, L., Jones, R., 2005. *Soil Atlas of Europe*. European Soil Bureau Network, European Commission. Office for Official Publications of the European Communities, Luxembourg, Luxembourg.
- Kasper, J., Leuschner, C., Walentowski, H., Petritan, A.M., Weigel, R., 2022. Winners and losers of climate warming: Declining growth in *Fagus* and *Tilia* vs. stable growth in three *Quercus* species in the natural beech-oak forest ecotone (western Romania). *For. Ecol. Manag.* 506, 119892. <https://doi.org/10.1016/j.foreco.2021.119892>.
- Kendall, M.G., 1975. ed. *Rank Correlation Methods*. Charles Griffin, London, UK https://scholar.google.com/scholar?hl=fr&as_sdt=0%2C5&q=Kendall%2C+M.G.%2C+1975.+ed.+Rank+Correlation+Methods.&btnG=.
- Kermavnar, J., Kutnar, L., 2024. Three decades of understorey vegetation change in *Quercus*-dominated forests as a result of increasing canopy mortality and global change symptoms. *J. Veg. Sci.* 35, e13317. <https://doi.org/10.1111/jvs.13317>.
- Kern, Z., Patkó, M., Kázmér, M., Fekete, J., Kele, S., Pályi, Z., 2013. Multiple tree-ring proxies (earlywood width, latewood width and $\delta^{13}\text{C}$) from pedunculate oak (*Quercus robur* L.), Hungary. *Quat. Int.* 293, 257–267. <https://doi.org/10.1016/j.quaint.2012.05.037>.
- Klesse, S., Bigler, C., 2025. Growth trends in basal area increments: the underlying problem, consequences for research and best practices. *Dendrochronologia* 90, 126296. <https://doi.org/10.1016/j.dendro.2025.126296>.
- Knutzen, F., Averbek, P., Barrasso, C., Bouwer, L.M., Gardiner, B., Grünzweig, J.M., Hänel, S., Haustein, K., Johannessen, M.R., Kollet, S., Müller, M.M., Pietikäinen, J.-P., Pietras-Couffignal, K., Pinto, J.G., Rechid, D., Rousi, E., Russo, A., Suarez-Gutierrez, L., Veit, S., Wendler, J., Xoplaki, E., Gliksman, D., 2025. Impacts on and damage to European forests from the 2018–2022 heat and drought events. *Nat. Hazards Earth Syst. Sci.* 25, 77–117. <https://doi.org/10.5194/nhess-25-77-2025>.
- Konópka, B., Yuste, J.C., Janssens, I.A., Ceulemans, R., 2005. Comparison of fine root dynamics in Scots pine and pedunculate oak in sandy soil. *Plant Soil* 276, 33–45. <https://doi.org/10.1007/s11104-004-2976-3>.
- Kostić, S., Kesić, L., Matović, B., Orlović, S., Stojanović, D.B., 2021. Soil properties are significant modifiers of pedunculate oak (*Quercus robur* L.) radial increment variations and their sensitivity to drought. *Dendrochronologia* 67, 125838. <https://doi.org/10.1016/j.dendro.2021.125838>.
- Kowalska, N., Šigut, L., Stojanović, M., Fischer, M., Kyselova, I., Pavelka, M., 2020. Analysis of floodplain forest sensitivity to drought. *Philos. Trans. R. Soc. B Biol. Sci.* 375, 20190518. <https://doi.org/10.1098/rstb.2019.0518>.
- Kroes, D.E., Schenk, E.R., Noe, G.B., Benthem, A.J., 2015. Sediment and nutrient trapping as a result of a temporary Mississippi River floodplain restoration: the Morganza Spillway during the 2011 Mississippi River Flood. *Ecol. Eng.* 82, 91–102. <https://doi.org/10.1016/j.ecoleng.2015.04.056>.
- Kunz, J., Löffler, G., Bauhus, J., 2018. Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *For. Ecol. Manag.* 414, 15–27. <https://doi.org/10.1016/j.foreco.2018.02.016>.
- Labuhn, I., Daux, V., Girardclos, O., Stievenard, M., Pierre, M., Masson-Delmotte, V., 2016. French summer droughts since 1326 CE: a reconstruction based on tree ring cellulose $\delta^{18}\text{O}$. *Clim* 12, 1101–1117. <https://doi.org/10.5194/cp-12-1101-2016>.
- Lacointe, A., 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Ann. For. Sci.* 57, 521–533. <https://doi.org/10.1051/forest:2000139>.
- Lang-Delus, C., François, D., Gille, E., 2016. Quel est le débit le plus fréquent d'un cours d'eau? *Physio-Géo* 10, 1–19. <https://doi.org/10.4000/physio-geo.4739>.
- Larsson, L., 2014. CooRecorder and Cdendro programs of the CooRecorder/Cdendro package version 7.7. (<http://www.cybis.se/forfun/dendro>).
- Lebourgeois, F., Cousseau, G., Ducos, Y., 2004. Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé ("Futaie des Clos", Sarthe, France). *Ann. For. Sci.* 61, 361–372. <https://doi.org/10.1051/forest:2004029>.
- Lebourgeois, F., Drénou, C., Bouvier, M., Lemaire, J., 2015. Caractérisation de la croissance des chênaies pédonculées atlantiques dépérissantes: effets des sécheresses et relation avec l'architecture des houppiers. *Rev. For. Fr.* 67, 333–351. <https://doi.org/10.4267/2042/59289>.
- Lebourgeois, F., Mérian, P., 2011. La sensibilité au climat des arbres forestiers a-t-elle changé au cours du XXe siècle. *Rev. For. Fr.* 63, 17–32. <https://doi.org/10.4267/2042/43091>.
- Lebourgeois, F., 1997. RENEFOFOR: Etude dendrochronologique des 102 peuplements du réseau. Office National des Forêts, Département des Recherches Techniques, Fontainebleau, France.
- Leonova, A., Heger, A., Váscónez Navas, L.K., Jensen, K., Reisdorff, C., 2022. Fine root mortality under severe drought reflects different root distribution of *Quercus robur*

- and *Ulmus laevis* trees in hardwood floodplain forests. *Trees* 36, 1105–1115. <https://doi.org/10.1007/s00468-022-02275-3>.
- Leuschner, C., Fuchs, S., Wedde, P., R  ther, E., Schuldt, B., 2024. A multi-criteria drought resistance assessment of temperate *Acer*, *Carpinus*, *Fraxinus*, *Quercus*, and *Tilia* species. *Perspect. Plant Ecol. Evol. Syst.* 62, 125777. <https://doi.org/10.1016/j.ppees.2023.125777>.
- Leuzinger, S., Zotz, G., Ashoff, R., K  rner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiol.* 25, 641–650. <https://doi.org/10.1093/treephys/25.6.641>.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>.
- Lloret, F., Siscart, D., Dalmases, C., 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Glob. Change Biol.* 10, 2092–2099. <https://doi.org/10.1111/j.1365-2486.2004.00870.x>.
- Lobo, A., Torres-Ruiz, J.M., Burlett, R., Lemaire, C., Parise, C., Francioni, C., Truffaut, L., Tom  skova, I., Hansen, J.K., Kj  r, E.D., Kremer, A., Delzon, S., 2018. Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. *For. Ecol. Manag.* 424, 53–61. <https://doi.org/10.1016/j.foreco.2018.04.031>.
- Mann, H.B., 1945. Nonparametric tests against trend. *Econometrica* 13, 245–259. <https://doi.org/10.2307/1907187>.
- Marchetti, Z.Y., Massa, E.S., Brunnich, F., 2020. Sediment and nutrient deposition in different riparian forests and floods of the Middle Parana River. *Ecohydrology* 13, e2153. <https://doi.org/10.1002/eco.2153>.
- Marks, C.O., Yellen, B.C., Wood, S.A., Martin, E.H., Nislow, K.H., 2020. Variation in tree growth along soil formation and microtopographic gradients in riparian forests. *Wetlands* 40, 1909–1922. <https://doi.org/10.1007/s13157-020-01363-9>.
- Matisons, R., Brumelis, G., 2012. Influence of climate on tree-ring and earlywood vessel formation in *Quercus robur* in Latvia. *Trees* 26, 1251–1266. <https://doi.org/10.1007/s00468-012-0701-z>.
- Maxwell, R.S., Larsson, L.-A., 2021. Measuring tree-ring widths using the CooRecorder software application. *Dendrochronologia* 67, 125841. <https://doi.org/10.1016/j.dendro.2021.125841>.
- Medici, G., Lorenzi, V., Sbarbati, C., Manetta, M., Petitta, M., 2023. Structural classification, discharge statistics, and recession analysis from the springs of the Gran Sasso (Italy) carbonate aquifer; comparison with selected analogues worldwide. *Sustainability* 15, 10125. <https://doi.org/10.3390/su151310125>.
- Meeran, K., Grabner, M., Schott, K., Wachter, E., van Loo, M., Watzinger, A., 2025. Tree size and site environment affects sessile oak growth and intrinsic water-use efficiency response to wet-dry years. *For. Ecol. Manag.* 577, 122413. <https://doi.org/10.1016/j.foreco.2024.122413>.
- Merian, P., Bontemps, J.-D., Berges, L., Lebourgeois, F., 2011. Spatial variation and temporal instability in climate-growth relationships of sessile oak (*Quercus petraea* [Matt.] Liebl.) under temperate conditions. *Plant Ecol.* 212, 1855–1871. <https://doi.org/10.1007/s11258-011-9959-2>.
- Merian, P., Pierrat, J.-C., Lebourgeois, F., 2013. Effect of sampling effort on the regional chronology statistics and climate-growth relationships estimation. *Dendrochronologia* 31, 58–67. <https://doi.org/10.1016/j.dendro.2012.07.001>.
- Meteo-France, 2025. Bilan climatique de l'annee 2024. (<https://meteofrance.fr/actualite/presse/bilan-climatique-2024-en-france>).
- Michelot, A., Breda, N., Damesin, C., Dufrene, E., 2012. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For. Ecol. Manag.* 265, 161–171. <https://doi.org/10.1016/j.foreco.2011.10.024>.
- Mikac, S., Zmegac, A., Trlin, D., Paulic, V., Orsanic, M., Anic, I., 2018. Drought-induced shift in tree response to climate in floodplain forests of Southeastern Europe. *Sci. Rep.* 8, 16495. <https://doi.org/10.1038/s41598-018-34875-w>.
- Mu, M., De Kauwe, M.G., Ukkola, A.M., Pitman, A.J., Guo, W., Hobeichi, S., Briggs, P.R., 2021. Exploring how groundwater buffers the influence of heatwaves on vegetation function during multi-year droughts. *Earth Syst. Dyn.* 12, 919–938. <https://doi.org/10.5194/esd-12-919-2021>.
- Naiman, R.J., Decamps, H., McClain, M.E., 2010. *Riparia: Ecology, Conservation, and Management of Streamside Communities*. Elsevier, Burlington, USA.
- Nechita, C., Camarero, J.J., 2025. Hotter winter-spring droughts accelerated the growth decline of marginal pedunculate oak (*Quercus robur*) populations in dry sites from Romania. *Dendrochronologia* 92, 126369. <https://doi.org/10.1016/j.dendro.2025.126369>.
- Netsvetov, M., Prokopuk, Y., Puchaika, R., Koprowski, M., Klisz, M., Romenskyy, M., 2019. River regulation causes rapid changes in relationships between floodplain oak growth and environmental variables. *Front. Plant Sci.* 10. <https://doi.org/10.3389/fpls.2019.00096>.
- Neuwirth, B., Rabbel, I., Bendix, J., Bogena, H.R., Thies, B., 2021. The European heat wave 2018: the dendroecological response of oak and spruce in Western Germany. *Forests* 12, 283. <https://doi.org/10.3390/f12030283>.
- Nosenko, T., Schroeder, H., Zimmer, I., Buegger, F., Orgel, F., Burau, I., Padmanaban, P. B.S., Ghirardo, A., Bracker, R., Kersten, B., Schnitzler, J.-P., 2025. Patterns of adaptation to drought in *Quercus robur* populations in central European temperate forests. *Glob. Change Biol.* 31, e70168. <https://doi.org/10.1111/gcb.70168>.
- Okonski, B., 2017. Radial growth of pedunculate oak and European ash on active river terraces. Hydrologic and climatic controls. *Infrastruktur. Ekol. Teren. Wiew. nr III/1*. <https://doi.org/10.14597/infraco.2017.3.1.083>.
- Ols, C., Klesse, S., Girardin, M.P., Evans, M.E.K., DeRose, R.J., Trouet, V., 2023. Detrending climate data prior to climate-growth analyses in dendroecology: a common best practice? *Dendrochronologia* 79, 126094. <https://doi.org/10.1016/j.dendro.2023.126094>.
- Parry, S., Hannaford, J., Lloyd-Hughes, B., Prudhomme, C., 2012. Multi-year droughts in Europe: analysis of development and causes. *Hydrol. Res.* 43, 689–706. <https://doi.org/10.2166/nh.2012.024>.
- Percolla, M.I., Fickle, J.C., Rodriguez-Zaccaro, F.D., Pratt, R.B., Jacobsen, A.L., 2021. Hydraulic function and conduit structure in the xylem of five oak species. *IAWA J.* 42, 279–298. <https://doi.org/10.1163/22941932-bja10059>.
- Perez-de-Lis, G., Olano, J.M., Rozas, V., Rossi, S., Vazquez-Ruiz, R.A., Garca-Gonzalez, I., 2017. Environmental conditions and vascular cambium regulate carbon allocation to xylem growth in deciduous oaks. *Funct. Ecol.* 31, 592–603. <https://doi.org/10.1111/1365-2435.12789>.
- Perez-de-Lis, G., Rossi, S., Vazquez-Ruiz, R.A., Rozas, V., Garca-Gonzalez, I., 2016. Do changes in spring phenology affect earlywood vessels? Perspective from the xylogenesis monitoring of two sympatric ring-porous oaks. *N. Phytol.* 209, 521–530. <https://doi.org/10.1111/nph.13610>.
- Perry, L.G., Andersen, D.C., Reynolds, L.V., Nelson, S.M., Shafroth, P.B., 2012. Vulnerability of riparian ecosystems to elevated CO2 and climate change in arid and semiarid western North America. *Glob. Change Biol.* 18, 821–842. <https://doi.org/10.1111/j.1365-2486.2011.02588.x>.
- Pettitt, A.N., 1979. A non-parametric approach to the change-point problem. *J. R. Stat. Soc. Ser. C. Appl. Stat.* 28, 126–135. <https://doi.org/10.2307/2346729>.
- Piegay, H., Pautou, G., Ruffioni, C., 2003. *Les forets riveraines des cours d'eau: ecologie, fonctions et gestion*. CNPF-IDF, Paris, France.
- Pilcher, J.R., Gray, B., 1982. The relationships between oak tree growth and climate in Britain. *J. Ecol.* 70, 297–304. <https://doi.org/10.2307/2259880>.
- Ponti, F., Minotta, G., Cantoni, L., Bagnaresi, U., 2004. Fine root dynamics of pedunculate oak and narrow-leaved ash in a mixed-hardwood plantation in clay soils. *Plant Soil* 259, 39–49. <https://doi.org/10.1023/B:PLSO.0000020949.61458.76>.
- Ponton, S., Dupouey, J.-L., Breda, N., Dreyer, E., 2002. Comparison of water-use efficiency of seedlings from two sympatric oak species: genotype × environment interactions. *Tree Physiol.* 22, 413–422. <https://doi.org/10.1093/treephys/22.6.413>.
- R Core Team, 2024. *R: A language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria. (<https://www.R-project.org/>).
- Radakovic, N., Stajic, B., 2021. Climate Signals in Earlywood, Latewood and Tree-Ring Width Chronologies of Sessile Oak (*Quercus petraea* (Matt.) Liebl.) from Majdanpek, North-Eastern Serbia. *Drv. Ind.* 72, 79–87. <https://doi.org/10.5552/drvidm.2021.2016>.
- Rameau, J.C., Mansion, D., Dume, G., Gauberville, C., 2018. *Flore forestiere franaise tome 1, Plaines et collines: Nouvelle edition revue et augmentee*. CNPF-IDF, Paris, France.
- Rivas, R., Rodriguez-Gonzalez, P.M., Albuquerque, A., Pinheiro, A.N., Egger, G., Ferreira, M.T., 2013. Riparian vegetation responses to altered flow regimes driven by climate change in Mediterranean rivers. *Ecohydrology* 6, 413–424. <https://doi.org/10.1002/eco.1287>.
- Rozas, V., 2005. Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. *Ann. For. Sci.* 62, 209–218. <https://doi.org/10.1051/forest:2005012>.
- Rust, S., Roloff, A., 2002. Reduced photosynthesis in old oak (*Quercus robur*): the impact of crown and hydraulic architecture. *Tree Physiol.* 22, 597–601. <https://doi.org/10.1093/treephys/22.8.597>.
- Rybnicek, M., ˇCermak, P., Zid, T., Kolar, T., Trnka, M., Buntgen, U., 2015. Exploring growth variability and crown vitality of Sessile Oak (*Quercus petraea*) in the Czech Republic. *Geochronometria* 42, 17–27. <https://doi.org/10.1515/geochr-2015-0003>.
- Salomon, R.L., Peters, R.L., Zweifel, R., Sass-Klaassen, U.G.W., Stegehuis, A.L., Smljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B.J.W., Lindner, M., Martineze-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bar, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiler, D., Blazenc, M., Cada, V., Carraro, V., Cecchini, S., Chan, T., Conedera, M., Delpierre, N., Delzon, S., Ditmarova, L., Dolezal, J., Dufrene, E., Edvardsson, J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Guney, A., Heinrich, I., Hentschel, R., Janda, P., Jezık, M., Kahle, H.-P., Knusel, S., Krejza, J., Kuberski, ., Kucera, J., Lebourgeois, F., Mikolas, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbel, I., Rathgeber, C.B.K., Salmon, Y., Saunders, M., Scharnweber, T., Sitkova, Z., Stangler, D.F., Sterenczak, K., Stojanovic, M., Strelcova, K., Svetlık, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavrcık, H., Vejprustkova, M., Walthert, L., Wilmsing, M., Zin, E., Zou, J., Steppe, K., 2022. The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. *Nat. Commun.* 13, 28. <https://doi.org/10.1038/s41467-021-27579-9>.
- Sanchez-Perez, J.M., Lucot, E., Bariac, T., Tremolieres, M., 2008. Water uptake by trees in a riparian hardwood forest (Rhine floodplain, France). *Hydrol. Process* 22, 366–375. <https://doi.org/10.1002/hyp.6604>.
- Santini, A., Bottacci, A., Gellini, R., 1994. Preliminary dendroecological survey on pedunculate oak (*Quercus robur* L.) stands in Tuscany (Italy). *Ann. Sci. For.* 51, 1–10. <https://doi.org/10.1051/forest:19940101>.
- Schnabel, F., Purrucker, S., Schmitt, L., Engelmann, R.A., Kahl, A., Richter, R., Seel-Dilbat, C., Scladaresis, G., Wirth, C., 2022. Cumulative growth and stress responses to the 2018–2019 drought in a European floodplain forest. *Glob. Change Biol.* 28, 1870–1883. <https://doi.org/10.1111/gcb.16028>.
- Schuldt, B., Buras, A., Arend, M., Vitase, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., K rner, C., Larysch, E., Lubbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of

- the extreme 2018 summer drought on Central European forests. *Basic Appl. Ecol.* 45, 86–103. <https://doi.org/10.1016/j.baae.2020.04.003>.
- Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. *Curr. For. Rep.* 6, 185–200. <https://doi.org/10.1007/s40725-020-00119-2>.
- Šenfeldr, M., Horák, P., Kvasnica, J., Šrámek, M., Hornová, H., Maděra, P., 2021. Species-specific effects of groundwater level alteration on climate sensitivity of floodplain trees. *Forests* 12, 1178. <https://doi.org/10.3390/f12091178>.
- Singer, M.B., Sargeant, C.I., Piégay, H., Riquier, J., Wilson, R.J.S., Evans, C.M., 2014. Floodplain ecohydrology: Climatic, anthropogenic, and local physical controls on partitioning of water sources to riparian trees. *Water Resour. Res.* 50, 4490–4513. <https://doi.org/10.1002/2014WR015581>.
- Singer, M.B., Stella, J.C., Dufour, S., Piégay, H., Wilson, R.J.S., Johnstone, L., 2013. Contrasting water-uptake and growth responses to drought in co-occurring riparian tree species. *Ecohydrology* 6, 402–412. <https://doi.org/10.1002/eco.1283>.
- Skiadaresis, G., Schwarz, J.A., Bauhus, J., 2019. Groundwater extraction in floodplain forests reduces radial growth and increases summer drought sensitivity of pedunculate oak trees (*Quercus robur* L.). *Front. For. Glob. Change* 2. <https://doi.org/10.3389/ffgc.2019.00005>.
- Sochová, I., Kolář, T., Árvai, M., Bošeľa, M., Čufar, K., Kern, Z., Kyncl, J., Marcíš, P., Mészáros, I., Morgós, A., Mursa, A., Popa, A., Roibu, C.-C., Sopushynskyy, I., Rybníček, M., 2024. The palaeoclimatic potential of recent oak tree-ring width chronologies from Southwest Ukraine. *Dendrochronologia* 84, 126168. <https://doi.org/10.1016/j.dendro.2024.126168>.
- Sohar, K., Helama, S., Läänelaid, A., Raisio, J., Tuomenvirta, H., 2014a. Oak decline in a southern Finnish forest as affected by a drought sequence. *Geochronometria* 41, 92–103. <https://doi.org/10.2478/s13386-013-0137-2>.
- Sohar, K., Läänelaid, A., Eckstein, D., Helama, S., Jaagus, J., 2014b. Dendroclimatic signals of pedunculate oak (*Quercus robur* L.) in Estonia. *Eur. J. For. Res.* 133, 535–549. <https://doi.org/10.1007/s10342-014-0783-9>.
- Soubeyroux, J.-M., Dubuisson, B., Bernus, S., Samacoïts, R., Rousset, F., Schneider, M., Drouin, A., Madec, T., Tardy, M., Corre, L., 2024. A quel climat s'adapter en France selon la TRACC ? *Metéo-France*, Toulouse, France.
- Speer, J.H., 2010. *Fundamentals of Tree-ring Research*. University of Arizona Press, Tucson, USA.
- Sperry, J.S., Hacke, U.G., Pittermann, J., 2006. Size and function in conifer tracheids and angiosperm vessels. *Am. J. Bot.* 93, 1490–1500. <https://doi.org/10.3732/ajb.93.10.1490>.
- Stojanović, D.B., Levanić, T., Matović, B., Orlović, S., 2015. Growth decrease and mortality of oak floodplain forests as a response to change of water regime and climate. *Eur. J. For. Res.* 134, 555–567. <https://doi.org/10.1007/s10342-015-0871-5>.
- Stojanović, D.B., Levanić, T., Matović, B., Stjepanović, S., Orlović, S., 2018. Growth response of different tree species (oaks, beech and pine) from SE Europe to precipitation over time. *Dendrobiology* 79, 97–110. <https://doi.org/10.12657/denbio.079.009>.
- Tetens, O., 1930. *Über einige meteorologische Begriffe*. *Z. Geophys* 6, 297–309.
- Tockner, K., Stanford, J.A., 2002. Riverine flood plains: present state and future trends. *Environ. Conserv* 29, 308–330. <https://doi.org/10.1017/S037689290200022X>.
- Treydte, K., Liu, L., Padrón, R.S., Martínez-Sancho, E., Babst, F., Frank, D.C., Gessler, A., Kahmen, A., Poulter, B., Seneviratne, S.I., Stegehuis, A.I., Wilson, R.J.S., Andreu-Hayles, L., Bale, R.J., Bednarz, Z., Boettger, T., Berninger, F., Büntgen, U., Daux, V., Dorado-Liñán, I., Esper, J., Friedrich, M., Gagen, M., Grabner, M., Grudd, H., Gunnarsson, B.E., Gutiérrez, E., Hafner, P., Haupt, M., Hiltunen, E., Heinrich, I., Helle, G., Jalkanen, R., Jungner, H., Kalela-Brundin, M., Kessler, A., Kirchhefer, A., Klesse, S., Krapiec, M., Levanić, T., Leuenberger, M., Linderholm, H.W.,
- McCarroll, D., Masson-Delmotte, V., Pawelczyk, S., Pazdur, A., Planells, O., Pukienė, R., Rinne-Garmston, K.T., Robertson, I., Saracino, A., Saurer, M., Schleser, G.H., Seftigen, K., Siegwolf, R.T.W., Sonninen, E., Stievenard, M., Szychowska-Krapiec, E., Szymaszek, M., Todaro, L., Waterhouse, J.S., Weigl-Kuska, M., Weigt, R.B., Wimmer, R., Woodley, E.J., Vitas, A., Young, G., Loader, N. J., 2024. Recent human-induced atmospheric drying across Europe unprecedented in the last 400 years. *Nat. Geosci.* 17, 58–65. <https://doi.org/10.1038/s41561-023-01335-8>.
- Tumajer, J., Tremli, V., 2016. Response of floodplain pedunculate oak (*Quercus robur* L.) tree-ring width and vessel anatomy to climatic trends and extreme hydroclimatic events. *For. Ecol. Manag.* 379, 185–194. <https://doi.org/10.1016/j.foreco.2016.08.013>.
- Ulrich, E., 1995. Le réseau renecofor: objectifs et réalisation. *Rev. For. Fr.* 47, 107–124. <https://doi.org/10.4267/2042/26634>.
- Urli, M., Lamy, J.-B., Sin, F., Burlett, R., Delzon, S., Porté, A.J., 2015. The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*. *Plant Ecol.* 216, 177–187. <https://doi.org/10.1007/s11258-014-0426-8>.
- van der Maaten, E., Pape, J., van der Maaten-Theunissen, M., Scharnweber, T., Smljanić, M., Cruz-García, R., Wilmking, M., 2018. Distinct growth phenology but similar daily stem dynamics in three co-occurring broadleaved tree species. *Tree Physiol.* 38, 1820–1828. <https://doi.org/10.1093/treephys/tpy042>.
- van der Werf, G.W., Sass-Klaassen, U.G.W., Mohren, G.M.J., 2007. The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia* 25, 103–112. <https://doi.org/10.1016/j.dendro.2007.03.004>.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science* 323, 521–524. <https://doi.org/10.1126/science.1165000>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Villar, M., Chevalier, R., Dufour, S., 2025. Ripisylves et forêts alluviales. Connaissances et gestion en contexte de changements globaux. Quae, Paris, France.
- Ward, J.V., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul. Rivers Res. Manag.* 15, 125–139. [https://doi.org/10.1002/\(SICI\)1099-1646\(199901/06\)15:1<3%253C125::AID-RRR523%253E3.0.CO;2-E](https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1<3%253C125::AID-RRR523%253E3.0.CO;2-E).
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Appl. Meteorol. Clim.* 23, 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023%253C0201:OTAVOC%253E2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023%253C0201:OTAVOC%253E2.0.CO;2).
- Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38, 431–436. <https://doi.org/10.1111/ecog.01335>.
- Zang, C.S., Buras, A., Esquivel-Muelbert, A., Jump, A.S., Rigling, A., Rammig, A., 2020. Standardized drought indices in ecological research: why one size does not fit all. *Glob. Change Biol.* 26, 322–324. <https://doi.org/10.1111/gcb.14809>.
- Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees* 26, 557–569. <https://doi.org/10.1007/s00468-011-0617-z>.
- Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate Warming-Related Growth Decline Affects *Fagus sylvatica*, but not other broad-leaved tree species in central European mixed forests. *Ecosystems* 18, 560–572. <https://doi.org/10.1007/s10021-015-9849-x>.