

Tree growth, wood anatomy and carbon and oxygen isotopes responses to drought in Mediterranean riparian forests

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ABSTRACT

Mediterranean riparian forests have been altered by past use and are also negatively impacted by climate and hydrological droughts. However, we lack data on their historical changes in extent combined with multi-proxy, long-term assessments of tree growth and leaf gas exchange responses to climate, drought severity and river flow. These evaluations must also consider their current stand structure and the amount of lying deadwood which are proxies of river dynamics and forest maturity. To fill these research gaps, we studied four riparian tree species (*Populus alba*, *Populus nigra*, *Fraxinus angustifolia* and *Ulmus minor*) inhabiting a Mediterranean riparian forest located in north-eastern Spain. We quantified and analyzed: stand structure; lying deadwood; radial growth; relationships between growth, climate variables, the SPEI drought index and river flow; stable C ($\delta^{13}\text{C}$) and O ($\delta^{18}\text{O}$) isotopes in wood of *P. alba*, *P. nigra* and *F. angustifolia*; and earlywood anatomy in *F. angustifolia*. Mature sites were dominated by *P. nigra* and *F. angustifolia* and showed the highest amount of decayed lying deadwood. Radial growth was reduced by drought and low spring-summer river flow. We found the highest growth responses to 3- (*P. nigra*, $r = 0.62$; *P. alba*, $r = 0.46$) or 12-month SPEI (*F. angustifolia*, $r = 0.54$; *U. minor*, $r = 0.53$). The coordinated decrease in $\delta^{18}\text{O}$ and intrinsic water-use efficiency (WUE) in *P. alba* and *P. nigra* could involve an increase in stomatal conductance rate. *P. alba* and *P. nigra* were more enriched in $\delta^{18}\text{O}$ than *F. angustifolia*, suggesting the former used more enriched shallow groundwater in dry periods. The *F. angustifolia* WUE and *P. nigra* $\delta^{18}\text{O}$ series were positively and negatively correlated with the SPEI, respectively. The *F. angustifolia* hydraulic diameter decreased in response to drought, whereas its vessel density and WUE were positively associated. Overall, *P. nigra* and *F. angustifolia* were the species most responsive to drought.

1. Introduction

In August 2022 several major European rivers recorded very low flow levels due to dry winter and spring conditions followed by summer heatwaves. Such drought negatively impacted power generation, irrigation, agricultural production, navigation and threatened the viability of many riparian forests (Toreti et al., 2022). According to models, the rivers of western and southern Europe will face more frequent hydrological and climatic droughts as that of 2022 by 2100, under a warmer climate scenario (Satoh et al., 2022). Therefore, it is advisable to investigate how riparian forests are responding to climatic and hydrological droughts given the high probability of future warmer and more arid conditions. These investigations are needed for drought-prone regions such as the Mediterranean basin with an increasing water demand.

Mediterranean riparian forests are among the most threatened wetland habitats because urban and agricultural land uses greatly reduced their extent and climate warming and biotic stressors (e.g., invasive pathogens) are negatively impacting on their growth, productivity and functioning (Stella et al., 2013b, Dufour et al., 2018, Stella and Bendix, 2019). In these seasonally dry regions, drought may induce canopy dieback, decrease radial growth and increase the mortality rate of riparian tree species (Scott et al., 2000, Horner et al., 2009, Stella et al., 2013a, Valor et al., 2020, Turczański et al., 2021). However, long-term assessments on the impacts of climate variability and drought on the radial growth, wood anatomy and functioning (e.g., water-use efficiency) of Mediterranean riparian forests are still few (but see Gomes Marques et al., 2018, Camarero et al., 2021, Rodríguez-González et al., 2021). The menaced conservation status of most Mediterranean riparian

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trees and their elevated but variable growth rates, which greatly depend on the access to shallow soil water (Singer et al., 2013), justify studying their responses to drought from a multi-proxy approach, i.e. comparing several variables (radial growth, wood anatomy, C and O isotopes).

We propose following a multiproxy approach to better understand and forecast the dynamics of Mediterranean riparian forests in response to drought and other disturbances. First, stand structure and the amount and decay of lying deadwood allow inferring how past disturbances (logging, drought, floods) have shaped the current successional dynamics of riparian forests (e.g., Oettel et al., 2022). Second, tree-ring variables (width, wood anatomy, C and O isotopes) allow quantifying how the main tree species have responded to those disturbances in terms of wood production and water-gas exchange, i.e. they allow reconstructing tree functioning in response to disturbances (e.g., Singer et al., 2013). The multiproxy approach enables linking the stand, tree and individual scales for improving forecasts of the responses of Mediterranean riparian forests to warmer and more arid conditions.

Mediterranean riparian forests are abundant along the Ebro river (Rodríguez-González et al., 2021), which is located in north-eastern Spain and it forms the third largest basin in southern Europe. Recent studies in this basin have shown that riparian tree species such as narrow-leaved ash (*Fraxinus angustifolia*) respond to climate and river flow and that these responses can be evaluated using their tree rings and studying their wood anatomy (Camarero et al., 2021, Rodríguez-González et al., 2021). Here we capitalize on those previous results: (i) to characterize the structure (density, basal area, amount and decay of lying wood) of riparian forests as related to their past dynamics, (ii) to relate radial growth (ring-width indices) of four tree species (the more phreatophytic *Populus alba* and *Populus nigra* vs. the less phreatophytic *Fraxinus angustifolia* and *Ulmus minor*), coexisting in Mediterranean riparian forests, with climate variables, river flow and a drought index, (iii) to use stable C ($^{13}\text{C}/^{12}\text{C}$) and O ($^{18}\text{C}/^{16}\text{C}$) isotopes in wood of three of these species (*P. alba*, *P. nigra*, *F. angustifolia*) to assess the responses of water-use efficiency and photosynthesis rates to climate conditions, river flow and drought, and (iv) to quantify earlywood anatomy data in *F. angustifolia* as related to climate, river flow, drought and C and O isotope discrimination. The selection of the ash species is justified by two reasons. First, its less phreatophytic behavior due to its shallow roots, dependent on capillary water rise and not adapted to low oxygen (Carlier et al., 1992, Köcher et al., 2009), which should make it more coupled to climatic drought than phreatophytes such as poplar species whose growth and isotope data should be more linked to hydrological drought and changes in river flow (Scott et al., 1999, Horton et al., 2001, Rood et al., 2003, Andersen, 2016, Schook et al., 2020). Second, ash species are keystone components of European riparian forests, menaced by climate warming and also by invasive fungal pathogens, showing increasing crown defoliation and mortality rates (George et al., 2022). We argue that following a multi-proxy approach focused on several, coexisting riparian tree species, and also measuring earlywood anatomy in *F. angustifolia*, will improve our understanding on the responses of these forests to climate variability and drought stress.

We inferred the intrinsic water-use efficiency (hereafter abbreviated as WUE), i.e. the ratio between the photosynthesis rate (A) and the stomatal conductance rate to H_2O (g), using wood C isotope ratios ($\delta^{13}\text{C}$) (Farquhar and Sharkey, 1982, Saurer and Voelker, 2022), whereas wood O isotope ratios ($\delta^{18}\text{O}$) were used to infer changes in g (Barbour et al., 2002, Grams et al., 2007, Allen et al., 2022). The combined quantification of wood $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ as proxies of tree functioning (dual-isotope approach) allows inferring water-gas exchange responses to drought and river flow. For instance, an increase in WUE could be due to a rise in A , a decline in g or both, whereas an increase in wood $\delta^{18}\text{O}$ can be interpreted as leaf water ^{18}O enrichment due to decreased g (e.g., Granda et al., 2018), among other causes (Roden et al., 2000, 2022). We expect a stronger coupling of WUE and $\delta^{18}\text{O}$ in the most phreatophytic species (*P. alba*, *P. nigra*) than in the less phreatophytic species (*F. angustifolia*, *U. minor*), which should present stronger growth-, WUE- and

$\delta^{18}\text{O}$ -drought relationships.

2. Materials and methods

2.1. Study area and selected tree species

The study area is located in the “Reserva Natural de los Sotos de Alfaro” (1.74° W, 42.20° N, 273 m), declared as a protected area in 2001, including 476 ha of well-preserved riparian forests and situated in Alfaro, La Rioja, north-eastern Spain (Fig. 1a).

These forests are located in the Middle Ebro basin, where the river flows over the main floodplain with a low slope and forms meandering channels (Ollero, 1991, 1996). The Ebro basin drainage area occupies 85,611 km² and it represents the largest hydrographic basin in Spain. The Ebro river length is 987 km.

Dynamics of riparian forests in the study area are rapid because of changes in the Ebro river flow (Ollero, 1991). In addition, historical alterations of these riparian have been widespread due to intensive agricultural and urban land uses. To assess how natural dynamics impacted changes in the cover of the study forests we compared aerial photographs of the study area taken in 1927 and 2014 (Fig. 1b). In the study area mean river flow is 234.1 m³ s⁻¹, with a high year-to-year and monthly variability peaking from January to April and showing a minimum in summer (Camarero et al., 2021).

Climate in the study area is semi-arid, Mediterranean continental with a mean annual temperature of 13.9 °C and annual precipitation amount of 370 mm (data from Alfaro [1.75° W, 42.08° N, 300 m a.s.l.] and Cadreita [1.69° W, 42.22° N, 288 m a.s.l.] climatic stations for the period 1980–2006, which are located at 2.5 and 3.8 km, respectively, from the study area). The precipitation of the hydrological year (from previous October to current September) is 405 mm. The annual potential evapotranspiration is 769 mm and the water deficit peaks in July and August, albeit dry conditions can last from April to October. January and July are the coldest (mean of 5.5 °C) and warmest (mean of 23.1 °C) months, respectively. Frosts can occur from November to March.

In the study area, riparian forests are dominated by tamarisks (*Tamarix* spp.), white willow (*Salix alba* L.) and silver poplar (*Populus alba* L.), mainly situated near the river shore and over gravel or sandy substrates, black poplar (*Populus nigra* L.) located in the transition zone, and ash (*Fraxinus angustifolia* Vahl.) with scattered elm trees (*Ulmus minor* Mill.) forming mature floodplain forests, inland. Elms with big diameter are usually affected by the Dutch elm disease (*Ophiostoma* spp.) and die. Introduced or invasive tree species can also be found including *Laurus nobilis* L. and *Acer negundo* L. Vines such as *Vitis vinifera* L. and *Humulus lupulus* L. are also common. Substrates are marls and gypsum producing basic, loamy-sandy soils.

We selected the study tree species based on: (i) their abundance in the sampled riparian forests, (ii) the production of annual, conspicuous rings, and (iii) their different phreatophytic behavior. This led to the selection of two more phreatophytic species (*P. alba*, *P. nigra*) and two less phreatophytic species (*F. angustifolia*, *U. minor*).

2.2. Climate, drought and river flow data

To avoid problems of heterogeneity and gaps in climate records, we used monthly mean temperature and precipitation data for the period 1920–2018 from the 0.25°-gridded E-OBS climate dataset (Cornes et al., 2018). We used the Standardized Precipitation Evapotranspiration Index (SPEI) to characterize drought intensity and duration as a function of rainfall amount and temperature-driven evapotranspiration (Vicente-Serrano et al., 2010). The SPEI data were obtained at weekly temporal resolution (period 1961–2018) and considering 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) long temporal scales from the 1.1-km² gridded SPEI Spanish dataset (Vicente-Serrano et al., 2017). These data are available at the webpage <https://monitordesequia.csic.es>. We considered appropriate using weekly SPEI data at 3–9 monthly

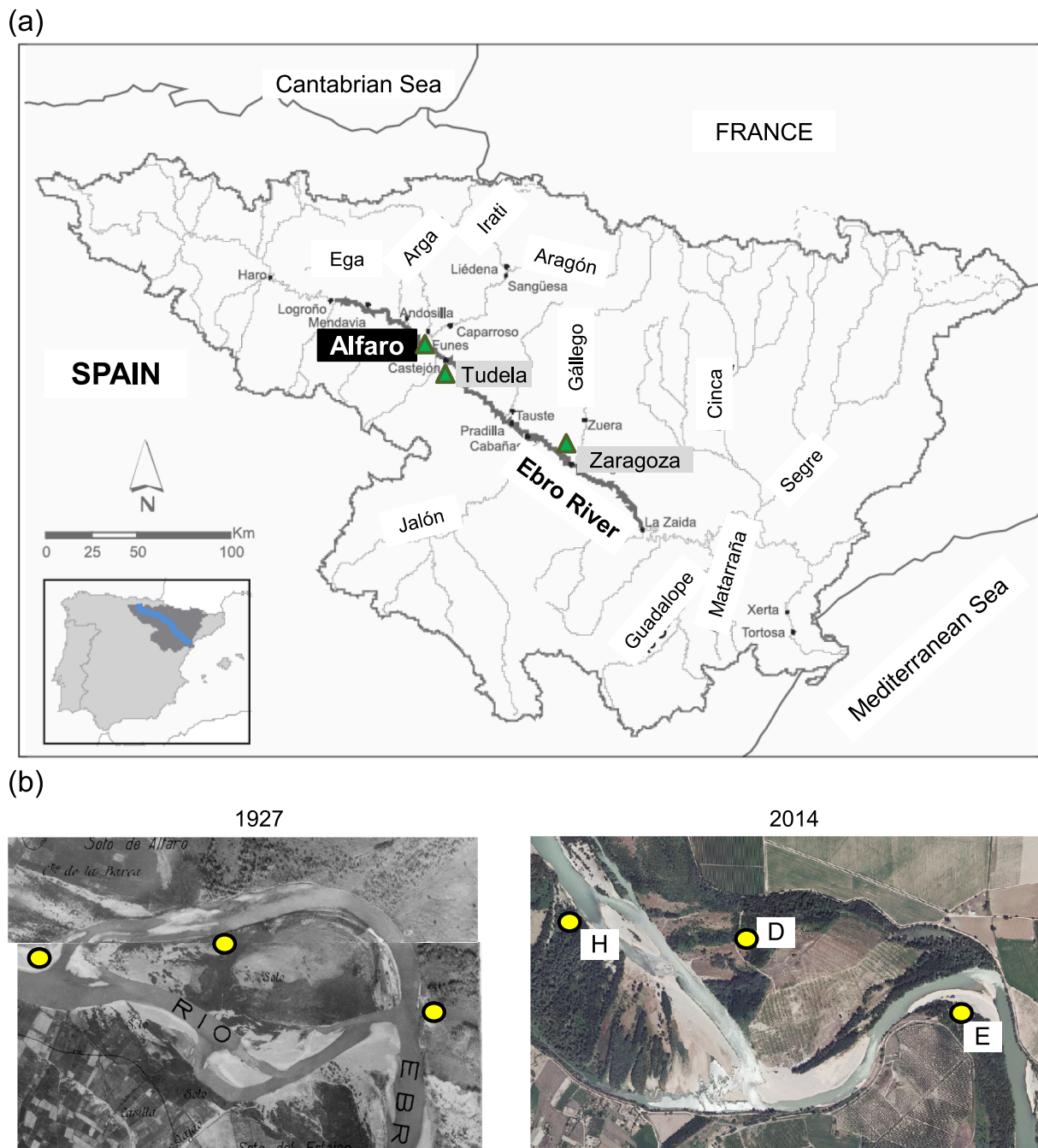


Fig. 1. (a) Study area in Alfaro and its location in north-eastern Spain with major cities and towns in the region (Alfaro, Tudela, Zaragoza) located downstream. The inset shows the Iberian Peninsula and the Ebro river basin (dark grey patch). (b) Comparison of two aerial photographs taken in 1927 and 2014 showing the approximate location (yellow dots) of the studied riparian forests (H, Soto del Hormiguero; D, Soto de la Duquesa; E, Soto del Estajao) situated near Alfaro town. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resolutions since the main phases of xylem development (cell division and enlargement) occurs at weekly to biweekly long scales (Larson, 1994).

Lastly, river flow data were obtained from the Spanish National Flow and Discharge Database (Centro de Estudios y Experimentación de Obras Públicas, data available at <https://ceh.cedex.es>). Flow data were obtained from the Castejón gauging station located in a bridge over the Ebro river (1° 41' W, 42° 11' N, 260 m a.s.l.; period 1970–2018) and situated 5 km downstream from the study sites. The average annual discharge of the Ebro river registered in this gauging station was 7,177 hm³. The drained area of the gauged station is 25,194 km². We also got monthly data of water table depth from a piezometer located near the

Ebro river (1.585° W, 42.132° N, 258 m; period 2006–2017), located at about 14 km downstream from the study site (data are available at the webpage <https://www.chebro.es/web/guest/red-piezometrica-oficial>). Water table depth showed maximum values from October to April (mean 2.03 m) and minimum values from May to September (mean 1.08 m). Monthly river flow and water table depths were negatively related but considering a 4-month lag ($r = -0.62$, $p < 0.001$, $n = 114$ measurements).

2.3. Field sampling

Three mature, relatively little disturbed sites were sampled in

autumn 2017 and 2018: “Soto del Hormiguero” (1.75° W, 42.20° N, 278 m), “Soto del Estajao” (1.72° W, 42.20° N, 275 m), and “Soto de la Duquesa” (1.73° W, 42.20° N, 274 m). The word “soto” is the local Spanish name for riparian forest. The “Soto de la Duquesa” was located on the best-preserved reaches, whereas the “Soto del Hormiguero” was subject to stronger channel alteration. In this last site, we detected Eurasian beaver (*Castor fiber* L.) scars in the base of several willow trees located near the river. Beaver was re-introduced in the Middle Ebro basin during the 1990s.

To characterize stand structure and to estimate the amount of lying woody debris and its degree of decay four 50-m transects were established perpendicular to the river main flow. We measured one transect in each site excepting the best-preserved “Soto de la Duquesa” site where two transects were measured. Transect dimensions were scaled by tree height to capture variability in wood spatial patterns and maximize efficiency (Van Pelt et al., 2004).

First, to estimate the density and basal area of the main tree and vine species we used the point-centered quarter method (Cottam and Curtis, 1956; Mueller-Dombois and Ellenberg, 2002). Along the transect, we measured every 2 m the distance from the sampling point to the nearest tree (distance <5 m) located in each quarter, determined its species and measured its diameter at breast height (dbh, measured at 1.3 m) and its total height using tapes and a rangefinder (Nikon Forestry Pro II). This was done for all woody plants with dbh >1 cm. We also noted if the measured individual was living or dead. Lastly, we calculated the importance value of each species, which was the average between the relative values of density and basal area within each transect (Mueller-Dombois and Ellenberg, 2002).

Second, the line-intersecting sampling method was used to estimate the volume of lying deadwood per area in the same transects (Woodall et al., 2009). We measured the diameter of wood pieces (with threshold size >5 cm) intersecting the transect (Van Wagner, 1968). Five classes of wood decay were considered (cf. Harmon et al., 1986; Maser et al., 1988): I, well preserved wood with intact bark and branches; II, moderately preserved wood with intact bark and branches, but without branchlets; III, scarcely preserved wood with decomposing bark, without branches and branchlets and breaking sapwood; IV, poorly preserved wood without bark and, branches and sapwood breaking into small pieces; V, decomposing wood without bark and branches, and sapwood showing a fragile texture with heartwood starting to break.

2.4. Tree-ring width data

To quantify past radial growth rates we used dendrochronology (Fritts, 1976). We sampled mature, healthy individuals of four species: *P. alba*, *P. nigra*, *F. angustifolia* and *U. minor*. We sampled from 12 to 25 individuals per species located in the “Soto de la Duquesa” site, where the trees with the largest diameters and oldest ages were found. Three cores were extracted at 1.3 m from each individual using 5-mm increment borers. Two cores were used to measure growth and the third core was used for isotope analyses.

In the laboratory, cores were air dried, glued in wooden supports and sanded using sandpapers of fine grits to clearly distinguish the ring boundaries. Tree rings were visually cross-dated under a binocular microscope. Then, their widths were measured along each core with a resolution of 0.01 mm using a measuring LINTAB device (Rinntech, Heidelberg, Germany). The visual cross-dating was further checked using the program COFECHA, which compares individual ring-width series with the master chronology (mean series) of each species using Pearson correlations (Holmes, 1983).

To remove radial-growth trends due to the increase in tree stem area and age, individual ring-width series were standardized and detrended using the program ARSTAN ver. 44 (Cook and Krusic, 2005). Linear or negative exponential functions were fitted to ring-width data to obtain tree-ring indices which contain mid- to high-frequency variability. Then, most of the first-order autocorrelation was removed from these indexed

series by fitting first-order autoregressive models (Fritts, 1976). The resulting series were averaged using bi-weight robust means to pre-whitened or residual chronologies for each species.

We calculated several statistics to characterize the ring-width data (Briffa and Jones, 1990): mean, standard deviation (SD) and first-order autocorrelation (AR1) of raw data, and mean correlations of individual indexed series and the species mean series. We also calculated the Expressed Population Signal (EPS), to assess the coherence and robustness of the chronologies.

2.5. Ash earlywood anatomy

We focused on earlywood vessels as they account for most total vessel area and hydraulic conductivity in ring-porous ash species such as *F. angustifolia* (Tulik et al., 2010). To measure earlywood anatomical variables we followed Scholz et al. (2013) and Camarero et al. (2021). The surfaces of ash cores for earlywood anatomy analyses were transversally cut using a sledge microtome (Gärtner and Nievergelt, 2010). We selected five mature ash trees whose ring-width series were significantly ($p < 0.05$) and positively correlated with the mean site series of the species.

Transversal, 15– to 20 μm thick wood sections were prepared from each core by dividing it into 2-cm long pieces. Samples were stained with safranin (1%) and astra blue (2%) and images were captured at 20–40x magnification using a light microscope (Olympus BH2). Earlywood vessels were considered those with lumen diameters larger than 50 μm (Camarero et al., 2021) and located in the first half of the ring along the radial direction. Radial vessel diameters were measured in a window of 4 mm (core width) along the period 1990–2016 using the ImageJ software (Schneider et al., 2012).

After measuring the diameter of all earlywood vessels (d) we calculated: the vessel density, the maximum vessel diameter and the hydraulic diameter (Dh), which was defined as (cf. Sperry et al., 1994):

$$Dh = \left(\sum d^5 / d^4 \right) \quad (1)$$

where d is the diameter for $i = 1$ to n measured vessels. Then, the potential hydraulic conductivity (Kp , in $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) was determined using the formula (cf. Tyree and Ewers, 1991):

$$Kp = (\pi \rho / 128 \eta A) [\sum Dh_i^4] \quad (2)$$

where A is the field area, ρ is the density of water (998.2 kg m^{-3} at 20°C) and η is the viscosity of water ($1.002 \times 10^{-9} \text{ MPa s}^{-1}$ at 20°C).

2.6. Wood $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data

Both C ($\delta^{13}\text{C}$) and O ($\delta^{18}\text{O}$) isotope data were only measured in wood of the three species *P. alba*, *P. nigra*, and *F. angustifolia*, whereas *U. minor* was excluded because its ring-width series were the shortest and presented the lowest common coherence (Table 3). As in the case of earlywood anatomy, cores for isotope analyses were not sanded to avoid mixing material between rings but their surfaces were transversally cut using a sledge microtome (Gärtner and Nievergelt, 2010). In each species, five cores from mature trees showing significant ($p < 0.05$) positive correlations with their respective mean species series were selected.

Annual rings were separated under the binocular using scalpels. Then, the five samples were mixed year by year to obtain annual pools for each species considering the common period 1989–2018. Wood samples were milled and homogenized using a ball mixer mill (Retsch MM301, Haan, Germany). We used whole wood instead of cellulose because previous studies on hardwood species showed that they lead to similar trends and results considering $\delta^{13}\text{C}$ (D'Alessandro et al., 2004). In the case of $\delta^{18}\text{O}$ data, we are aware this may lead to some bias.

In the case of $\delta^{13}\text{C}$, wood aliquots (0.50–0.70 mg) were weighed on a microbalance (AX205 Mettler Toledo, OH, USA) into tin foil capsules

and combusted to CO₂ using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., MA, USA). For δ¹⁸O, 0.50–0.70 mg of dry wood was weighed into silver foil capsules and combusted using a Carlo Erba 1108 elemental analyzer (Carlo Erba Instruments Ltd, Milan, Italy) interfaced with a Finnigan Deltaplus XP isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Bremen, Germany).

Isotope analyses were carried out at the Stable Isotope Facility of the University of California (Davis, USA). Stable isotope ratios were expressed as per mil deviations using the δ notation relative to Vienna Pee Dee Belemnite (VPDB) for C and the Vienna Standard Mean Ocean Water standard for O. The standard deviation for repeated analyses was better than 0.1‰.

We obtained WUE values from tree-ring wood C isotope ratios (δ¹³C) using the following framework. First, we calculated C isotope discrimination in wood (Δ¹³C) from δ¹³Ca (δ¹³C of atmospheric CO₂) and plant δ¹³Cp following Farquhar and Richards (1984):

$$\Delta^{13}C = (\delta^{13}Ca - \delta^{13}Cp) / (1 + \delta^{13}Cp/1000) \quad (3)$$

δ¹³Ca was obtained from Belmecheri and Lavergne (2020). Second, we calculated WUE using the equations proposed by Farquhar et al., (1982, 1989):

$$WUE = Ca[1 - (Ci/Ca)]0.625 = A/g \quad (4)$$

where Ca is the atmospheric CO₂ concentration, Ci is the CO₂ concentration in the sub-stomatal cavity of leaves, and 0.625 is the relation among the conductance of H₂O compared to the conductance of CO₂. To determine Ci we followed Francey and Farquhar (1982):

$$Ci = Ca(\delta^{13}Cp - \delta^{13}Ca + 1) / (b - a) \quad (5)$$

where a is the diffusion fractionation across the boundary layer and the stomata (+4.4‰) and b is the Rubisco enzymatic biologic fractionation (+27.0‰).

2.7. Statistical analyses

Differences among species regarding tree-ring data were tested using

Table 1

Main structural variables (diameter at breast height -dbh, height, tree density, basal area) and importance value estimated for the main tree and vine species located in the study riparian forests. The importance value refers to living trees. Dbh and height values are means ± SD.

Site	Transect	Species *	Dbh (cm)	Height (m)	Density of living/dead trees (ind ha ⁻¹)	Basal area of living/dead trees (m ² ha ⁻¹)	Importance value
Soto del Hormiguero	1	Sa	26.9 ± 13.5	9.7 ± 2.7	300	20.63	0.35
Soto de la Duquesa	1	Pn	12.4 ± 7.1	7.1 ± 2.2	1250	19.77	0.65
		Cm	5.5 ± 0.1	4.0 ± 0.1	50	0.12	0.01
		Vv	3.3 ± 0.4	6.3 ± 0.4	100	0.08	0.03
		Ta	6.0 ± 0.1	4.5 ± 0.2	50	0.14	0.01
		Fa	18.5 ± 5.7	6.4 ± 0.8	200	5.76	0.09
		Pn	45.8 ± 8.5	10.2 ± 2.4	500	28.61	0.28
		Pa	64.1 ± 25.0	15.8 ± 3.4	550	59.02	0.44
		Um	15.8 ± 2.9/24.4 ± 3.3	6.6 ± 1.4/8.1 ± 1.3 [#]	300/250 [#]	9.18/11.86 [#]	0.13
	2	Cm	5.8 ± 0.2	3.0 ± 0.1	100	0.27	0.04
		Ln	20.0 ± 0.2	6.8 ± 0.3	100	3.15	0.05
Pn		75.8 ± 28.8	16.9 ± 1.4	200	99.93	0.47	
Um		9.1 ± 4.1/19.4 ± 1.1	3.8 ± 1.8/7.0 ± 0.7 [#]	450/100 [#]	3.43/1.71 [#]	0.20	
Soto del Estajao	1	Fa	45.3 ± 13.6	9.6 ± 3.6	350	21.94	0.23
		Um	4.0 ± 0.1	2.0 ± 0.1	50	0.06	0.02
		Fa	5.0 ± 0.1	4.0 ± 0.2	50	0.10	0.02
		Pa	52.0 ± 28.3	15.3 ± 2.5	150	24.54	0.18
		Pn	39.3 ± 19.7	10.3 ± 3.3	300	45.86	0.34
		Sa	33.4 ± 8.9	10.6 ± 1.9	500	46.60	0.44

* Species' abbreviations: Pa, *Populus alba*; Pn, *Populus nigra*; Sa, *Salix alba*; Fa, *Fraxinus angustifolia*; Um, *Ulmus minor*; Ta, *Tamarix* spp.; Cm, *Crataegus monogyna*; An, *Acer negundo*; Ma, *Morus alba*; Pc, *Prunus cerasus*; Ln, *Laurus nobilis*; Vv, *Vitis vinifera*.

[#] Dead individuals.

Mann-Whitney tests. Trends in WUE and δ¹⁸O were quantified using the non-parametric Mann-Kendall (τ) test.

Monthly environmental variables (mean, maximum and minimum temperatures, total precipitation, river flow) and species' chronologies were correlated using Pearson correlations. Correlations were calculated from previous October to current September to account for lagged climate-growth effects and based on previous studies (see Camarero et al., 2021). Since all earlywood anatomy variables were correlated among them, we only show significant correlations of Dh with monthly, bimonthly or seasonal climate variables, river flow data or SPEI considering the period when most earlywood is formed (February–April; see Sass-Klaassen et al., 2011). We also considered the prior summer to winter climate variables since climate of the previous year affects earlywood formation the following year in ring-porous species (e.g., Alla and Camarero, 2012).

3. Results

3.1. Forest structure and lying deadwood

The tallest and thickest individuals corresponded to *P. nigra*. The “Soto del Hormiguero” and “Soto del Estajao” sites were dominated by *S. alba* and *P. alba*, respectively (Table 1).

In the most mature “Soto de la Duquesa” site, both poplar species showed the highest importance values, followed by *U. minor* and *F. angustifolia*. In the two transects from this site, dead *U. minor* trees had significantly (Mann-Whitney test, *p* < 0.05) larger diameters than living conspecific trees (Table 1).

Regarding the amount and decay of lying deadwood, the “Soto del Hormiguero” presented the highest volume since it was located close to the river shore where more sedimentation of woody debris could occur (Fig. 1b, Table 2). However, the decay degree was higher in the “Soto de la Duquesa” site in agreement with its more advanced successional status. The “Soto del Estajao” presented the lowest volume of lying deadwood and intermediate decay degree.

Table 2

Volume of lying deadwood per area estimated in the three study sites and percentage according to its decay degree. Decay classes are: I, well preserved wood with intact bark and branches; II, moderately preserved wood with intact bark and branches, but without branchlets; III, scarcely preserved wood with decomposing bark, without branches and branchlets and breaking sapwood; IV, poorly preserved wood without bark and, branches and sapwood breaking into small pieces; V, decomposing wood without bark and branches, and sapwood showing a fragile texture with heartwood starting to break.

Site	Transect	Volume of deadwood (m ³ m ⁻²)	Volume of deadwood according to decay class (%)				
			I	II	III	IV	V
Soto del Hormiguero	1	0.026	0.77	85.36	13.87	0.00	0.00
Soto de la Duquesa	1	0.010	0.00	14.32	35.82	49.86	0.00
	2	0.020	0.00	0.00	16.20	83.80	0.00
Soto del Estajao	1	0.004	0.00	2.82	78.87	18.31	0.00

3.2. Radial growth variability

The species with largest diameters (77.8 cm) and highest age (57 years) was *P. nigra*, whereas the species with smallest diameter (28.8 cm) and lowest age (32 years) was *U. minor* (Table 3). The widest rings were formed by *P. alba* (6.69 mm) and the narrowest ones by *U. minor* (2.67 mm), which presented the highest first-order autocorrelation (0.70) but the lowest mean correlation with the mean species series (0.25). On the contrary, *F. angustifolia* presented the highest correlation (0.65) indicating a high coherence in growth variability among conspecific individuals.

There were notable increases (e.g., 1992–1993, 1997) and decreases (e.g., 1995–1996, 2012) in growth which usually corresponded to wet and dry years, respectively (Fig. 2 and S1). It is remarkable the sharp drop in growth rates (-67%) detected in *F. angustifolia* during the year 2002 with respect to the prior year after very low December temperatures were recorded in 2001 (Fig. S2). A similar growth decline with respect to the prior year (-57%) was also detected during 2002 in *P. alba*.

Considering the period 1995–2018 common to all species, the mean series of ring-width indices showed positive and significant relationships in both poplar species ($r = 0.50$, $p = 0.016$) and *P. alba* and *F. angustifolia* ($r = 0.42$, $p = 0.049$). In the case of *P. nigra* and *U. minor*, their chronologies were positively correlated with that of *F. angustifolia* ($r = 0.38$, $p = 0.070$).

3.3. Relationships between climate, river flow, growth and wood C and O isotopes

Warm winter conditions enhanced growth in *P. alba* and *F. angustifolia*, whereas elevated temperatures in May and June reduced growth in all species (Table 4). *P. alba* also responded negatively to high minimum temperatures in the prior October and the current May. High precipitation in May and June increased growth of *P. nigra* (Fig. 3), whilst wet conditions in the prior winter increased *F. angustifolia* growth (Fig. 3). The growth of *P. alba* also increased if July–August precipitation did. The *U. minor* growth was enhanced by wet conditions in the prior October and also in current March, suggesting an early start of the growing season. Growth indices were positively correlated with river flow from prior December up to September, with the highest correlations occurring in December and summer (Fig. 3).

The WUE of *P. nigra* and *F. angustifolia* increased in response to warmer June conditions (Table 4). In *P. alba*, the WUE was negatively

correlated with May precipitation (Fig. 4a), whereas negative correlations with July–August river flow were found in *P. nigra* and *F. angustifolia*.

For instance, a sharp drop in *P. alba* WUE during 2008 corresponded to a peak in May precipitation (Fig. 4a). Dry May conditions and warm June conditions increased $\delta^{18}\text{O}$ in *P. nigra* and *F. angustifolia* (Table 4). In *P. alba*, warm-wet conditions in the prior autumn–winter lead to a decrease of $\delta^{18}\text{O}$. High river flow in summer months also lead to a decrease of $\delta^{18}\text{O}$ in *P. nigra* and *F. angustifolia*.

3.4. Relationships between growth indices and wood C and O isotopes

Only the *F. angustifolia* WUE series showed a marginally significant negative trend, particularly after 2004 ($\tau = -0.25$, $p = 0.056$; Fig. 4a), while the three species showed negative $\delta^{18}\text{O}$ trends (*P. alba*, $\tau = -0.29$, $p = 0.026$; *P. nigra*, $\tau = -0.25$, $p = 0.056$; *F. angustifolia*, $\tau = -0.26$, $p = 0.048$; Fig. 4a). The WUE series of *P. nigra* and *F. angustifolia* were positively and significantly related ($r = 0.46$, $p = 0.01$), whereas those of *P. alba* and *P. nigra* were marginally related ($r = 0.34$, $p = 0.063$). Moreover, the three species $\delta^{18}\text{O}$ series were positively correlated with the highest correlation found for *P. nigra* – *F. angustifolia* series ($r = 0.55$, $p = 0.002$) and the lowest one for *P. alba* – *F. angustifolia* series ($r = 0.42$, $p = 0.022$). This coherence among species is illustrated by synchronous increases (declines) of $\delta^{18}\text{O}$ in years 1990, 1994 and 2009 (1996, 2003 and 2008) (Fig. 4).

The WUE of *F. angustifolia* (mean $\pm$ SD, $81.3 \pm 6.4 \mu\text{mol mol}^{-1}$) was significantly ($p < 0.001$) higher than that of *P. nigra* ($72.9 \pm 2.9 \mu\text{mol mol}^{-1}$) and *P. alba* ($70.4 \pm 6.3 \mu\text{mol mol}^{-1}$) WUEs (Fig. 4b). Analogously, the $\delta^{18}\text{O}$ of *F. angustifolia* ($23.7 \pm 0.4 \text{‰}$) was significantly ($p = 0.006$) lower than those of *P. nigra* ($24.0 \pm 0.5 \text{‰}$) and *P. alba* ($24.1 \pm 0.5 \text{‰}$). Only the *F. angustifolia* WUE presented a significant and positive first-order autocorrelation ($r = 0.64$, $p < 0.001$), indicating a high year-to-year persistence.

We found positive and significant relationships between WUE and $\delta^{18}\text{O}$ in *P. alba* ($r = 0.47$, $p = 0.008$) and *P. nigra* ($r = 0.59$, $p = 0.0006$), but not in *F. angustifolia* (Fig. 4b). When separately considering dry (hydrological year precipitation $<$ mean $- 1$ SD) vs. wet years (hydrological year precipitation $>$ mean $+ 1$ SD), the WUE– $\delta^{18}\text{O}$ correlations remained significant only in *P. nigra*. Lastly, relationships between ring-width indices vs. WUE or $\delta^{18}\text{O}$ were negative but not significant in all species, indicating a low coupling in year-to-year variability between C and O isotope data and growth rates.

Table 3

Tree-ring data and statistics of the four study tree species. Values are means $\pm$ SD. The Expressed Population Signal (EPS) was calculated for the 1989–2018 common period. Different letters indicate significant ($p < 0.05$) differences among species based on Mann-Whitney tests.

Species	No. trees (No. radii)	Diameter at 1.3 m (cm)	Age at 1.3 m (yrs.)	Period	Tree ring-width (mm)	First-order autocorrelation	Correlation with species mean series	EPS
<i>Populus alba</i>	15 (20)	$53.3 \pm 9.6\text{ab}$	$42 \pm 5\text{a}$	1962–2018	$6.69 \pm 2.25\text{b}$	0.54 ± 0.22	$0.35 \pm 0.12\text{ab}$	0.69
<i>Populus nigra</i>	12 (17)	$77.8 \pm 18.7\text{b}$	$57 \pm 8\text{b}$	1936–2018	$4.46 \pm 1.80\text{ab}$	0.59 ± 0.25	$0.28 \pm 0.11\text{a}$	0.55
<i>Fraxinus angustifolia</i>	25 (34)	$41.9 \pm 9.8\text{ab}$	$50 \pm 9\text{ab}$	1953–2018	$3.17 \pm 1.52\text{a}$	0.60 ± 0.26	$0.61 \pm 0.18\text{b}$	0.92
<i>Ulmus minor</i>	16 (22)	$28.8 \pm 8.9\text{a}$	$32 \pm 12\text{a}$	1968–2018	$2.67 \pm 1.41\text{a}$	0.70 ± 0.28	$0.29 \pm 0.12\text{a}$	0.74

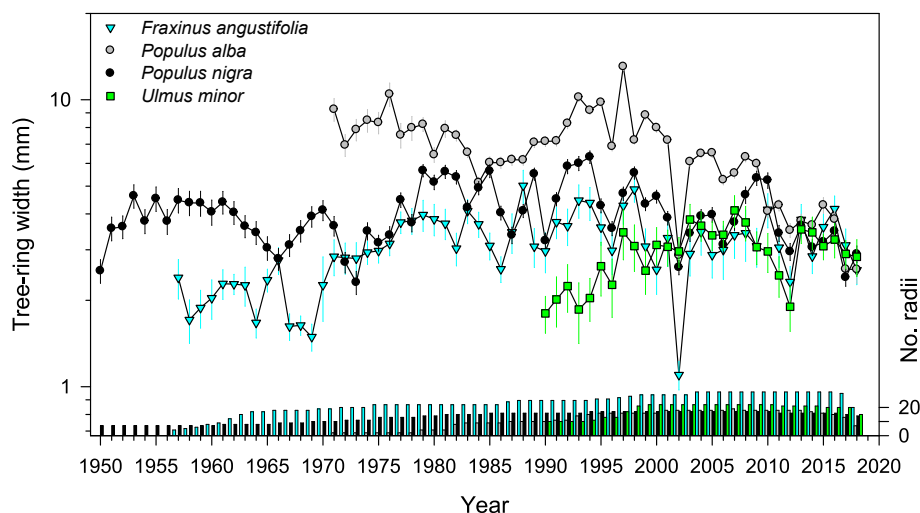


Fig. 2. Tree-ring width series of the four study species (values are means $\pm$ SE; note the logarithmic scale). The right y axis shows the sample size or number of radii considered each year to calculate the mean values. Note the sharp drop in growth of ash observed in 2002 and the growth decrease detected in 2012 in all species.

Table 4

Significant ($p < 0.05$) Pearson correlations calculated by relating tree growth rates (ring-width indices), intrinsic water-use efficiency (WUE), $\delta^{18}\text{O}$ and environmental variables at monthly resolution (TMx, mean maximum temperature; TMn, mean minimum temperature; Prec, precipitation; Flow, river flow). Months abbreviated by lowercase and uppercase letters correspond to the prior and current years, respectively. Species' abbreviations: Pa, *Populus alba*; Pn, *Populus nigra*; Fa, *Fraxinus angustifolia*; Um, *Ulmus minor*.

Variable	Environmental variable	Species	Month											
			o	n	d	J	F	M	A	M	J	J	A	S
Ring-width index	TMx	Pa												
		Pn												
		Fa												
		Um												
	TMn	Pa	−0.39		0.36			−0.37						
		Pn												
		Fa			0.38									
		Um												
	Prec	Pa								−0.39				
		Pn								0.36	0.38	0.39	0.37	
		Fa			0.38									
		Um	0.36					0.37						
	Flow	Pa												
		Pn				0.43			0.36		0.51	0.39	0.51	
		Fa				0.59	0.46			0.39	0.43	0.50	0.43	0.46
		Um					0.39	0.58	0.40	0.42	0.41		0.49	
WUE	TMx	Pa												
		Pn												
		Fa												
		Um												
	TMn	Pa												
		Pn												
		Fa												
		Um												
	Prec	Pa								−0.49				
		Pn												
		Fa												
		Um												
	Flow	Pa												
		Pn												
		Fa												
		Um												
$\delta^{18}\text{O}$	TMx	Pa		−0.39										
		Pn												
		Fa												
		Um												
	TMn	Pa												
		Pn												
		Fa												
		Um												
	Prec	Pa												
		Pn												
		Fa												
		Um												
	Flow	Pa												
		Pn												
		Fa												
		Um												

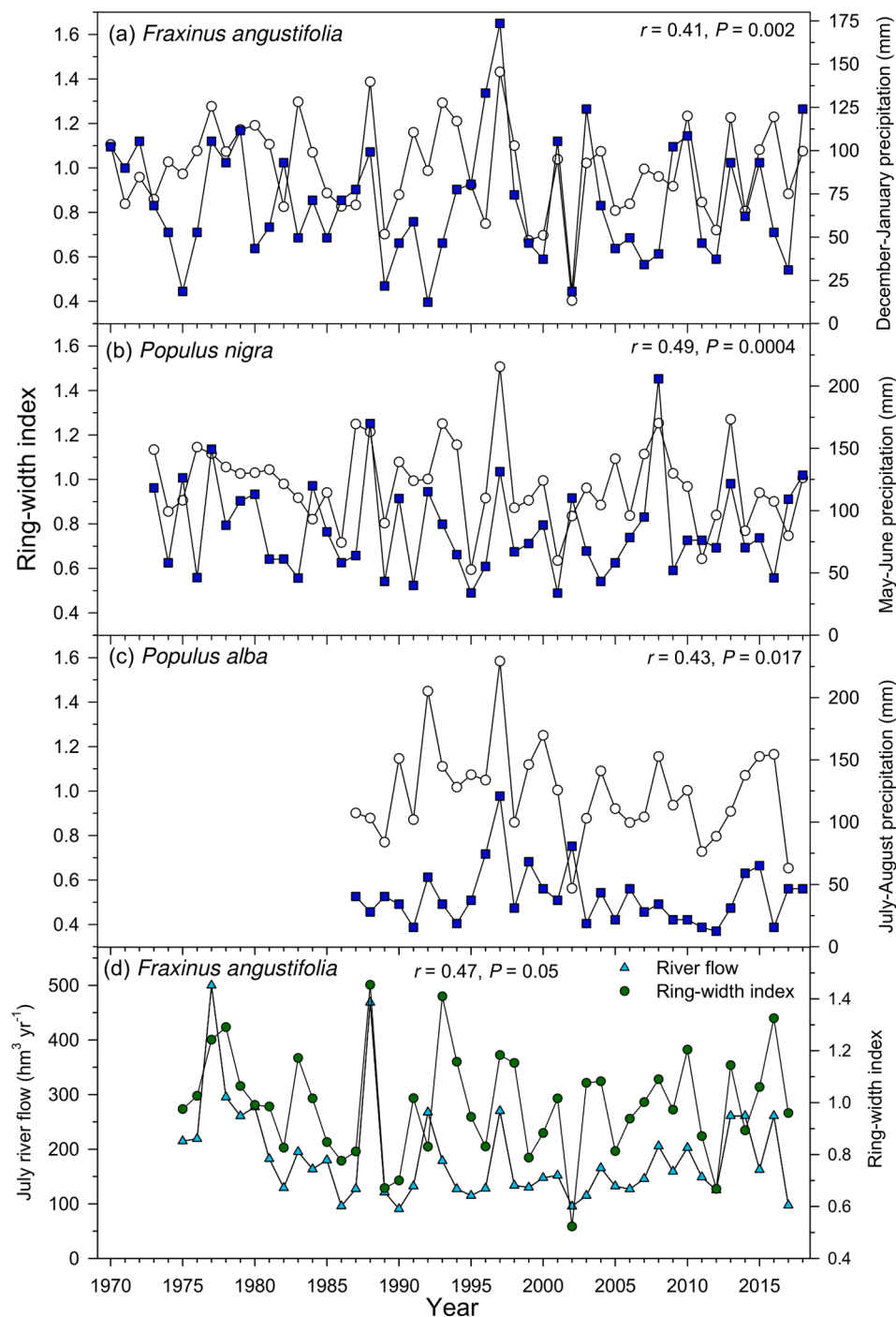


Fig. 3. Some relationships found between bimonthly climate variables (blue squares in plots a, b, c; right y axes) or river flow (triangles in plot d) and ring-width indices of the three study species (a, b and c, white circles; d, green circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Relationships between growth indices and drought

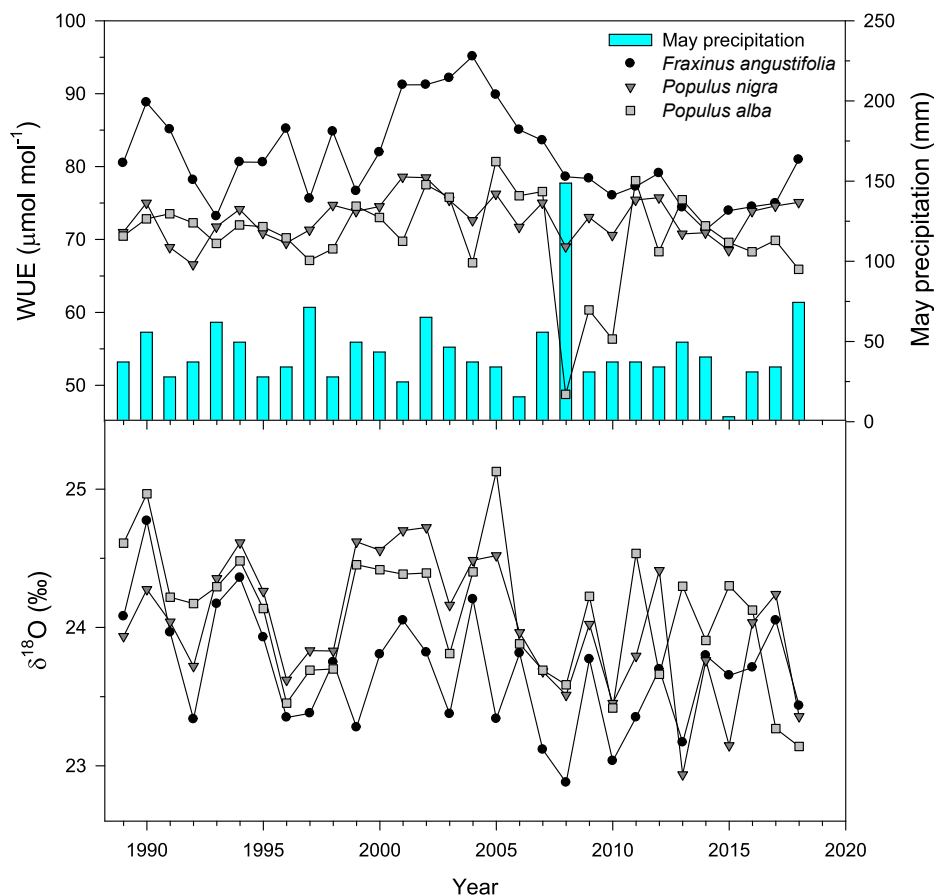
The four species showed different correlation values and timings between their series of ring-width indices and the SPEI drought index (Fig. 5). The most responsive species was *P. nigra* with highest correlations ($r = 0.62$) in late June corresponding to short droughts (SPEI3). Then, *F. angustifolia* growth indices mainly responded ($r = 0.54$) to long droughts (SPEI9, SPEI12) in early July. In the case of *U. minor*, growth indices were reduced in response to droughts of long duration (SPEI9, SPEI12) in May and July ($r = 0.53$). Finally, *P. alba*, correlations peaked in August ($r = 0.46$) considering droughts of short duration (SPEI3).

3.6. Relationships between drought and C and O isotopes in wood

Among, the three species considered *P. alba* was the least responsive to SPEI in terms of WUE or $\delta^{18}\text{O}$, whereas *F. angustifolia* WUE and *P. nigra* $\delta^{18}\text{O}$ series were the most responsive, respectively (Figs. 6 and 7).

Both *P. nigra* and *F. angustifolia* showed negative associations between their WUE series and short-term drought (SPEI3) in August and Early September indication that water shortage since June was affecting WUE (Fig. 6). In the case of *P. nigra*, these negative correlations were also found for longer droughts (SPEI6 and SPEI9), albeit they were

(a)



(b)

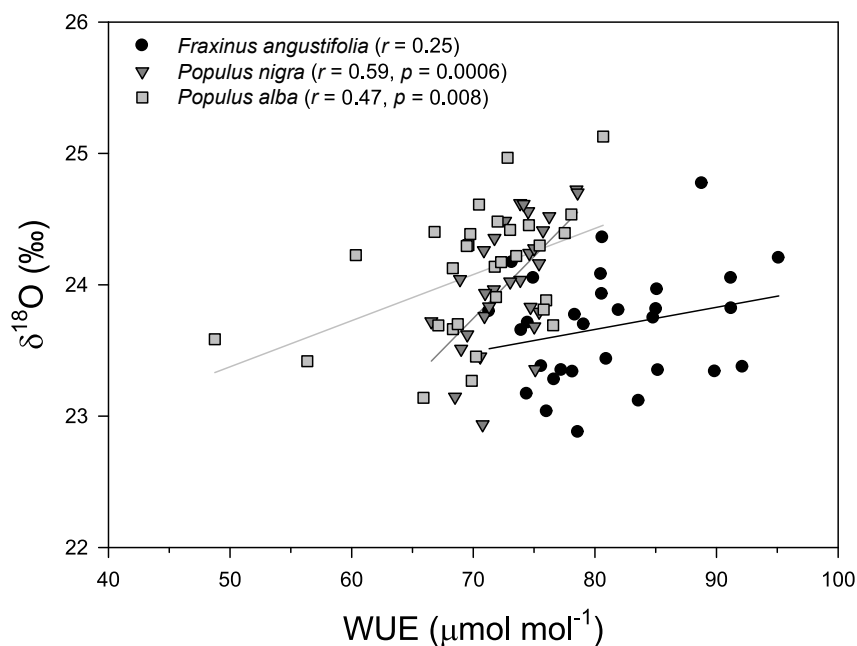


Fig. 4. (a) Relationships between intrinsic water-use efficiency (WUE), $\delta^{18}\text{O}$ and May precipitation (bars), which was negatively related to *P. alba* WUE (see Table 4). (b) Relationships between WUE and $\delta^{18}\text{O}$ calculated for each species (the colors of symbols and lines correspond to each species). Pearson correlations were significant ($p < 0.05$) in the case of the two *Populus* species.

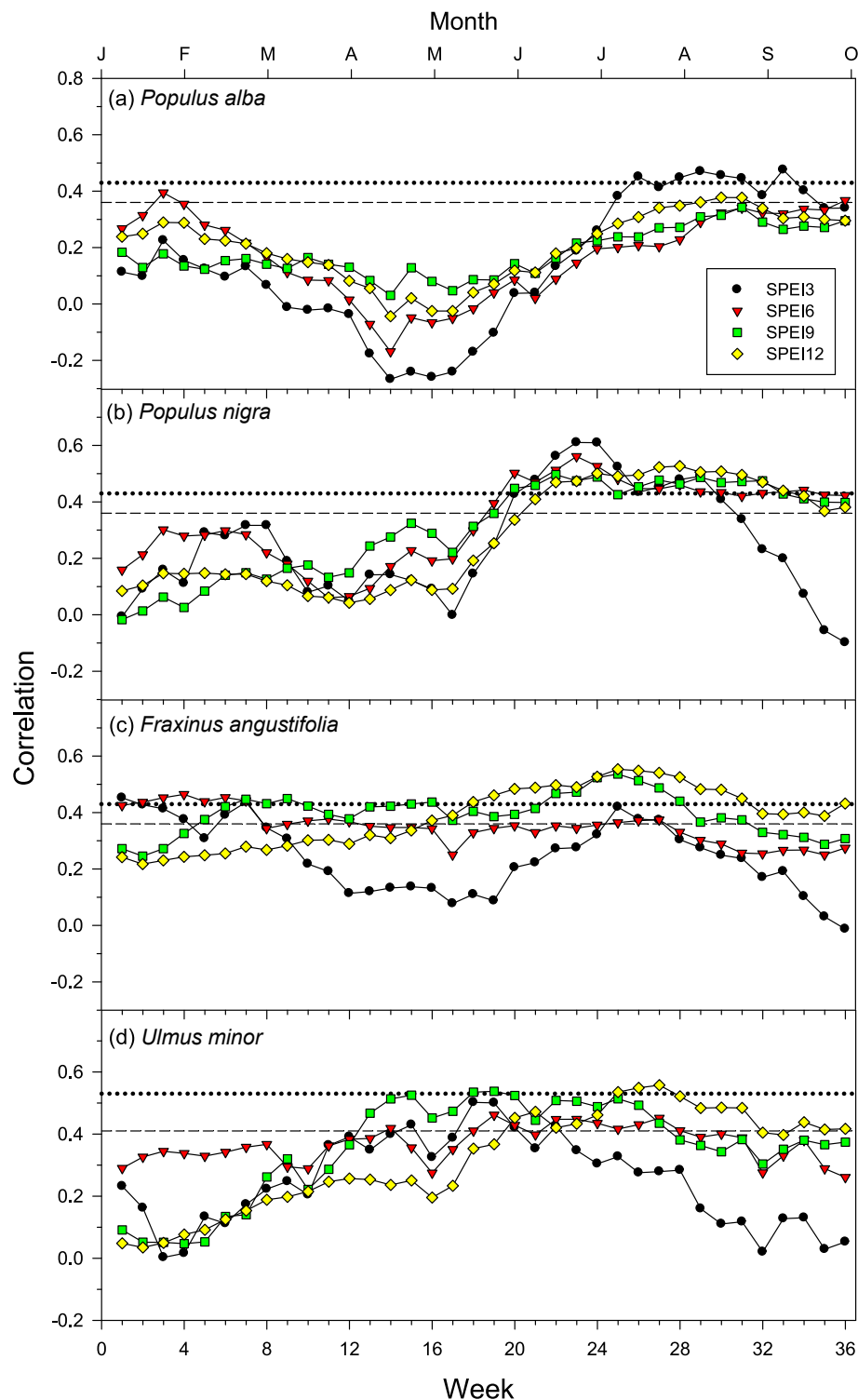


Fig. 5. Relationships (Pearson correlation coefficients) between series of ring-width indices of the four study species and weekly values of the SPEI drought index calculated at 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) long temporal scales. The dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

weaker.

In the case of $\delta^{18}\text{O}$ series we also found negative correlations from June to October and considering long droughts (SPEI6, SPEI9) (Fig. 7). Shorter droughts (SPEI3) from February to April also showed negative correlations with $\delta^{18}\text{O}$, particularly in the two poplar species.

3.7. Ash earlywood anatomy responses to climate, river flow and drought

The mean ash earlywood vessel density was 9 vessels mm^{-2} and it significantly ($p < 0.001$) increased in 2002 (14 vessels mm^{-2}) and 2008 (12 vessels mm^{-2}) (Fig. 8).

Interestingly, the earlywood vessel density explained 27% of variability in *F. angustifolia* WUE since both were positively related ($r = 0.52$,

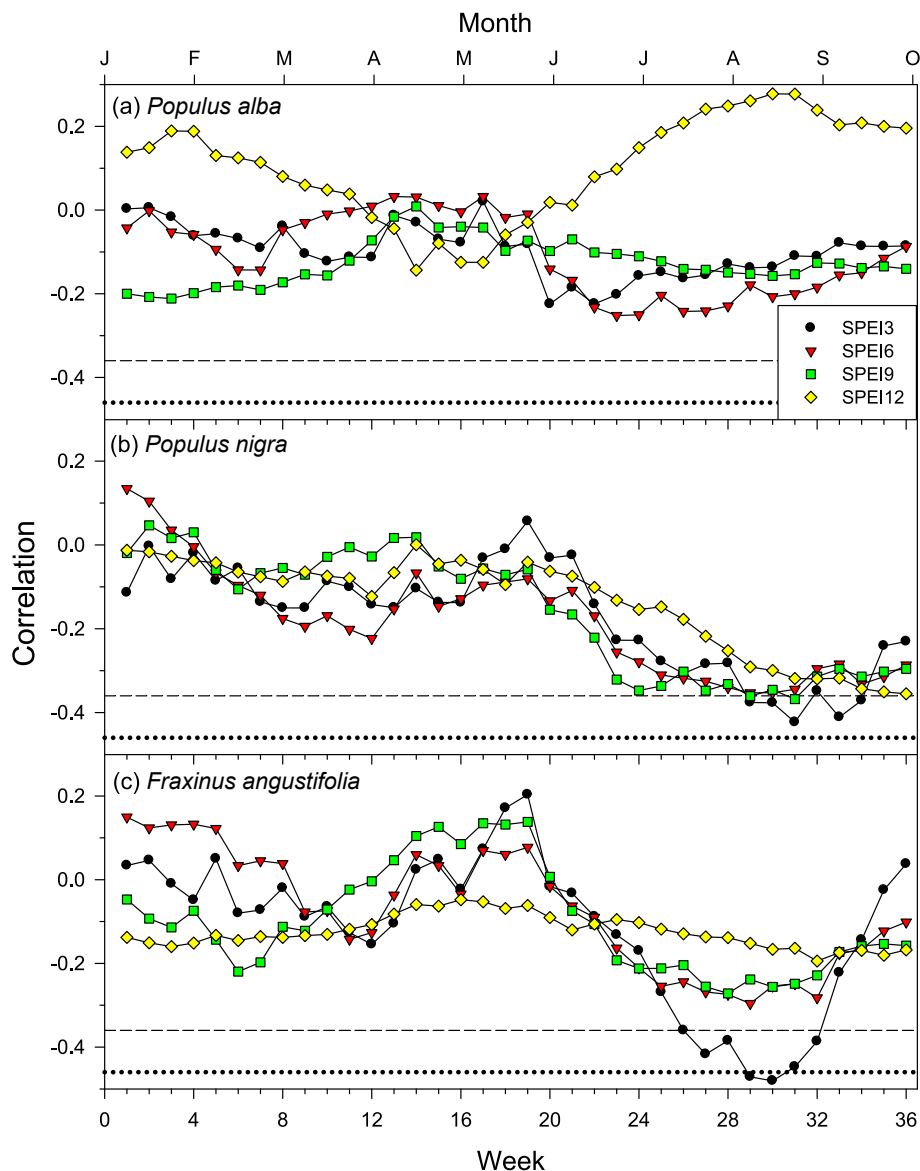


Fig. 6. Relationships (Pearson correlation coefficients) between WUE series of three study species and weekly values of the SPEI drought index calculated at 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) long temporal scales. The dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

$p = 0.005$; Fig. S3). The mean Dh was 198 μm and the mean maximum vessel diameter was 248 μm . As expected, the earlywood Dh and the mean maximum diameter were positively correlated ($r = 0.91$, $p < 0.001$), whilst earlywood vessel density was negatively related to the other anatomical variables (Dh , maximum diameter, Kp). The Dh in years 1998 (218 μm), 2010, 2015 and 2016 (213–216 μm) was significantly higher than the average value ($p < 0.01$), but it was lower in years 2002 (174 μm), 2007 (180 μm) and from 2011 to 2013 (186–190 μm). Accordingly, the Kp (mean $\pm$ SD, $2.8 \cdot 10^{-9} \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$) showed increases in 1998 (maximum value, $4.4 \cdot 10^{-9} \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$), 2010 and 2015–2016, and decreases in 2002 (minimum value, $1.7 \cdot 10^{-9} \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$), 2007 and 2011–2013.

The Dh was positively correlated with the precipitation of the prior August ($r = 0.56$, $p = 0.002$), November ($r = 0.44$, $p = 0.02$) and November–December ($r = 0.48$, $p = 0.01$). The Dh was also positively correlated with the river flow of the prior December ($r = 0.38$, $p = 0.05$) and summer months, particularly in August ($r = 0.57$, $p = 0.002$) and considering the total summer flow ($r = 0.59$, $p = 0.001$).

The earlywood vessel density negatively responded to the drought

index, peaking the correlation, in absolute terms, with SPEI9 from late January to early March (Fig. 9). Consequently, the SPEI and Dh showed positive correlations, with the highest correlation values found in mid to late February for SPEI9 and in January for SPEI12.

4. Discussion

We found that the most mature sites were dominated by *P. nigra* and *F. angustifolia* and showed the highest amount of decayed lying deadwood. This suggests they are less subjected to a lower influence of river dynamics than stands located near the river edge, dominated by *P. alba*. Since *P. nigra* and *F. angustifolia* presented high growth rates, were the species most responsive to drought and *F. angustifolia* showed the highest WUE, we expect an expansion and future dominance of the ash species in riparian forests located away from the river edge. The most phreatophytic poplar species would dominate stands located near the river edge, but warmer and more arid conditions during the growing season and low river flow could trigger growth decline and dieback of *P. nigra*.

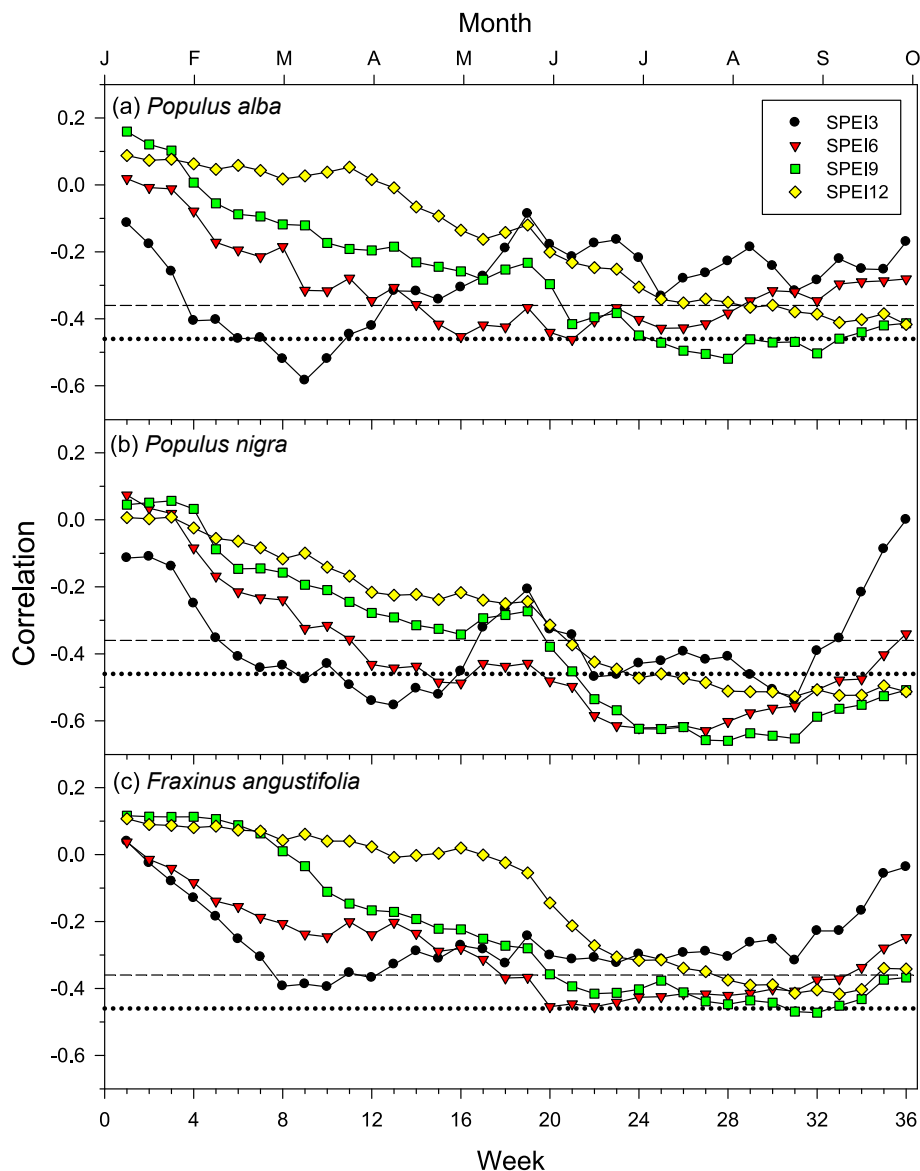


Fig. 7. Relationships (Pearson correlation coefficients) between $\delta^{18}\text{O}$ series of three study species and weekly values of the SPEI drought index calculated at 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) long temporal scales. The dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

The comparison of aerial photographs, the description of the stand structure and the quantification of the amount and decay degree of lying deadwood allow recognizing the high dynamism that the Ebro river and the study forests experienced during the past century. These dynamics, and also the past historical use, could explain the relative scarcity of very large trees showing the hydromorphological changes that characterize sites with higher level of naturalness. We further discuss how these historical dynamics may have shaped the current stand structure of the study riparian forests, including lying deadwood amount, and their growth and isotope responses to climate variables, drought severity and river flow.

4.1. Structure and amount of lying deadwood in Mediterranean riparian forests

The sites located near the river edge and subjected to stronger dynamics (“Soto del Hormiguero”) were dominated by pioneer, more phreatophytic species such as willows (*S. alba*) and contained the highest amount of lying deadwood, particularly less decayed pieces,

revealing relatively high and recent dynamics, probably resulting of low return period floods (Ollero, 1996). This finding partially concurs with a recent study in south-eastern Europe where highly decayed deadwood was found in sites closer to the river edge (Oettel et al., 2022). The discrepancy regarding decay degree may be explained by the different spatial scales analyzed since we focused on a small scale near the Ebro river, whereas Oettel et al. (2022) considered a larger scale in the Danube basin. In both cases, the lying deadwood volume decreases as distance from the river edge increases. In our study, the decayed lying deadwood was more abundant in the most mature stands located in the “Soto de la Duquesa” site and dominated by big *P. nigra* individuals.

In general, *P. nigra* was abundant in the three study sites, even in the best-preserved “Soto de la Duquesa” site where the highest amount of lying, very decayed deadwood was found. The presence of *P. nigra* in this site may result from past its proximity of the channel. The individuals of this species were among the largest and oldest ones among sampled species, and considering the wide lateral mobility of the Ebro river channel in the last decades (Fig. 1b), it might be that current old *P. nigra* trees have established in “Soto de la Duquesa” in a position closer to the

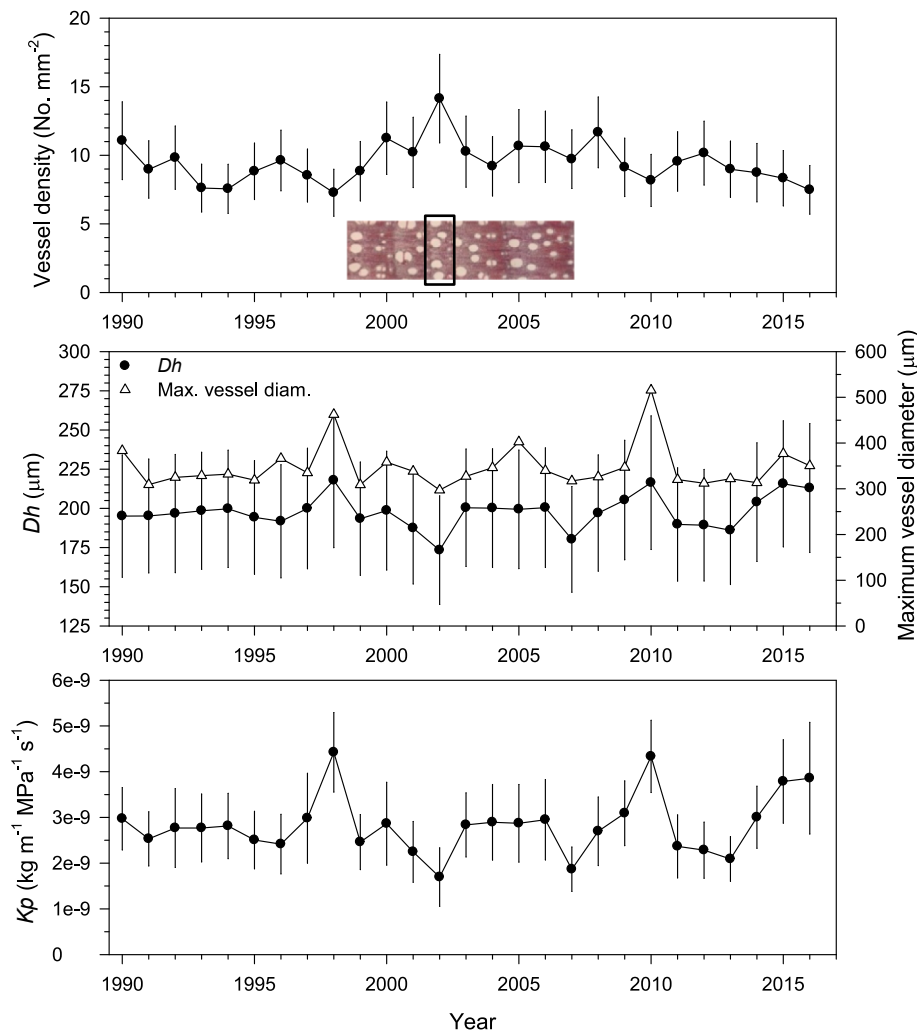


Fig. 8. Ash earwood anatomy data: vessel density, hydraulic (D_h) and maximum vessel diameters, and potential hydraulic conductivity (K_p). In all cases values are means $\pm$ SE. The image shows the narrow 2002 ring in the uppermost plot.

former margin of the river channel, probably lower in elevation and consequently, closer to the water level, taking a window opportunity for recruitment in an abandoned channel (Stella et al., 2011). Currently, although far from the channel, their root system is likely allowing them to reach water level even located farther from the channel. This suggests this species may be playing now an intermediate functional role between more (*P. alba*) and less phreatophytic (*F. angustifolia*) species.

The aforementioned results agree with data showing that, in addition to climate, drought and river flow, changes in river channel elevation also affect growth and recruitment of riparian tree species such as *Fraxinus excelsior* (Dufour and Piégay, 2008). It is also remarkable the abundance of dead *U. minor* trees, which showed a size-dependent mortality rate (Table 1). This high mortality is due to Dutch elm disease, which preferentially affected the trees with biggest diameters in the best-preserved “Soto de la Duquesa” site. Naturalized or introduced species such as *L. nobilis* are still exceptional, perhaps because their performance in terms of growth or WUE is lower as compared to native species (González-Muñoz et al., 2015).

4.2. Contrasting growth responses to climate, drought and river flow

We expected that the less phreatophytic species such as *F. angustifolia* would show higher growth–drought and growth–flow correlations than more phreatophytic species such as *P. alba*. This was the case since *P. alba* was the least responsive to river flow and the drought index in

terms of growth changes. For instance, growth indices of all species, excepting that of *P. alba*, positively responded to river flow, particularly in summer. The *P. alba* growth increased in response to cool-wet summer conditions. However, *F. angustifolia* was not the most responsive species but *P. nigra*. Therefore, we can reject our hypothesis that a higher growth–drought coupling should be expected for the less phreatophytic *F. angustifolia* and *U. minor*. Instead, these two species tended to respond to longer droughts than *P. alba* and *P. nigra*, indicating that they are able to extract deeper groundwater as compared with the poplar species which would depend on punctual, shallow water sources (Singer et al., 2013). The relationships found between growth or C and O isotope discrimination and river flow are further supported by the negative association between river flow and water table depth in the study sites. This confirms that river flow is a reliable proxy of soil water availability for the study riparian tree species, excepting *P. alba* which should mainly use shallow river water and depend on spring-summer rainfall justifying its low responsiveness.

Our findings agree with results from riparian forests in south eastern France, where drought and water table suppression reduced more growth of *P. nigra* than *F. excelsior* (Singer et al., 2013). These authors also reported that *P. nigra* and *F. excelsior* showed 1-year lagged response between dry years and growth drops. A similar lagged response was observed in our site with growth reductions observed one year after severe droughts (e. g., 1994–1995, 2011–2012). This could be explained because of the responses to long drought observed in *F. angustifolia* and

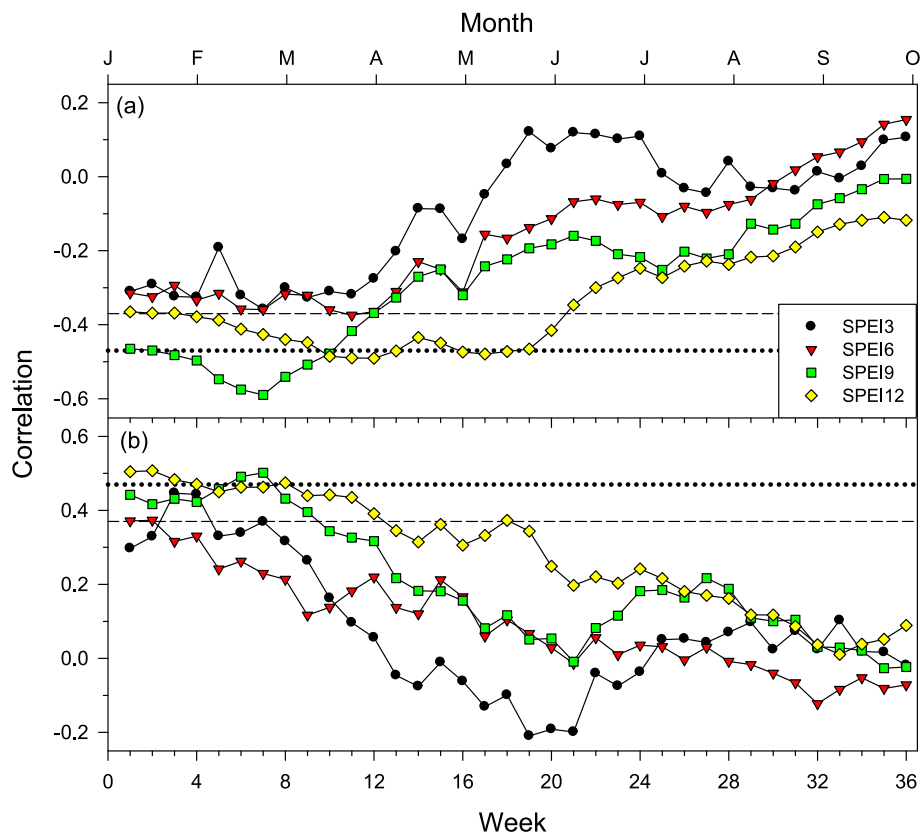


Fig. 9. Relationships (Pearson correlation coefficients) between earlywood anatomical series of *F. angustifolia* (a, vessel density; b, *Dh*, hydraulic diameter) and weekly values of the SPEI drought index calculated at 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) long temporal scales. The dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

U. minor, in agreement with what Rodríguez-González et al. (2021) reported for *F. angustifolia* in several Mediterranean rivers. The high responsiveness of *F. angustifolia* to climate and changes in groundwater availability was also observed in a floodplain forest located in central Europe (Šenfeldr et al., 2021).

In another central European floodplain forest, consecutive hotter droughts induced growth legacies or carryover effects as WUE increased (Schnabel et al., 2022). *Fraxinus angustifolia* and *U. minor* showed the highest first-order autocorrelation in growth data and *F. angustifolia* WUE also showed year-to-year persistence. Therefore, such less phreatophytic species would be more susceptible to present legacy effects of drought (*sensu* Anderegg et al., 2015). Nonetheless, individuals of more phreatophytic species such as *Populus deltoides* could also show similar legacies when growing far from the active channel and relying on shallow unconfined aquifers and rainfall to meet water demands (Andersen, 2016). Future research could investigate these drought legacies in other riparian forests and species, and determine if drought contributes to growth decline and tree death in *U. minor* before symptoms associated to Dutch elm disease develop.

The 2002 narrow ring observed in *F. angustifolia* and *P. alba* could have been caused due to carryover effects of the low minimum temperatures recorded in December 2001. Such drop in temperature could have triggered xylem embolism of the latewood formed in 2001 through freeze-thaw cycles (Sperry et al., 1994; Kitin and Funada, 2016), with cascading negative effects on the 2002 ring formation, particularly in the ring-porous ash species. This negative impact of a dry cold spell on *P. alba* growth also concurs with its thermophilic behavior across the Mediterranean basin (Dickmann, 2001). Therefore, this species would be particularly vulnerable to similar cold spells if climate variability increases.

4.3. Isotope (WUE, $\delta^{18}\text{O}$) responses to climate, drought and river flow

We expected a stronger coupling of WUE and $\delta^{18}\text{O}$ in the most phreatophytic species (*P. alba*, *P. nigra*) than in the less phreatophytic species (*F. angustifolia*). According to the dual-isotope conceptual model (Scheidegger et al., 2000; Ripullone et al., 2009), the combined decrease in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (or WUE) in *P. alba* and *P. nigra* would imply either an increase in *g* with relatively constant *A* or a decrease in *A* with relatively constant *g*. The slower decrease of $\delta^{18}\text{O}$ in *F. angustifolia* suggests a similar scenario but with higher WUE, particularly in dry periods (e.g., late 1990s, early 2000s), which agrees with its positive response to June temperature and the negative correlation with late-summer, short droughts (SPEI3). The sharp decrease of WUE in *P. alba* during 2008, with a synchronous growth enhancement and a decline in $\delta^{18}\text{O}$, corresponded to a very elevated May precipitation which could have led to a higher growth rate and might indicate a rise in *g*, at least proportionally higher than the increase in *A*. However, these findings might be taken with caution since more phreatophytic tree species tend to use $\delta^{18}\text{O}$ -enriched water from the vadose zone so the different impacts of evaporative demand or low precipitation on tree-ring $\delta^{18}\text{O}$ wood might be difficult to disentangle.

The commented associations between WUE and $\delta^{18}\text{O}$ could be also influenced by competition among trees, but we always sampled dominant trees forming the overstory in relatively open stands. Furthermore, the study poplar species are considered pioneer, shade-intolerant species and share similar leaf and cambial phenology with ash (Sass-Klaassen et al., 2011).

Nevertheless, these interpretations must be taken with caution since the application of the dual-isotope model is problematic due to several untested assumptions (e.g., similar source water and atmospheric vapor $\delta^{18}\text{O}$ inputs, common humidity in complex forest canopies, etc.; see

Roden et al., 2022). The $\delta^{18}\text{O}$ values in wood result from different sources of variability and its interpretation may be complex ($\delta^{18}\text{O}$ of source water and water vapor, air temperature, relative humidity, evaporative exchanges between the leaf and atmosphere, etc.; Barbour et al., 2002, Allen et al., 2022). In addition, our results based on $\delta^{18}\text{O}$ might be biased because we analyzed whole wood and not alpha-cellulose (Helle et al., 2022).

Riparian forests respond to changes in the availability of water within the vadose and phreatic zones (Scott et al., 2000). The more phreatophytic *P. alba* and *P. nigra* were more enriched in $\delta^{18}\text{O}$ than *F. angustifolia*, concurring with what Singer et al. (2013) found. This suggests poplars used more enriched water from the vadose zone than the ash as the water table was suppressed. As in a mountain mixed conifer forest (Marshall and Monserud, 2006), it was also found that co-existing species showed similar year-to-year $\delta^{18}\text{O}$ variability, albeit *P. alba* showed a stronger $\delta^{18}\text{O}$ depletion than the other two species. This means that the three species, particularly *P. alba*, could be increasingly extracting more depleted water, presumably from greater depths (phreatic zone), during the growing season. Moreover, groundwater is likely sourced from $\delta^{18}\text{O}$ -depleted high-elevation precipitation and soil recharge in the early growing season derives disproportionately from winter and spring precipitation (Jasechko, 2019).

If precipitation is generally enriched in $\delta^{18}\text{O}$ compared with groundwater because of evaporative demand, then discrimination in $\delta^{18}\text{O}$ can be used to compare the relative contributions of phreatic vs. vadose zone water sources to wood formation in riparian trees (cf. Singer et al., 2013). The mean $\pm$ SD value for regional precipitation $\delta^{18}\text{O}$ was -6.27 ± 0.72 ‰ at the Zaragoza station (1.04° W, 41.66° N, 261 m, period 2000–2015), also located in the Middle Ebro basin, according to data from the Global Network for Isotopes in Precipitation (Rodríguez-Arévalo et al., 2011). The measured $\delta^{18}\text{O}$ signature in surface waters of the Ebro river and groundwater were -8.2 ‰ and -9.0 ‰, respectively (Négrel et al., 2016). These data support using $\delta^{18}\text{O}$ data as proxies of source water use in the study site.

Ash species show greater sub-annual source water variability than poplars which tend to use more $\delta^{18}\text{O}$ -depleted water derived from hyporheic discharge and forming the phreatic zone (Sargeant and Singer, 2016). However, a decline in phreatic water access could lead to a convergence in water source uptake between more and less phreatophytic species. This could explain our finding that wood $\delta^{18}\text{O}$ values gradually declined in the studied species. Co-occurring riparian trees with different rooting depths can challenge the interpretation of seasonal changes in source-water utilization because trees integrate different water source reservoirs and droughts alter hydrological conditions (Singer et al., 2013).

Positive (negative) correlations between tree-ring $\delta^{18}\text{O}$ and vapor pressure deficit (precipitation) have been reported for north-eastern American temperate forests with abundant summer precipitation (Levesque et al., 2019). This is in line with our correlations showing positive (negative) responses of tree-ring $\delta^{18}\text{O}$ to maximum growing-season temperature (precipitation), i.e. high vapor pressure deficit, in *P. nigra* and *F. angustifolia*. It also concurs with their negative correlations with river flow in summer, a result also observed with annual river discharge in *F. excelsior* (Singer et al., 2013). Furthermore, *P. nigra* $\delta^{18}\text{O}$ series showed the strongest responses to the SPEI drought index, whilst in the case of WUE it was *F. angustifolia*, at least regarding short-term droughts (SPEI3). *P. nigra* showed a greater $\delta^{18}\text{O}$ sensitivity to river discharge than *F. excelsior*, indicating a more consistent phreatic water usage in *P. nigra* whilst *F. excelsior* would depend more on water from the vadose zone. Further, these observations are consistent with data on floodplain rooting depths, which show that poplars root deeply into phreatic zone gravels (Singer et al., 2013), while ash has more difficulty to go through coarse substrates (e.g., gravel layers) that characterize riparian zones (Sánchez-Pérez et al., 2008). Our results confirm that *P. nigra* may be more vulnerable to drought than *F. angustifolia* potentially affecting structure, composition and soil water availability in riparian forests.

This pattern might be exacerbated for *P. nigra* populations that established in former riparian conditions and are currently farther (both in distance and elevation) from the channel and potentially less often in contact to phreatic level in global warming and/or geomorphological alteration scenarios such as channel incision (Stella et al., 2013a). Similar results on the vulnerability of riparian poplar stands to groundwater decline and climatic drought have been recently reported in southern California (Williams et al., 2022).

4.4. Earlywood wood anatomy in *F. angustifolia*

Despite the highest growth and $\delta^{18}\text{O}$ responsiveness to drought of *P. nigra* compared to *F. angustifolia*, the earlywood anatomy of *F. angustifolia* provided additional information. The *Dh* decreased in response to long droughts (SPEI9, SPEI12) culminating in late winter. Consequently, long droughts starting in the prior winter-spring, i.e. 9–12 months before earlywood vessels start forming, lead to a reduction in vessel diameters, *Kp* and may explain part of the *F. angustifolia* growth reduction due to long droughts. The earlywood vessel density was positively related to WUE and both increased in response to dry conditions, albeit at short to long temporal scales, respectively. This suggests linkages between anatomical and hydraulic properties of the xylem and leaf water–gas exchange, such as the larger WUE for individuals with smaller vessel cross-section area (higher vessel density) observed in some ring-porous oak species (Ponton et al., 2001).

The associations reported between river flow and *Dh* agree with what has been found for *F. angustifolia* in several Mediterranean rivers, particularly under dry climatic conditions (Camarero et al., 2021), and also with findings from floodplain *F. excelsior* forests in Poland, where warm spring conditions reduced the number of earlywood vessels but a high river flow increased their area (Okoński and Koprowski, 2016). Analogous relationships have been observed in other ash species from different biomes. For instance, vessel area depended on spring discharge in *Fraxinus nigra* floodplain forests from Canada (Tardif et al., 2021). However, in *Fraxinus mandshurica* forests from wet north-eastern China, warm conditions lead to the formation of wider vessels, thus improving hydraulic efficiency (Zhu et al., 2021).

4.5. Caveat of the study and implications for management

A caveat of our study is the consideration of four tree species in a single study area. Nevertheless, similar results have been found for *F. angustifolia* growth (Rodríguez-González et al., 2021) and earlywood anatomy data (Camarero et al., 2021) in other sites of the Middle Ebro basin, under similar climate conditions. Therefore, we are confident that our analyses, at least on *F. angustifolia*, can be extended to other drought-prone riparian forests. However, further studies should consider additional sites with long series of water table depths.

Our analyses illustrate the responses of riparian forests to climate variability, drought severity and river flow in terms of radial growth, C (WUE) and O isotope discrimination and earlywood anatomy. More importantly, some of these responses and the current stand features (scarce old and large trees, abundant lying deadwood in best-preserved site) are conditioned by the Ebro river dynamics during the past decades. Such dynamism may have favored the establishment of *P. nigra* in the “Soto de la Duquesa” site, in locations situated farther from the channel. These stands may become more vulnerable to climate and hydrological droughts than *F. angustifolia* so their growth and vigor (changes in canopy cover, mortality rate) could be monitored and the river-forest dynamics should be restored if possible. According to our findings, these stands are prone to drought-induced dieback during periods when the water table declines. Finally, the earlywood anatomy of *F. angustifolia* is a sensitive proxy of drought stress so this ash species could be used to monitor the conservation status of similar riparian forests subjected to seasonal water deficit.

5. Conclusions

The assessment of historical changes in forest and river dynamics and radial growth combined with the characterization of current stand structure and the amount of lying deadwood allowed describing the maturity degree and successional status of riparian forests. Past dynamics of riparian forests shape their current structure and drive their responses to climate variables and drought stress. Our multi-proxy (growth, wood anatomy, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) approach provides an illustrative framework to retrospectively assess the responses of growth and functioning of riparian forests to climate, drought and river flow changes. In general, the dichotomy between more (*P. alba*, *P. nigra*) and less phreatophytic species (*F. angustifolia*, *U. minor*) was fuzzy, excepting the extreme cases of *P. alba* and *U. minor*. The most mature sites showed a higher amount of decayed deadwood and were dominated by *P. nigra* and *F. angustifolia*, which were the most responsive species to drought in terms of growth, WUE (*F. angustifolia*) and $\delta^{18}\text{O}$ (*P. nigra*).

In general, growth was reduced by drought and low spring-summer river flow. *P. alba* and *P. nigra* were more enriched in $\delta^{18}\text{O}$ than *F. angustifolia*, suggesting they used more enriched shallow groundwater, particularly during dry periods, than the ash species. Both WUE and $\delta^{18}\text{O}$ responded to drought which suggests the use of more depleted groundwater of the study species in agreement with their decrease in wood $\delta^{18}\text{O}$. The *F. angustifolia* earlywood anatomy was a sensitive proxy of changes in soil water availability since the *Dh* decreased in response to drought. Riparian trees are vulnerable to drought and water table declines.

CRedit authorship contribution statement

J. Julio Camarero: Conceptualization, Formal analysis, Funding acquisition, Writing – original draft. **Michele Colangelo:** Data curation, Methodology, Writing – review & editing. **Patricia M. Rodríguez-González:** Data curation, Methodology, Writing – original draft, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120710>.

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