



# Environmental influences on climate-driven growth of Mediterranean pollarded willows

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## ABSTRACT

Anthropogenic woodlands dominated by pollarded trees are iconic landscapes common in Europe, where they represent unique cultural, aesthetic, ecological and economic values. A special type of these woodlands are riparian pollarded willows (*Salix* spp.), which show a strong coupling with shallow soil water sources and streamflow. Willows are fast-growing, pioneer species formerly used to obtain key resources for rural communities. However, the long-term responses of these species to pollarding abandonment and warmer and drier conditions are unknown, particularly in Mediterranean, seasonally dry areas. We also lack a good understanding on the diameter, age and growth rates of pollarded willows growing under different ecohydrological situations. Here, we sampled five willow (*Salix alba*) stands, located in north eastern Spain and growing under Mediterranean conditions, characterized by warm and dry summers, and analyzed them using tree-ring data. Lower-basin dry sites near intermittent streams and upper-basin cold-wet sites near permanent streams were compared. We compared these stands with two coexisting poplar (*Populus nigra*) populations. Growth in lower-basin sites located near intermittent streams was constrained by low precipitation and soil moisture from spring to summer, whereas growth in upper-basin sites situated near permanent streams and with deep soils was constrained by winter waterlogging, dry spring conditions and low summer temperatures. Willow growth declined in response to short-term spring-summer droughts. The different responses of Mediterranean pollarded willows to climate variables and river flow depend on their contrasting ecohydrological situations which condition their use and management.

## 1. Introduction

In Europe, woodlands formed by pollarded trees represented traditional agroforestry systems, and constituted vital resources for rural economies since at least the Middle Age (Grove and Rackham, 2003). These anthropogenic iconic woodlands were created through secular tree pollarding by cutting all branches at a certain height above the ground, to keep the crowns out of the reach of livestock (Read, 2008). A particular case of pollarded stands are riparian woodlands dominated by poplar and willow species, which use shallow groundwater. These species are expected to respond more to reductions in streamflow and water table depth, leading to dry conditions (Singer et al., 2013).

Willows (*Salix* spp.) are widely distributed, pioneer, dioecious, fast-growing tree and shrub species found in riparian and floodplain forests of both hemispheres, and used for ecosystem restoration, bioengineering, as nature-based flood defenses, and as a source of bioenergy (Kuzovkina and Quigley, 2005; Baker et al., 2022; van Wesenbeeck et al., 2022). Willows are often planted and grown to produce biomass through short rotation coppice systems (Ceulemans et al., 1996). Their regeneration and growth dynamics are linked to hydrologic regimes, and they show adaptations to changes in soil moisture and river flow, including flooding (González et al., 2018). For instance, willows germinate on moist surfaces, they present high genetic variability and hybridization rates, produce extensive root systems, form branches with

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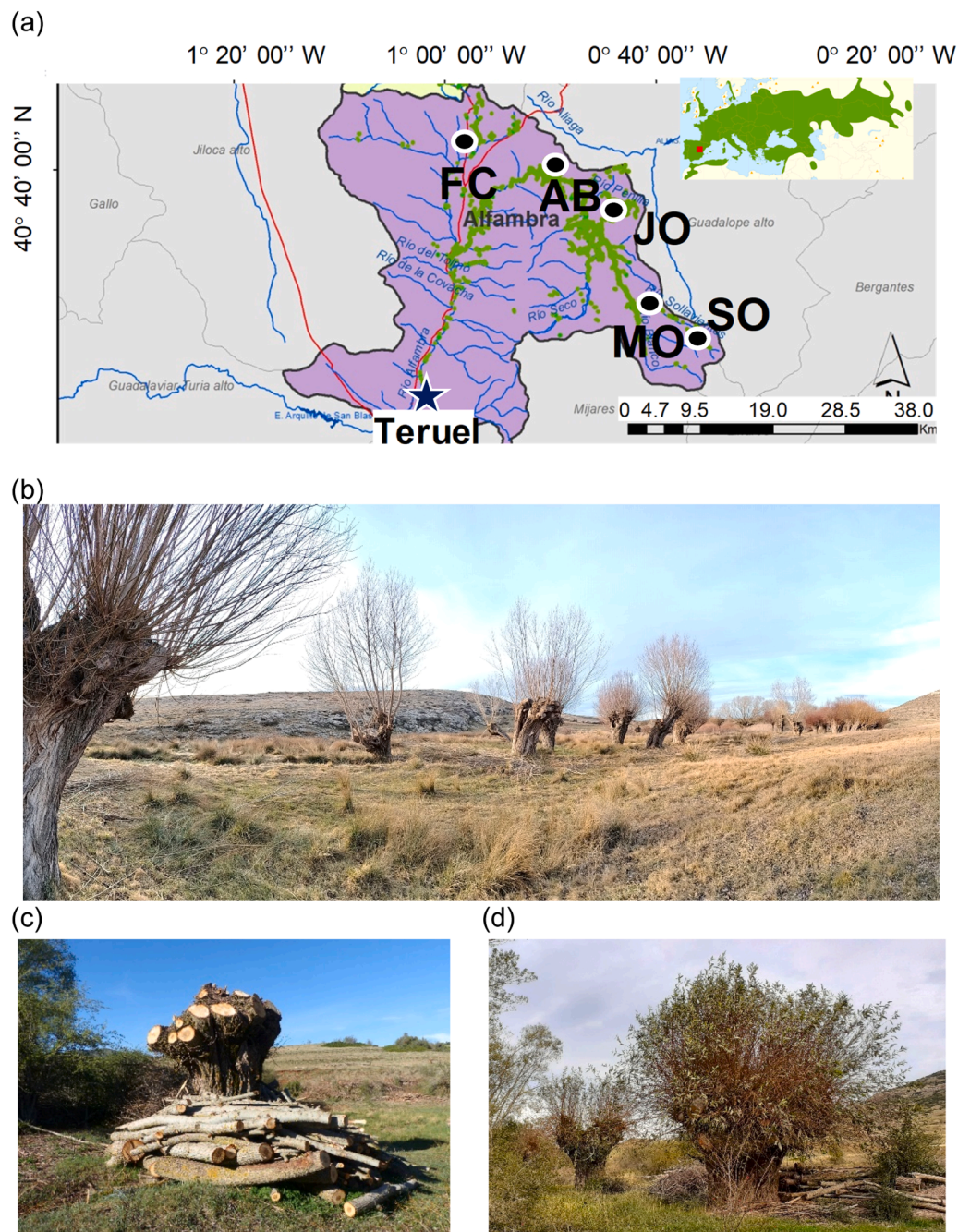
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**Fig. 1.** (a) Approximate location of sampled sites (circles) and the Teruel stream gauge (star) in the Alfambra river basin, Teruel province, north eastern Spain, indicating the main riparian forests (green points) dominated by poplars (the small map shows the distribution of *Salix alba* –green patches– and the location of the study area in Spain–red square), (b) landscape view of a sampled stand (site FC), (c) recently pollarded willow, and (d) willows re-sprouting after pollarding.

a high bending stability, and rapidly re-sprout after disturbances (Beismann, 2000; Karrenberg et al., 2002).

Most studies have focused on young willow stands as bioenergy and bioengineering solutions. However, old pollarded willows also play a key biodiversity role in European cultural woodlands and riparian forests (Rotherham, 2022). In most European countries, the management of these iconic landscapes along riversides was abandoned after the mid-twentieth century, threatening some of them due to the lack of pollarding. For instance, in the English countryside, many veteran willow trees are collapsing (big branches and poles break out) and being removed by farmers (Rotherham, 2022). Pollarded willows, mainly *Salix alba* L., were pruned at around 2.5–3.0 m height on a 'bole' and re-cut every few years, to produce firewood, timber, osier, and fodder, which

created a large woody 'head' bearing around twenty sprouts (Rotherham et al., 2021). Such pollarding practices are linked to the persistence of ancient willows in formerly grazed, riparian areas, but the ages and growth rates of those veteran trees are unknown. Obtaining this information is critical for the management and preservation of old willow stands since periodic pollarding prolongs lifespan (English Nature, 1999). The lack of management of formerly pollarded willows results in uneven growth in the boles on the pollard, decay and hollowing of the main stem, which threaten them and challenge their accurate dating using tree rings (Rotherham, 2022).

The persistence of pollarded riparian forests could be further menaced by land-use changes reducing river flow (e.g., dam building, draining for intensive agriculture; see Sanz-Zubizarreta et al., 2025),

**Table 1**

Geographical, ecohydrological and structural features of the five study sites. Diameter (dbh) and height values are means  $\pm$  SE. Different letters indicate significant ( $p < 0.05$ ) differences between sites according to  $t$  tests. The last column shows the closest gridpoint of climate data (4-km gridded Terraclimate dataset).

| Site name         | Site code | Ecohydrological conditions                     | Latitude (°N) | Longitude (°W) | Elevation (m a.s.l.) | No. sampled trees | dbh (cm)          | Pollarding height (m) | Closest grid of climate data |
|-------------------|-----------|------------------------------------------------|---------------|----------------|----------------------|-------------------|-------------------|-----------------------|------------------------------|
| Ababuj            | AB        | Karstic area, intermittent stream, lower basin | 40.552        | 0.791          | 1293                 | 12                | 106.9 $\pm$ 6.2b  | 3.2 $\pm$ 0.1b        | 40.549° N, 0.808° W          |
| Fuentes Calientes | FC        | Karstic area, meandering stream, lower basin   | 40.711        | 0.981          | 1235                 | 16                | 93.1 $\pm$ 7.9a   | 2.8 $\pm$ 0.1b        | 40.700° N, 0.976° W          |
| Jorcas            | JO        |                                                | 40.547        | 0.760          | 1326                 | 19                | 76.5 $\pm$ 4.6a   | 3.2 $\pm$ 0.1b        | 40.547° N, 0.760° W          |
| Motorritas        | MO        | Deep soils, upper basin                        | 40.409        | 0.656          | 1668                 | 15                | 122.4 $\pm$ 10.6b | 3.3 $\pm$ 0.2b        | 40.409° N, 0.656° W          |
| Sollavientos      | SO        |                                                | 40.469        | 0.671          | 1544                 | 16                | 141.8 $\pm$ 8.3b  | 2.3 $\pm$ 0.1a        | 40.469° N, 0.671° W          |

**Table 2**

Timespan and tree-ring statistics (means  $\pm$  SE) of the best-replicated period (1994–2024). Different letters indicate significant ( $p < 0.05$ ) differences between sites according to  $t$  tests. Abbreviations: AC1, first-order autocorrelation; MSx, mean sensitivity.

| Site | Timespan  | No. radii | Ring width (mm)  | AC1              | MSx              | rbar |
|------|-----------|-----------|------------------|------------------|------------------|------|
| AB   | 2004–2024 | 22        | 8.23 $\pm$ 1.02b | 0.49 $\pm$ 0.05a | 0.65 $\pm$ 0.09b | 0.41 |
| FC   | 1925–2024 | 23        | 4.62 $\pm$ 0.26a | 0.57 $\pm$ 0.21b | 0.42 $\pm$ 0.09a | 0.37 |
| JO   | 1957–2024 | 23        | 4.53 $\pm$ 0.20a | 0.50 $\pm$ 0.18a | 0.40 $\pm$ 0.06a | 0.32 |
| MO   | 1979–2024 | 28        | 4.27 $\pm$ 0.24a | 0.49 $\pm$ 0.14a | 0.38 $\pm$ 0.06a | 0.48 |
| SO   | 1990–2024 | 26        | 6.49 $\pm$ 0.47b | 0.52 $\pm$ 0.20a | 0.37 $\pm$ 0.08a | 0.29 |

and also by climate warming and aridification, as has been observed in pollarded poplar (Camarero et al., 2022), oak (Camarero and Valeriano, 2023; Olano et al., 2023) and ash woodlands (Candel-Pérez et al., 2022). However, no comparable studies exist on pollarded willows subjected to seasonal water shortage in Mediterranean regions, to the best of our knowledge. Here, we address this research gap by: (i) sampling five pollarded willow stands located in north-eastern Spain and subjected to different environmental constraints; (ii) quantifying their size (diameter), growth and age; and (iii) relating radial growth variability to climate variables and river flow. To compare climate-growth relationships in willow and coexisting riparian species, we also sampled two pollarded poplar (*Populus nigra*) stands. We expect that stands subjected to comparable ecohydrological conditions will show more similar year-to-year growth variability and responses to climate variables.

## 2. Materials and Methods

### 2.1. Study sites

We sampled apparently old, pollarded willow (*S. alba*) trees in five sites situated in the Alfambra river basin (ca. 1412 km<sup>2</sup> large), Iberian Range, Teruel province, north eastern Spain (Fig. 1, Table 1; Fig. S1). We selected five sites corresponding to three contrasting ecohydrological situations and different geological substrates which characterize the riparian forests in the study area (De Jaime Loren and Herrero Loma, 2007; De Jaime Loren, 2017), namely: karstic area with deep soils, meandering and intermittent streams, lower basin (Ababuj site, AB); karstic area, meandering stream, lower basin (Fuentes Calientes and Jorcas sites, FC and JO, respectively), and riparian forest in the upper basin with deep soils (Motorritas and Sollavientos, sites MO and SO, respectively). All sites presented willows with recently (1–2 years ago) pollarded crowns, except site SO, where recently pollarded willows coexist with other willows which had not been pollarded for the past

15–40 years. This last case is common because most of these stands are not regularly pollarded due to shifts in agricultural uses driven by the loss of wood economic returns and the migration of rural population to cities in the 1960s (Burillo-Cuadrado et al., 2019). The height of sampled willow trees ranged 5.0–7.5 m in sites MO and SO, and 10.5–16.5 m in sites AB, FC, and JO.

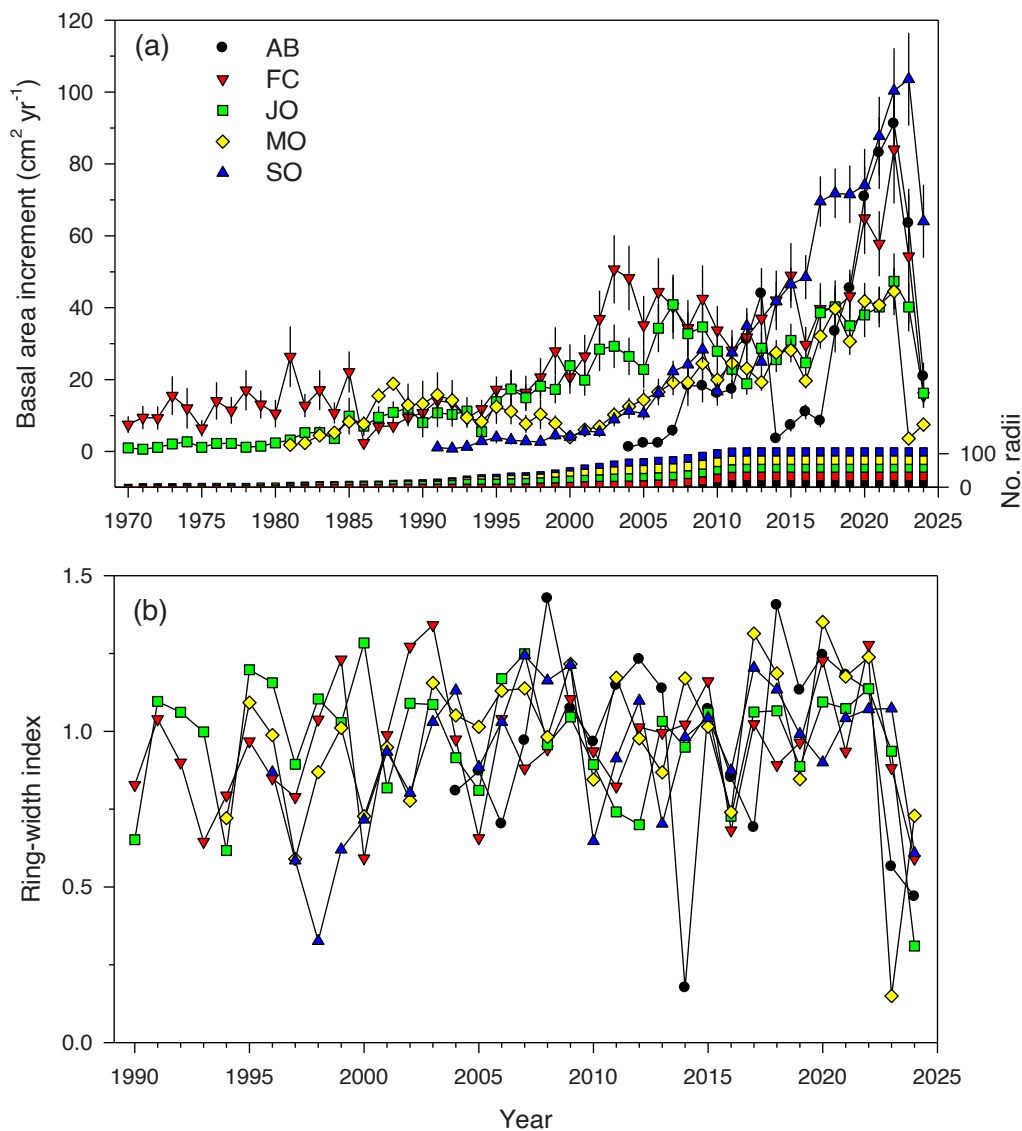
Climate in the study area is characterized by cold winters and warm-dry summers (Fig. S2). Mean annual temperatures ranges 10.6–12.6 °C, with minimum values in January (mean temperature is 1.6–4.4 °C) and warmest conditions in July (mean temperature is 20.3–21.6 °C). Annual precipitation ranges 420–650 mm with peaks in May and September and low values in July and January (Peña Monné et al., 2002). In the high-elevation, coldest sites (SO, MO), snow can fall and persist from winter to early spring, reaching a maximum depth of 0.5–1.5 m.

In the two high-elevation SO and MO sites, willows coexist with shrubs (*Juniperus sabina* L., *Juniperus communis* L., *Prunus spinosa* L., *Crataegus monogyna* Jacq., *Ribes alpinum* L., *Corylus avellana* L., *Rosa canina* L.), and are located near Scots pine (*Pinus sylvestris* L.) forests (see Fig. S1). In the other sites, willows co-occur with poplar (*Populus nigra* L.), ash (*Fraxinus angustifolia* Vahl) and shrubs (*C. monogyna*, *R. canina*, *Amelanchier ovalis* Medik., *Berberis hispanica* Boiss. & Reut., *Ligustrum vulgare* L., *Lonicera xylosteum* L., *Cornus sanguineum* L., *Genista scorpius* (L.) DC., *Thymus vulgaris* L., *Rhamnus saxatilis* Jacq.). Several willow species appear in the study sites (*Salix atrocinerea* Brot., *Salix purpurea* L., *Salix eleagnos* Scop.), but we focused on *S. alba*, which we distinguished by its hairy, narrow buds.

### 2.2. Sampling and processing tree-ring data

We sampled formerly pollarded, apparently old willow trees. In each site, from 12 to 19 willow stems, separated at least 10 m from each other, were selected. First, their diameter at 1.3 cm (dbh) and the pollarding height (where main poles were cut in the crown) were measured with tapes and a laser rangefinder (Nikon Forestry Pro 550 hypsometer), respectively. We also extracted cores, using the same methods, from old formerly pollarded poplars (*P. nigra*), in nearby sites Gúdar (GU, 40.43° N, 0.73° W, 1363 m,  $n = 12$  trees, timespan 1910–2020) and Allepuz (AL, 40.50° N, 0.75° W, 1328 m,  $n = 10$  trees, timespan 1877–2020) located near JO and MO sites, respectively, following Camarero et al. (2022). This was done to compare willow and poplar growth responses to climate under similar conditions in lower- and upper-basin sites.

Second, two cores were extracted at opposite sides of the stem and at 1.3 m using 5-mm wide Pressler increment borers (Haglöf, Sweden). Wood cores were air dried and then glued onto wooden mounts and sanded until tree rings were clearly visible (Fritts, 1976). Then, they were visually cross-dated, and tree-ring width was measured with a 0.01 mm resolution using scanned images (resolution 2400 dpi) and the CooRecorder-CDendro software (v. 9.8.1, Saltsjöbaden, Sweden) (Maxwell and Larsson, 2021). The visual cross-dating was checked using



**Fig. 2.** Sites' series of (a) basal area increment and (b) ring-width indices of the sampled willow sites. In plot (a) values are means  $\pm$  SE, and the right y axis shows the annual number of measured radii (bars with same colors as the study sites).

the COFECHA software, which calculates moving correlations between individual ring-width series and the mean sites series (Holmes, 1983).

To assess growth trends, tree-ring width data were converted into basal area increment (BAI) using the outside-in method and the following formula:

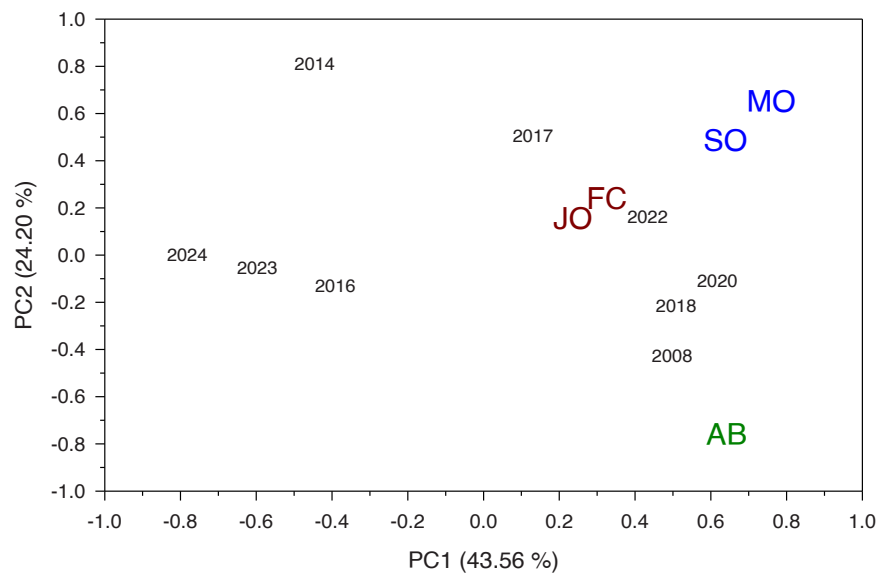
$$BAI = \pi \times (R_t^2 - R_{t-1}^2) \quad (1)$$

where  $R_t$  and  $R_{t-1}$  are the radii measured in years  $t$  and  $t - 1$ , which correspond to the cumulative sums of annual ring widths until years  $t$  and  $t - 1$ , respectively.

Most of the sampled large and old trees presented hollow stems with decayed heartwood and part of the sapwood. Therefore, we estimated the percentage of decayed area by sampling logged willow cross-sections in site JO ( $n = 10$  stems, diameter range 14–76 cm) during winter 2024–2025. We measured the radii of the wood cross-section and the decayed area in these basal samples and converted them into areas assuming a circular shape. Then, the cross-section and decayed areas were compared and a linear regression was fitted.

To assess year-to-year growth variability, each tree-ring width series was detrended by fitting a  $x$ -year cubic smoothing spline with a 50% frequency response cut-off, where  $x$  was 2/3 of the mean series length

(Fritts, 1976). This procedure preserved high-frequency variability mainly related to extreme climate events (e.g., droughts) and reduced the influence of biological trends due to changes in stem size or disturbances (Cook and Kairiukstis, 1990). Then, autoregressive models were applied to remove the first-order autocorrelation in detrended series and generate a series of residual ring-width indices. A bi-weight robust mean was computed to produce chronologies for each species and site. To summarize the variability of tree-ring data, several dendrochronological statistics (Briffa and Jones, 1990) were calculated over the best-replicated period (1994–2024): AR1, the first-order autocorrelation of raw data; MS, the mean sensitivity of standardized ring-width indices, i.e. a measure of relative changes in width between consecutive rings; rbar, the mean correlation among indexed ring-width series for each species in each site; and, EPS, the Expressed Population Signal (Wigley et al., 1984). Segments of mean ring-width series (chronologies) with  $EPS \geq 0.85$  are assumed to represent the population signal with sufficient quality, i.e. how well the tree-ring data represents an infinite population chronology. Site chronologies were calculated using the dplR package (Bunn, 2008, 2010; Bunn et al., 2025).



**Fig. 3.** PCA biplot showing the willow sites' loadings (sites' abbreviations) of the first (PC1) and second (PC2) components and the scores of years with very high (high PC1 scores) or low growth indices (low PC1 scores). The labels' colors indicate chronologies with similar growth patterns.

### 2.3. Climate and river flow data

To obtain homogeneous, long-record climate records we used the ~4-km gridded Terraclimate dataset and used data for the period 1960–2024 (Abatzoglou et al., 2018). We obtained climate variables from closest 4-km gridpoint to each site (see Table 1). We selected the following monthly variables: mean maximum (TMax) and minimum (TMin) temperatures, precipitation (Prec), climatic water deficit (Def), soil moisture (Soil m.), and vapor pressure deficit (VPD). The climatic water deficit was defined as the difference between potential and actual Evapotranspiration with higher values indicating stronger drought stress.

To assess drought severity, we used the Standardized Precipitation-Evapotranspiration Index (SPEI), which is a multi-scalar index based on the difference between water supply and demand (Vicente-Serrano et al., 2010). Positive values correspond to wetter than normal conditions, while negative values indicate drier than normal conditions. We obtained 1-km gridded, weekly SPEI data at 1- (SPEI 1), 3- (SPEI 3), and 6-month-long (SPEI 6) scales from the Spanish SPEI dataset (Vicente-Serrano et al., 2017).

We obtained monthly river flow data (period 1951–2024) from the Teruel station (40° 21' 30'' N, 1° 07' 13'' W, 885 m), which adequately represents the flow variability across the Alfambra river basin. River flow data were retrieved from the Spanish National Flow and Discharge Database ("Centro de Estudios y Experimentación de Obras Públicas", data available at the webpage <https://ceh.cedex.es/anuarioaforos/afo/estaf-datos.asp?indroea=8027>). River flow peaks from February to May (3.7–4.5 hm<sup>3</sup>), reaching the lowest values from July to September (1.6–1.9 hm<sup>3</sup>). In this regime, flow depends on precipitation and geological substrates such as limestones or clays, which can mitigate the reduction of flow in summer (Solans and Poff, 2013). Annual flow ranged 5–111 hm<sup>3</sup> (mean of 36.9 hm<sup>3</sup>), thus showing a high year-to-year variability. Note that sites AB, MO, and SO are located near the Alfambra river; whereas sites JO and FC are located near streams situated in the Alfambra river basin. Therefore, we assume that the flow and discharge data of the river are representative of the hydrological situation of those two smaller streams.

### 2.4. Statistical analyses

First, the normality of variables was checked using Shapiro-Wilk

tests. Second, after checking that compared variables fulfilled normality, tree diameter, pollarding and tree-ring statistics were compared between sites using *t* tests. Trends of monthly climate data (temperature, precipitation) and BAI were assessed using the non-parametric Mann-Kendall trend test (*S* statistic) because precipitation data did not follow normal distributions.

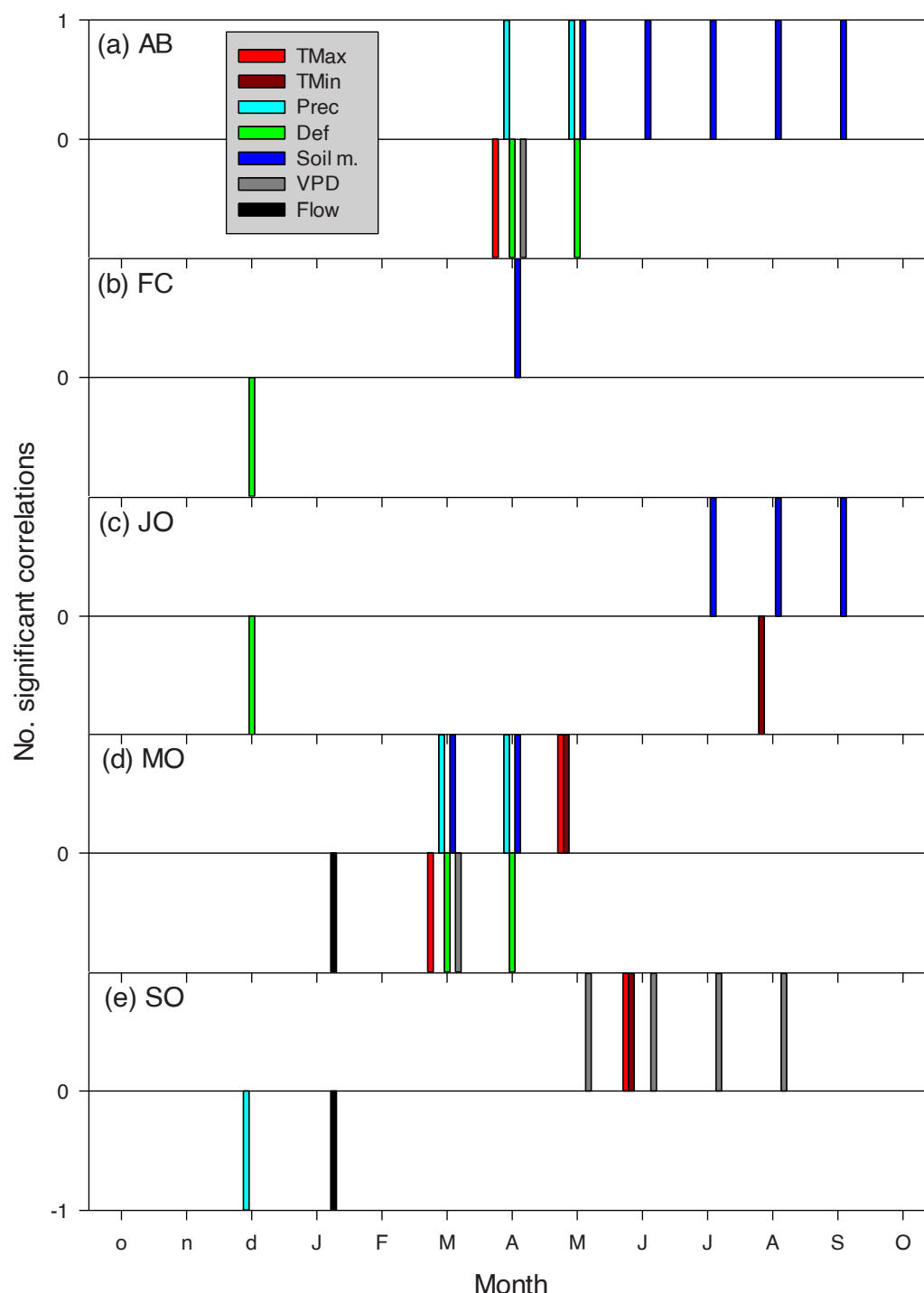
Site-to-site coherence in growth variability was evaluated by calculating Pearson correlation coefficients between site mean series of ring-width indices. In addition, to summarize the growth variability, we calculated a Principal Component Analysis on the variance-covariance matrix of indexed ring-width series, considering the period 1994–2024. We kept the first (PC1) and second (PC2) principal components since they accounted for most of 50% of the common growth variability. The PCA was calculated using the vegan R package (Oksanen et al., 2025).

Climate-growth relationships were assessed by calculating correlations between the mean series of ring-width indices and monthly climate variables and flow data. Pearson correlations were used for all climate variables, and Spearman correlations were used for precipitation, climatic water deficit, and river flow. In addition, correlations were calculated between PC1 and PC2 scores and the climate variables averaged for the sites showing highest loadings on each axis (sites AB, MO, and SO and sites FC and JO, respectively). Lastly, correlations were also computed between the sites' chronologies and the weekly SPEI values (SPEI 1, SPEI3, and SPEI 6). Correlations were calculated for the common period 1994–2024, except in the case of poplars (period 1990–2020). The window of analysis spanned from previous to current October. Climate-growth relationships were computed using the R package treeclim (Zang and Biondi, 2015). Analyses were carried out using the R software (R Development Core Team, 2025).

## 3. Results

### 3.1. Climate and flow trends, diameter, age and growth of pollarded willows

In all study sites, maximum and minimum monthly temperatures have significantly increased from 1960 to 2024 ( $p < 0.001$ ), whereas precipitation showed significant ( $p < 0.05$ ) negative trends indicating aridification (Fig. S3). The annual flow of the Alfambra river has also declined significantly ( $S = -609$ ,  $p = 0.002$ ; Fig. S4).

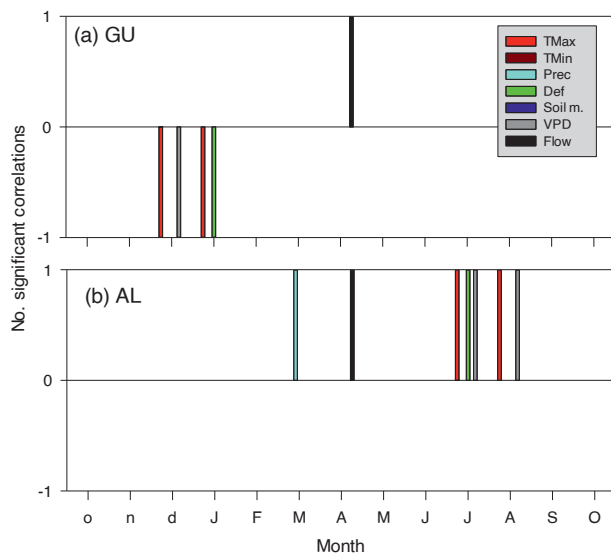


**Fig. 4.** Number of significant ( $p < 0.05$ ) correlations calculated between ring-width indices of the five willow sites (a, AB; b, FC; c, JO; d, MO; and e, SO) and monthly climate variables (TMax, mean maximum temperature; TMin, mean minimum temperature; Prec, precipitation; Def, climatic water deficit; Soil m., soil moisture; and VPD, vapor pressure deficit) and river flow. Correlations were calculated from prior to current October (x axes) with months of the previous and current years abbreviated by lowercase and uppercase letters, respectively. Positive and negative values indicate positive and negative correlations, respectively.

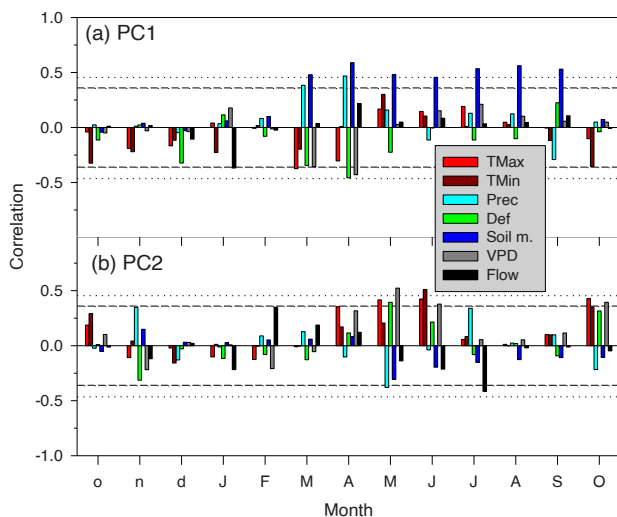
The thickest diameters (106.9 – 141.8 cm) were measured in sites AB, SO and MO (Table 1), and all sites showed similar pollarding heights (2.8 – 3.3 m) except site SO (2.3 m). Mean ring-width ranged from 4.27 (site MO) to 8.23 mm (site AB), and the youngest trees (20 years old) were sampled in site AB (Table 2). In contrast, the oldest willow, which was at least 100 years old, was found in site FC. In site JO, the total and decayed areas of the measured cross-sections were positively correlated, indicating potential to estimate age in hollow stems (Fig. S5). Site FC

showed higher first-order autocorrelation than the other sites, whereas site AB presented the highest mean sensitivity, with sites MO and SO showing the lowest mean sensitivity values. The  $r_{\text{bar}}$  values ranged 0.29 – 0.41, indicating moderate tree-to-tree coherence.

All sites showed significant ( $p < 0.001$ ) BAI increases according to Mann-Kendall trend tests, but some recent BAI drops were noticeable (Fig. 2). For instance, site AB showed a strong BAI drop from 2014 to 2017, and all sites showed abrupt BAI reductions in 2023 and 2024.



**Fig. 5.** Number of significant ( $p < 0.05$ ) correlations calculated between ring-width indices of the two poplar sites (a, GU; b, AL) and monthly climate variables. The rest of explanations are as in Fig. 4.



**Fig. 6.** Correlations calculated between the scores of the first (a, PC1) and second (b, PC2) principal components of willow ring-width indices and monthly climate variables. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively. The rest of explanations are as in Fig. 4.

Such recent growth decline was also observable in the series of ring-width indices.

The comparison of willow site chronologies based on Pearson correlations revealed moderate site-to-site coherence, particularly between FC, JO and MO sites, except site AB, which showed no significant ( $p > 0.05$ ) correlation with the other sites, and site SO, which only showed a significant positive correlation with site MO (Table S1). Significant positive correlations were also found between willow and poplar series of growth indices from sites JO and GU ( $r = 0.515$ ,  $p = 0.003$ ), and MO and AL ( $r = 0.555$ ,  $p = 0.003$ ).

Correlation analyses were in agreement with the PCA biplot which produced similar loadings for sites JO and FC (lower-basin sites located near intermittent streams), sites SO and MO (upper-basin sites located on deep soils and near permanent streams), and site AB situated near a water surge (Table 1, Fig. 3). The scores of the PCA highlighted years

with high (high PC1 scores; e.g., 2008, 2018, 2020, 2022) and low growth rates (low PC1 scores; e.g., 2014, 2016, 2023, 2024).

### 3.2. Climate-growth relationships in willow and poplar

Cool-wet conditions in April and moist soils from May to September enhanced willow growth in site AB which showed the strongest responses to soil moisture (Fig. 4). In the site JO, high soil moisture in summer and low August temperatures were positively correlated with higher willow growth rates (Figs. 4 and S6), whilst poplar growth in the nearby site GU increased as April flow did and decreased in response to warmer conditions in the prior winter (Figs. 5 and S7). In the cool-wet site MO, willow growth was enhanced by high precipitation and soil moisture from March to April (Fig. 4), whereas poplar growth in the nearby site AL also increased in response to wet March conditions and positively responded to April river flow (Fig. 5). In general, high soil moisture levels in spring and summer improved willow growth in all sites (e.g., sites AB and MO), except in site SO where growth positively responded to warm conditions and high VPD from May to August. In the upper-basin MO and SO sites, a high flow in January was related to low growth rates, whereas a high climate water deficit in the previous December reduced growth in sites FC and JO.

The correlation analyses between PC1 or PC2 scores and climatic variables identified two different responses corresponding to warm-dry and cold-wet sites, respectively (Fig. 6). The PC1 scores increased as spring-summer precipitation and soil moisture did and as April water deficit and VPD decreased. In contrast, the PC2 scores increased in response to warm May-June and October conditions, leading to high VPD.

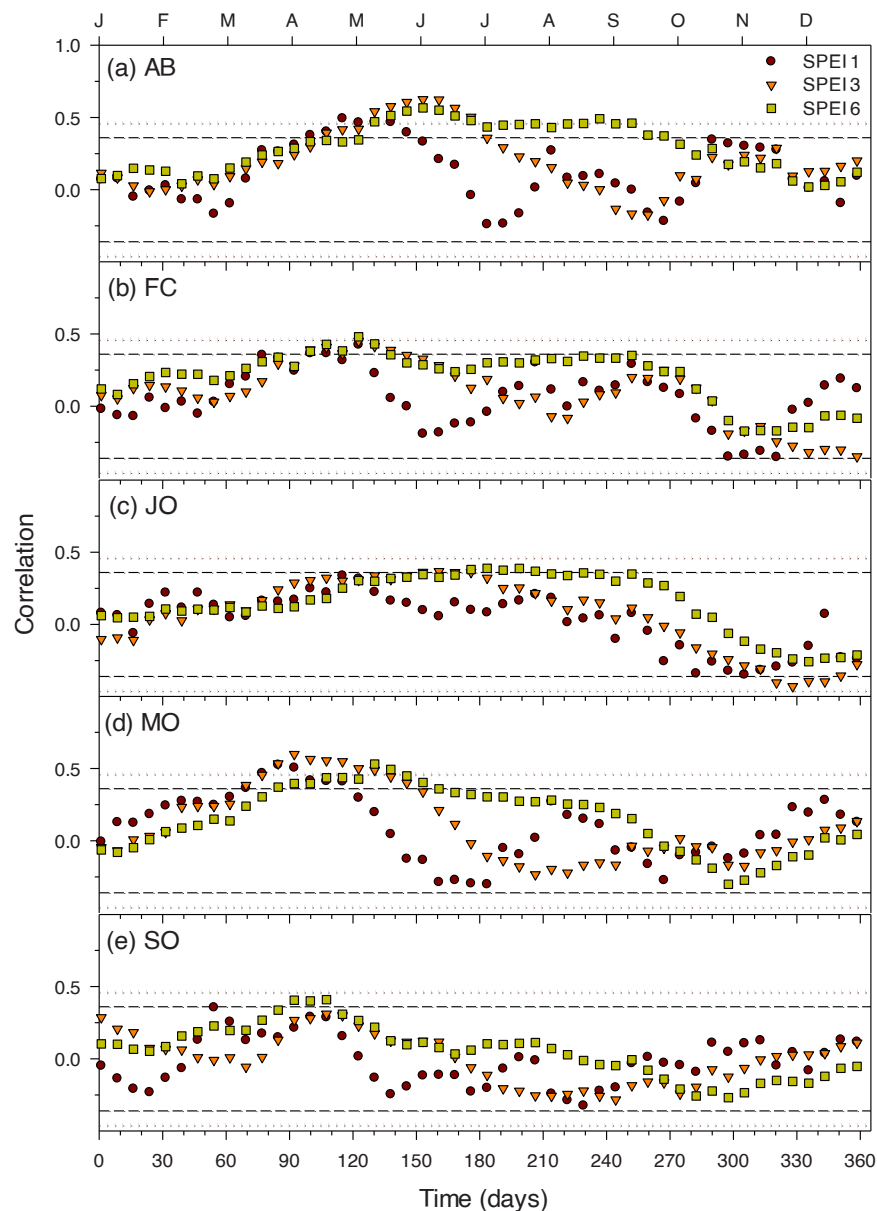
### 3.3. Drought-growth relationships

Willow sites showed very different growth responsiveness to the SPEI drought index (Fig. 7). The highest correlations between growth indices and the SPEI were found for 3-month-long scales in late March (site MO) or early June (site AB). In sites, FC, JO, and SO correlations peaked for 6-month-long SPEI values in April and June.

## 4. Discussion

Pollarded willow stands under Mediterranean conditions fulfilled our expectations, namely, stands experiencing comparable environmental conditions presented similar year-to-year growth variability and responses to climate variables. The first two axes of the PCA separated lower-basin, dry and less cold sites located near small and intermittent streams in a karstic area, and mountain, upper-basin, wet and colder sites located on deeper soils near permanent streams (Figs. 3 and 6). Overall, two extreme situations regarding willow climate-growth relationships were found (Fig. 6): lower-basin sites subjected to higher season water shortage, where growth was enhanced by wet-cool spring-summer conditions, and upper-basin mountain sites with more stable river flow, where warmer conditions and elevated VPD during the growing season improved growth.

Regarding the specific situations of each site, willows in site AB showed a remarkable sensitivity to spring-summer soil moisture, which is explained by its dependence on a water surge. Sites JO and FC also corresponded to conditions characterized by a more variable and lower water availability (karstic areas, meandering stream, lower basin; Table 1), which agrees with their responsiveness to spring and summer soil moisture (Fig. 4). Lastly, in the upper-basin sites MO and SO, willow growth increased as spring-summer temperature did indicating very different climatic constraints characterized by colder winters, a probable later growth onset in spring, and less variable soil moisture in summer. Nevertheless, these results must be interpreted with caution, given the shortness of willow chronologies and the high numbers of computed correlations, which can lead to spurious correlations



**Fig. 7.** Correlations calculated between ring-width indices of the five willow sites (a, AB; b, FC; c, JO; d, MO; and e, SO) and weekly SPEI data obtained at 1- (SPEI 1), 3- (SPEI 3), and 6-month-long (SPEI 6) scales. Upper and lower x axes show months and days of year, respectively. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively.

(Torbensoen et al., 2025).

The BAI data showed long-term increasing growth trends (Fig. 2a), which must be interpreted with caution because of the short lifespan of the oldest sampled willows (ca. 100 years), and considering that the outside-in method generates more reliable growth rates for recent than for past decades (Klesse and Bigler, 2025). Furthermore, BAI estimates are probably biased because many sampled trees presented some degree of hollow trunks due to wood decay, which increases proportionally to stem diameter and area. In fact, the presented equation obtained by relating stem and decayed areas may be used to correct BAI calculations in further studies (Fig. S5). This internal wood decay is a widely documented phenomenon caused by several white rot fungi and affecting fast-growing, short-living riparian tree species, including willows (Levin and Águeda Castro, 1998). Interestingly, no symptoms of canopy dieback or loss of vigor were observed in the sampled trees despite the common occurrence of wood decay.

Regarding the rooting-depth strategy of willows, we only found a

negative growth response to high January flow levels in the mountain, upper-basin sites (Fig. 3). This relationship could be explained by negative effects of waterlogging. In Portugal, willow (*Salix atrocinerea* Brot.) growth was constrained by elevated soil saturation levels (Rodríguez-González et al., 2010), possibly causing anaerobiosis in the rooting zone for trees growing near the river bank (Nakai and Kisanuki, 2007). The study performed in Portuguese riparian willows also found that growth was limited by low soil nutrient concentrations (Rodríguez-González et al., 2010), which requires future testing in our sites, where we did not measure soil nutrient availability. Nevertheless, most of these sites are grazed in summer by sheep and cows (see Fig. S1), which can fertilize soils. In contrast, high April flow levels enhanced poplar growth (Fig. 5), suggesting this species used shallow water pools in spring. Willows uptake water sources from shallow soil horizons (Marttila et al., 2018; Landgraf et al., 2022), and usually inhabit the riverbank, which may make them vulnerable to waterlogging and more sensitive to changes in soil moisture. Poplar growth showed weaker

correlations with soil moisture than willows (Figs. 4 and 5), suggesting less dependence on shallow soil water sources (Camarero et al., 2023). These findings concur with the high growth rates and elevated water demand, linked to low intrinsic water-use efficiency observed in riparian willow species by Schiffman et al. (2012). Furthermore, they explain the elevated growth sensitivity of riparian trees (poplars, willows) to long-term changes in streamflow (Meko et al., 2015, 2020).

In Mediterranean forests, dry conditions from the prior winter to early spring constrain tree growth by drying up the soil (Gazol et al., 2018) and reducing river discharge (Solans and Poff, 2013). However, the studied pollarded willows were more vulnerable to dry soil conditions in spring and summer, suggesting a lower dependence on winter-spring soil water recharge. Growth in sites AB and MO was very constrained by 3-month-long droughts, but the response peaks almost two months later in the first (early June) than in the second site (late March; Fig. 7). These different timings in the growth responses to drought suggest contrasting xylem phenological patterns, which are confirmed by other studies. For instance, *Salix viminalis* L. growing in Sweden under much colder conditions than the study sites showed a maximum cambium activity in July (Sennerby-Forsse, 1986). In the study sites, leaf flushing and leaf fall occur in late March and late November, respectively (*personal observation*); thus, matching the growing season of wood production.

Given the aridification trend observed in the study area and the decrease in river discharge, it could be expected that lower-basin willow stands will show a decrease in growth in response to short-term droughts as occurred in 2023 and 2024 (Figs. 2 and 3). In contrast, warmer conditions and lower flows would be linked to improved growth of upper-basin willow sites such as site SO (Fig. 4).

## 5. Conclusions

Riparian woodlands dominated by pollarded willows are iconic landscapes in Europe, but they have been little studied in Mediterranean mountain areas subjected to aridification and land-use changes. We obtained size and growth data of five Mediterranean willow (*Salix alba*) stands from north-eastern Spain using tree-ring data. This allowed identifying at least two growth responses to climate: a higher dependence on growing-season precipitation and soil moisture in lower-basin dry sites situated near intermittent streams, and a positive link with temperature in upper-basin, cold-wet sites near permanent streams. Such contrasting responses have clear implications for the management of these unique landscapes because the first sites are vulnerable to further warming and drying in spring and summer, whereas the coldest upper-basin sites show mixed responses, being constrained by winter waterlogging, reduced spring moisture and cool summer conditions. In contrast, growth of poplar was enhanced by high river flow levels in spring. Managing Mediterranean pollarded willows requires combining the knowledge on their responses to short-term droughts with pollarding of vigorous young individuals and preserving the oldest individuals. Climate warming would benefit growth of pollarded willows in mountain upper-basin sites, whereas aridification and reduced soil moisture would constrain growth in lower-basin sites.

## CRedit authorship contribution statement

**J. Julio Camarero:** Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jaime Loren Chabier:** Writing – review & editing, Validation, Software, Resources, Project administration, Methodology, Investigation, Conceptualization. **Cristina Valeriano:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Sánchez-Sancho José:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

## Declaration of Competing Interest

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

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2026.126551.

## Data availability

Data are available at: 10.5281/zenodo.20508706

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