Growth, earlywood anatomy and wood nutrients respond to precipitation and flow in semi-arid riparian tamarisk forests

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ARTICLE INFO	ABSTRACT
	Riparian forests from semi-arid regions with saline soils are dominated by facultative phreatophytes such as tamarisks (*Tamarix* spp.). Tamarisks tolerate drought and salt stress by using shallow and deep soil water sources depending on precipitation and flow variability in ephemeral or permanent streams. Therefore, their radial growth and wood anatomy would differently respond to precipitation and drought severity depending on stream ephemerality. To assess these responses, tree-ring-width, earlywood anatomy and sapwood nutrient concentrations were measured in five riparian tamarisk stands located in semi-arid north-eastern Spain. These sites experienced different aridity degrees and were located near ephemeral (e.g., Lanaja-dry site) or permanent streams in intensively irrigated agricultural areas (e.g., Valcuerna). Tree rings were widest in Peñaflor (2.94 mm) and narrowest in the driest Lanaja-dry site (1.11 mm), where tree-to-tree growth coherence was higher than in the other sites. Wet conditions during the water year enhanced growth, particularly in the most responsive Lanaja-dry site and in Lopín, whereas elevated flow increased the earlywood hydraulic diameter in Valcuerna. In the Lanaja-dry site, Ca, Cu, K and Mn wood concentrations were higher than in Valcuerna, but C and N concentrations were lower. Elevated Ca wood concentrations correspond to higher drought stress in the Lanaja-dry site, whereas higher N concentrations reflect eutrophication due to extensive use of agricultural fertilizers in Valcuerna. In sites near permanent streams such as Valcuerna, depth to groundwater may be a more robust proxy of growth than in drier sites located near more ephemeral streams such as Lanaja-dry site where tamarisk growth is constrained by 12-month long spring droughts.

1. Introduction

The spatiotemporal segregation in the use of different soil water sources is the basis of the hydrological niche (Silvertown et al., 2015). The partition of soil resources through mechanisms of water acquisition such as different root depths allows co-occurring plants to uptake nutrients (Moreno-Gutiérrez et al., 2012). In drylands, many tree and shrub species may use topsoil water during wet seasons, enhancing growth and nutrient use, and access the deep water table during drought when transpiration peaks and growth is constrained (Ehleringer et al., 1991). This represents a vertical decoupling between water and nutrient use with implications on nutrient uptake and growth (Querejeta et al., 2021). Facultative phreatophytes from arid and semi-arid regions, often found near ephemeral rivers, illustrate this spatial segregation in soil

water and nutrient uptake through the use of superficial and deep roots (Thomas, 2014).

Tamarisks (*Tamarix* spp., Tamaricaceae; also called saltcedars) tree and shrub species are facultative phreatophytes which tolerate seasonal drought stress by using shallow and deep soil water sources (Sala et al., 1996). Their dimorphic roots system (long lateral roots, deep taproot) allows them switching water sources from groundwater to unsaturated soil water when water table declines (Busch et al., 1992, Horton et al., 2003, Nippert et al., 2010). However, the unsaturated soil water used by tamarisks may also derive from groundwater sources (Sun et al., 2016). They inhabit hyperarid to semi-arid zones with saline soils in temperate and subtropical regions (Baum, 1978). Tamarisks are found along usually temporary or permanent streams, or in oasis and coastal habitats, usually forming riparian forests or growing in floodplains. The 67

Table 1
Characteristics of the sampled sites. MAT and TAP are the mean annual temperature and the total precipitation, respectively. Different letters indicate significant ($p < 0.05$) differences in tree-ring width among sites according to Mann-Whitney tests. Values are means ± SE.

Site	Latitude N	Longitude –W, E	Elevation (m a.s. l.)	Slope (º)	MAT (ºC)	TAP (mm)	No. sampled trees	Dbh (cm)	Description on site's water availability situation
Valcuerna	41.45	0.05	180	8	16.1	313	15	18.0 ± 2.3b	Permanent stream, irrigation surplus
Lanaja-dry site	41.71	-0.37	476	15	13.5	475	26	7.9 ± 0.6a	Temporary stream, upper basin
Lanaja-wet site	41.77	-0.35	379	7	13.7	463	13	9.1 ± 0.7a	Permanent stream, lower basin
Barranco Lopín	41.35	-0.51	186	5	15.0	330	14	15.4 ± 1.3b	Permanent stream, irrigation surplus
Peñaflor	41.77	-0.76	310	2	14.5	353	10	17.5 ± 1.8b	Temporary stream, lower basin

tamarisk species are native to Eurasia, including the Mediterranean region, and have become very invasive in semi-arid regions of SW North America (Baum, 1978). Their invasiveness depends on their high drought- and salt-stress tolerance and it is related to their high growth and evapotranspiration rates (Smith et al., 1998). First, tamarisk radial growth does not depend so much on groundwater distance as that of coexisting, native poplars (Gries et al., 2003). Second, due to such intense water use, tamarisks can lower the water table and, thus, induce a more intense drought stress to co-occurring tree and shrub species (Di Tomaso, 1998). Finally, post-drought recovery of tamarisk is very rapid upon rewatering (Devitt et al., 1997).

Tamarisk species grow in sites with saline soils and tolerate salt stress by extracting chemical elements from deeper soil profiles, excreting them through their foliar salt glands and depositing the enriched litter on shallow soils (Li et al., 2019; Newete et al., 2019, 2020). Tamarisks alter topsoil chemical properties by increasing the concentration of nutrients and exchangeable cations (Na^+, K^+, Mg^{2+} and Ca^{2+}) through salt excretion and litter decomposition (Sookbirsingh et al., 2010, Yin et al., 2010, Zhang et al., 2016). This could lead to a positive feedback because changes in topsoil performed by tamarisks (e.g., increased water content and nutrient concentrations in shallow soil) may enhance their growth and persistence as found in invaded South-African regions (Newete et al., 2019, 2020, Araya et al., 2022). Therefore, tamarisks can ameliorate growing conditions in semi-arid regions and sites with saline soils by influencing the variability of soil water content and nutrient availability (Cao et al., 2020).

Despite the relevance of tamarisks in regions with saline soils, which represent ca. 7 % of the Earth land area, there are still few studies investigating their radial growth responses to seasonal changes in water availability (precipitation, river flow) and associated changes in early-wood anatomy (e.g., hydraulic diameter) and wood nutrient concentrations (but see Xiao and Xiao, 2007, Fang et al., 2021). Analyses of leaf nutrient concentrations are more directly interpretable than those based on wood, but data on tree-ring wood nutrients provide a retrospective view (dendrochemistry) which can allow tracing changes in nutrient availability (e.g., Hevia et al., 2019) or soil salinity. Since both primary (e.g., branch length increment) and secondary growth (e.g., tree-ring width) in riparian trees are sensitive to variations in streamflow and ground water availability (Willms et al., 1998, Camarero et al., 2023), we expect that: (i) radial growth rates and earlywood vessel areas would be lower and (ii) wood concentrations of nutrients related to transpiration (e.g., Ca) would be higher in drier (more arid locations, ephemeral streams) than in wetter sites (less arid locations, permanent streams). We also hypothesize that growth responses to precipitation will depend on soil water-use strategies given the facultative phreatophytic behavior in tamarisk. Specifically, we expect a stronger growth dependence on spring precipitation in the driest sites located near ephemeral streams. Regarding earlywood anatomy, we expect that the transversal diameter of vessels will increase in response to wet-cool conditions from prior autumn to current spring and also in response to

higher flow in the stand located near a permanent stream.

2. Material and methods

2.1. Study sites

The five study sites are located in riparian stands from the semi-arid Middle Ebro basin and the Monegros steppe, Aragón, north-eastern Spain (Table 1). The Valcuerna site is located in the "Barranco de la Valcuerna", which is the only permanent stream in the Monegros steppe, and its flow depends on irrigation surplus waters coming from the Monegros channel. The Barranco de Lopín (hereafter Lopín site) is also located in a permanent stream feeding from surplus of irrigation waters upstream. The Lanaja-wet site is located in the lower basin of the Valdelanaja stream, where water accumulation is greater and lasts longer. The last two sites are located along temporary streams, usually dry during most months (April to November). The Lanaja-dry site is located in the upper basin of the Valdelanaja stream, on steep slopes, and the Peñaflor site is located in a relatively flat site (Las Canteras) located at ca. 4 km from Peñaflor village. All sites are situated in stable terraces. The Valcuerna, Lanaja-wet and Lopín sites are located within agricultural landscapes with more (Valcuerna, Lanaja-wet) or less (Lopín) irrigation intensity, whereas the Lanaja-dry and Peñaflor sites are surrounded by Mediterranean woodlands and scrublands.

In the study region, tamarisks (mainly *Tamarix africana* Poir. and *Tamarix gallica* L.) are mainly found in riparian forests and on saline soils (Braun-Blanquet and Bolós, 1957, Fernández-González et al., 1990, Villar et al., 2022). They form halophilous tamarisk-dominated communities near rivers or temporary streams where the understory is dominated by halophytic shrubs such as *Atriplex halimus* L. and *Salsola vermiculata* L. Other trees such as poplars (*Populus alba* L.) and willows (*Salix purpurea* L.) can be found in riparian forests or floodplains, whereas far from the lowland sites vegetation is dominated by drought-tolerant shrub (e.g., *Salvia rosmarinus* Spenn., *Quercus coccifera* L., *Rhamnus lycioides* L., *Rhamnus alaternus* L., *Juniperus phoenicea* L., *Pistacia lentiscus* L.) and tree species (*Pinus halepensis* Mill.).

Climate in the study area is semi-arid, continental and Mediterranean with dry summers, an ample thermal amplitude and a high year-to-year rainfall variability (Fig. S1) according to climate diagrams (Zepner et al., 2021). Valcuerna is the warmest (MAT, mean annual temperature of 16.1 ºC) and driest site with only 313 mm of total annual precipitation (TAP) (Table 1). Lanaja is the wettest site with TAP of 463–475 mm, whereas Peñaflor and Lopín sites are also dry with TAP of 353 and 330 mm, respectively. Mean maximum and minimum temperatures range 18.0–19.7 º C and 5.5–7.7 ºC in Peñaflor and Lopín sites, respectively. Aridity is amplified by strong winds blowing from the NW (locally called "cierzo"), but in winter months (December, January) high-pressure conditions are associated to persistent fogs providing air humidity (Pedrocchi, 2000). Soils are basic, calcareous, saline and formed on limestones or gypsum substrates. For instance, in Valcuerna

the soil pH was 7.9, the electrical conductivity was 5.6 dS m^{-1}, N concentration was 0.38 %, the organic matter concentration was 12.0 %, the CaCO$_3$ concentration was 43.9 % and gypsum content was 3.4 %. In the Valcuerna site, the electrical conductivity of water samples was 13.2 dS m^{-1} (Berga Celma, 1993). In Peñaflor, the soil pH was 7.5, and the organic matter and CaCO$_3$ concentrations were 18.4 % and 36.6 %, respectively.

2.2. Study species

Tamarisks or saltcedar trees are native to Africa and Eurasia (Zohary, 1987). One of its diversity centres is the Mediterranean Basin where several tamarisk species coexist. They usually grow in riparian forests or floodplains on arid and semi-arid sites with saline soils where streams may be permanent or temporary and precipitation seasonality is high (Smith et al., 1998). They often have salt-secreting twigs and are considered halophytic, although a reduction in growth rates have been observed in response to elevated salt concentrations (Glenn et al., 1998). They show high concentrations of leaf osmolytes which allow them maintaining positive turgor and higher stomatal conductance at lower leaf water potential (Busch and Smith, 1995). Their wood is diffuse-porous to semi-ring-porous (Fahn, 1958).

2.3. Climate, drought and flow data

To obtain homogeneous and long-term climate records, we used the monthly mean maximum (Tx, diurnal) and minimum (Tn, nocturnal) temperature and total precipitation data for the period 1950–2018 from the 0.1º-gridded E-OBS climate dataset (Cornes et al., 2018). We also calculated the monthly climate water balance as the difference between precipitation and potential evapotranspiration (P-PET). The PET was estimated using the Hargreaves method (Hargreaves and Samani, 1985). Annual PET ranged from 800 (Lanaja) to ca. 1000 (Valcuerna) mm. The annual water balance was negative and varied from −410 (Lanaja) to −620 (Peñaflor, Lopín) and ca. −900 (Valcuerna) mm

To assess drought severity and duration at local scale we obtained 0.5º-gridded monthly SPEI data (period 1986–2020) from the SPEI Global Drought Monitor webpage (https://spei.csic.es/map/). The Lanaja-dry, Lanaja-wet and Peñaflor sites were located in the same 0.5º grid. These monthly SPEI data were downloaded at 1- to 24-month time scales. The SPEI has positive and negative values for wet and dry conditions, respectively, and it is based on a cumulative climatic water balance calculated as differences between precipitation and potential evapotranspiration (Vicente-Serrano et al., 2010).

Stream flow data were available near the Valcuerna site. Flow data were obtained from the Valcuerna gauging station (0.027º E, 41.465º N, 196 m a.s.l.; period 1986–2020) situated 2 km upstream from the sampled stand (Spanish National Flow and Discharge Database -Centro de Estudios y Experimentación de Obras Públicas, data available at https://ceh.cedex.es/anuarioaforos/afo/estaf-datos.asp?indroea=9231). The average annual discharge of the station was 18.4 hm^3, with maximum monthly flows in April, July and August and minimum flows in winter. The stream is about 35 km long and water is collected from an endorreic basin of 439 km^2.

2.4. Field sampling and wood samples

We sampled mature trees and measured their diameter at breast height (dbh, 1.3 m). Two cores were taken at 1.3 m from trees using a Pressler increment borer (Haglöf Sweden AB). In the case of thick stems (dbh > 15–20 cm), rotten heartwood was common, so we took cross-sections from other thinner stems of the same individual using a cordless pruning saw (Milwaukee M12, Brookfield, USA). Five additional trees were sampled in Valcuerna and Lanaja-dry sites and their cores were kept for dendrochemical analyses.

The collected wood samples were processed using standard dendrochronological methods (Fritts, 1976). Cores were air dried, mounted in wooden supports using glue and sanded with sandpapers of different grain until growth rings were visible. The cores for wood-anatomical and dendrochemical analyses were neither sanded nor glued but their surface was carefully prepared using a sledge microtome designed (Gärtner and Nievergelt, 2010). Then, samples were scanned at a resolution of 2400 dpi using an Epson Expression 10,000-XL scanner (Epson, Suwa, Japan). In the case of cores for wood anatomy, each analyzed radius was stained with black ink and the vessels were filled with chalk white powder to enhance contrast. Then, high-resolution images of the cross-sections were captured using a Canon EOS 7D camera mounted on a Leica S9D stereomicroscope. The images were stitched with PT-Gui (New House Internet Services BV, Rotterdam, NL) to create one composite image for each sample (Fig. S2).

Cores were visually cross-dated, and ring widths were measured to the nearest 0.001 mm from the pith to the bark considering two radii for each sampled tree. The CooRecorder and CDendro software (Larsson and Larsson, 2022) were used to cross-date and measure the samples. The quality of the visual cross-dating was assessed with the COFECHA software (Holmes, 1983). This process is based on the computation of correlations between the individual ring-width series of each sampled tree and the site mean chronology.

2.5. Quantitative wood anatomy

Earlywood anatomy was measured in two sites where tamarisks were subjected to contrasting hydrological conditions: the temporary stream in Lanaja-dry site and the permanent stream in Valcuerna. These data were obtained the period 2000–2020 and considering five trees per site which showed high correlations with their respective mean site series. Images of scanned tamarisk cores or cross-sections whose surface was prepared with the core microtome were used to measure earlywood anatomy. We measured earlywood vessel area and radial diameters (*d*) along one radius per tree and within a 4-mm tangential window using the ImageJ software (Schneider et al., 2012). Earlywood vessels were considered those formed in the first quarter of the ring and with a transversal diameter larger than 80 μm. Then, we calculated the hydraulic diameter (*Dh*) following Sperry et al. (1994):

$$Dh = (\sum d^5 / d^4) \tag{1}$$

where *d* is the diameter measured for $i = 1$ to *n* earlywood vessels. Then, the potential hydraulic conductivity (*Kp*, in kg m^{-1} MPa^{-1} s^{-1}) was calculated following Tyree and Ewers (1991):

$$Kp = (\pi\rho / 128\eta A) [\Sigma Dh_i^4] \tag{2}$$

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

2.6. Processing tree-ring width and wood anatomy series

To calculate climate-growth relationships, the individual ring-width series were converted into dimensionless ring-width indices through standardization and detrending (Fritts, 1976). This allows removing size-related trends in ring-width data and emphasize high-frequency growth variability by fitting 23-year cubic smoothing splines with a 50 % frequency response cut-off to individual ring-width series. Then, we obtained ring-width indices by dividing observed by fitted values. The length of the spline was selected to retain annual to decadal growth variability. Lastly, we fitted autoregressive models to remove most of the first-order autocorrelation in series of dimensionless ring-width indices. The obtained residual or pre-whitened individual series were averaged using a bi-weight robust mean to obtain residual series or chronologies for each site (Fritts, 1976). Finally, a best-replicated period (common interval) was defined for each site based on the values of the Expressed Population Signal (EPS). We considered the best-replicated period that

Table 2
Tree-ring width statistics calculated for the common, best-replicated period (1986–2020). Values are means ± SE. Different letters indicate significant ($p < 0.05$) differences in tree-ring width among sites according to Mann-Whitney tests.

Site	Timespan	Tree-ring width (mm)	AR1	MS	PC1 (%)	rbar	EPS (common interval)
Valcuerna	1970–2020	1.97 ± 0.33bc	0.50	0.36	54.6	0.41	0.81 (1991–2020)
Lanaja-dry site	1959–2020	1.11 ± 0.12a	0.49	0.42	59.5	0.46	0.83 (1982–2020)
Lanaja-wet site	1984–2020	1.40 ± 0.25b	0.49	0.43	34.4	0.33	0.72 (1996–2020)
B. Lopín	1986–2020	2.14 ± 0.30c	0.17	0.39	48.6	0.39	0.76 (1991–2020)
Peñaflor	1982–2020	2.94 ± 0.37 cd	0.33	0.37	41.0	0.38	0.73 (1986–2020)

with EPS ≥ 0.70 because none of the chronologies reached the 0.85 EPS threshold usually considered as approaching theoretically perfect chronologies (Wigley et al., 1984). We also characterized the site chronologies by calculating several statistics including: the mean ring-width values, the mean first-order autocorrelation of ring widths (AR1), which accounts for year-to-year persistence in growth, the mean sensitivity (MS), which reflects relative changes in ring width between consecutive rings, the common percentage of the first principal component (PC1), the mean inter-series correlation (rbar) and the EPS (Briffa and Jones, 1990).

2.7. Chemical analyses of sapwood elements

To compare sapwood element concentrations between the sites with permanent (Valcuerna) and temporary (Lanaja-dry) streams, we selected 5 trees per site and two cores per tree. We separated the outer 5

rings (period 2016–2020) by using clean scalpels and gloves to avoid contamination. Then, wood samples were ground and homogenized to a fine powder using a ball mill (Retsch MM301, Haan, Germany). Wood N and C concentrations were measured with an elemental analyser (TruSpec CN, Geleen, The Netherlands). The sapwood concentrations of the other elements were analysed using inductively coupled plasma optical emission spectrometry (ICP-OES, Thermo Icap 6500 DUO, Thermo Fisher Sci., Waltham, USA) after a microwave-assisted digestion with HNO3:H2O2 (4:1, v:v). All analyses were done in the Ionomics laboratory at CEBAS-CSIC (Murcia, Spain). Elements not reported (As, Be, Bi, Cd, La, Mo, Sb, Se and V) showed concentrations lower than the detection limit (0.01 mg kg^{-1}).

2.8. Statistical analyses

Mann-Whitney tests were used to compare several variables among
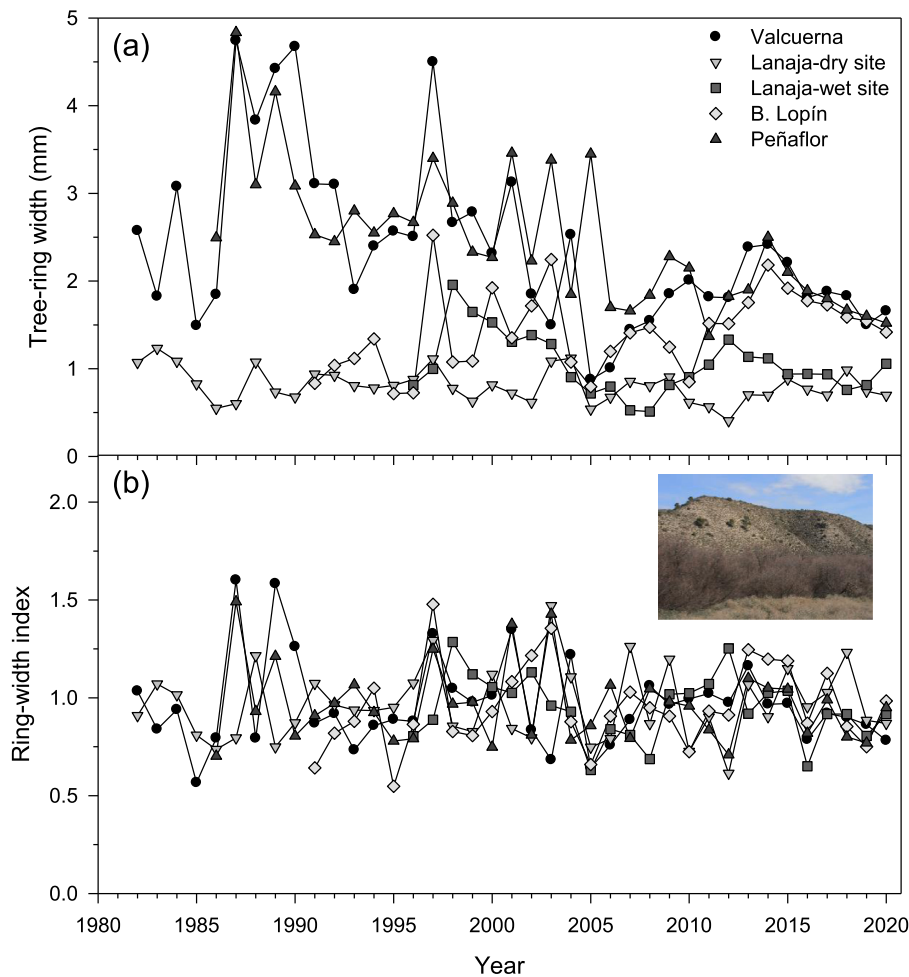
Fig. 1. Mean site series of (a) tree-ring width and (b) ring-width indices of the sampled tamarisk sites. The presented intervals correspond to the best-replicated periods (see Table 1). The image shows a view of a tamarisk riparian forest in winter with drought-tolerant shrub and tree species (*P. halepensis*) shown in the background.
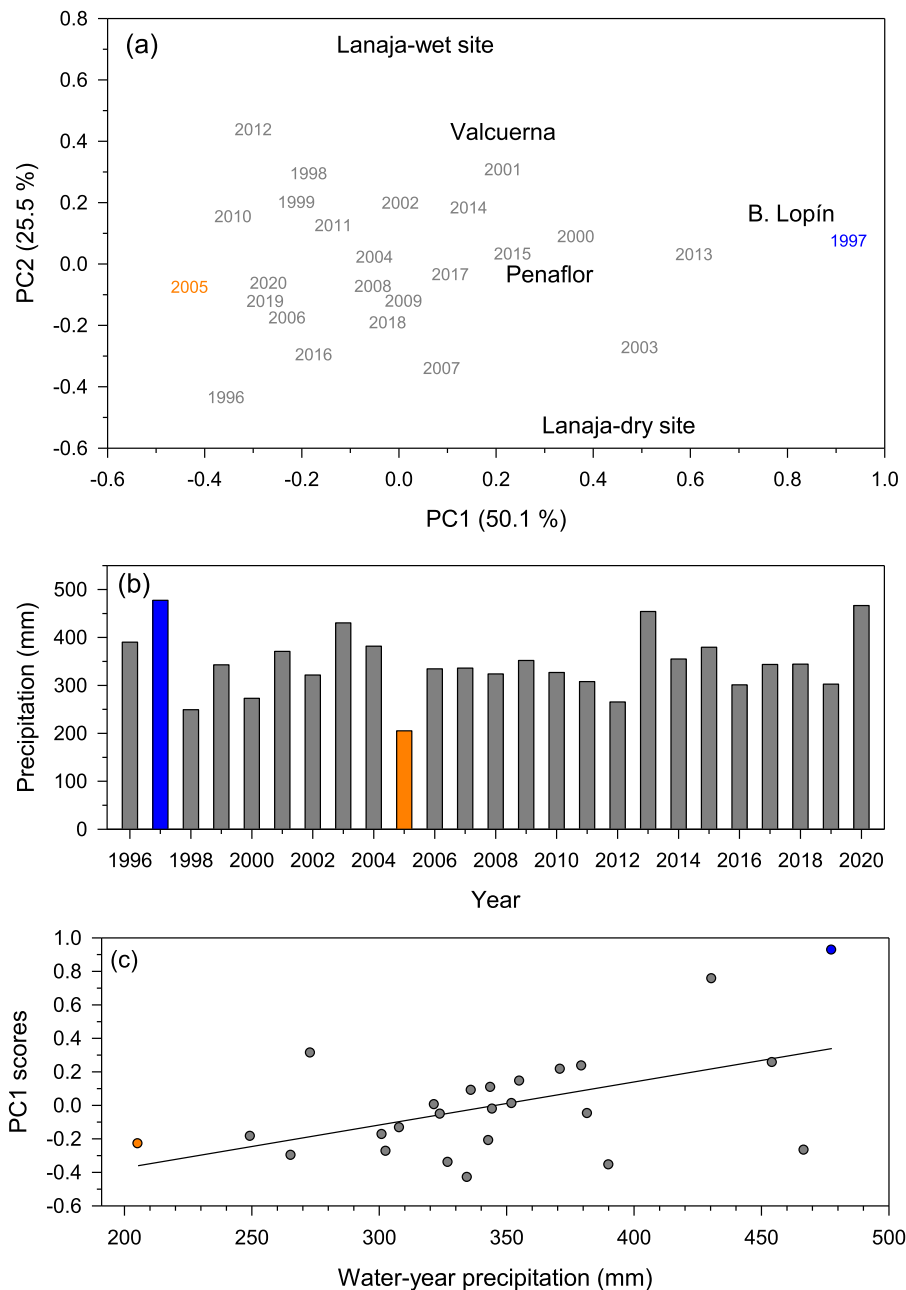
Fig. 2. (a) Biplot showing the sites' loadings (black letters) and years' scores (grey letters) along the first (PC1) and second (PC2) principal components (period 1996–2020). (b) Water year precipitation over the study area. The wet 1997 and dry 2005 years are indicated with blue and orange symbols (a, c) or bars (b), respectively. (c) Positive relationship between the PC1 scores and the regional water-year precipitation.

sites including tree diameter (dbh), tree-ring width and sapwood element concentrations.

To summarize the relationships among site series of growth indices, we calculated a Principal Component Analysis (PCA) on the variance-covariance matrix of residual chronologies considering the best-replicated period (1986–2020). We kept the two first principal components (PC1 and PC2) because they accounted for the most (75 %) of the variability. A PCA biplot showing the sites' loadings and the years' scores was drawn to assess the similarity among sites' growth series and years.

To assess how tamarisk growth and wood anatomy depend on climate conditions, drought stress, and flow, we calculated Pearson correlation coefficients between the site series of growth indices and monthly climate variables (Tx, Tn, P-PET), flow (only in Valcuerna), and SPEI data. In the case of climate and flow data, they were also detrended

using the same spline length as ring-width series again dividing observed by fitted values. Correlations were calculated for the common interval 1986–2020 and considering a temporal window from the previous September to current (growth year) September. A similar analysis was done for earlywood hydraulic diameter in the Valcuerna and Lanaja-dry sites, but in this case no detrending was applied because series were short. In addition, correlations were also calculated for seasonal (prior autumn, son; prior winter, dJF; current spring, MAM; current summer, JJA) climate data calculating mean temperatures and summed water balance.

Statistical analyses were performed using the R statistical software (R Development Core Team, 2023). The dplR package was used to process dendrochronological data including detrending and the calculation of statistics (Bunn, 2008, 2010, Bunn et al., 2023). The vegan package was used to calculate the PCA (Oksanen et al., 2024). The "dcc"
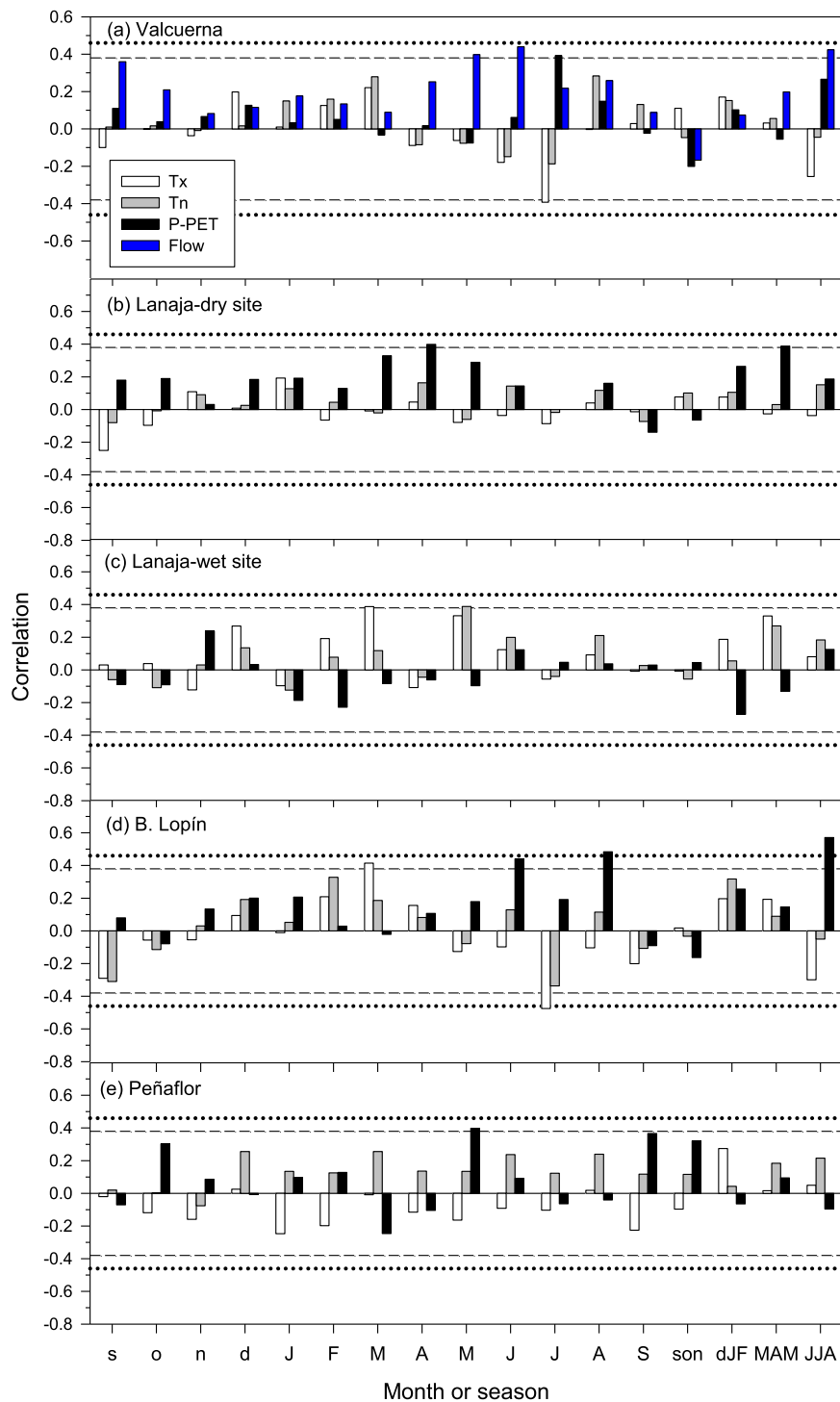
Fig. 3. Relationships (Pearson correlation coefficients) calculated between seasonal and monthly climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; P-PET, climate water balance) or flow and the site series of ring-width indices. Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. Correlations were calculated from September of the previous year (lowercase letters) up to September of the current year (uppercase letters).

function from the treeclim package was used to calculate correlations between climate variables or SPEI and series of ring-width indices (Zang and Biondi, 2015).

3. Results

3.1. Growth patterns

The oldest individuals (62 years old) were sampled at the Lanaja-dry site, where the diameters were the smallest, consistent with the lowest growth rates (ring width, 1.11 mm; Tables 1 and 2, Fig. 1). The highest growth rates corresponded to Peñaflor (2.94 mm). In Peñaflor and
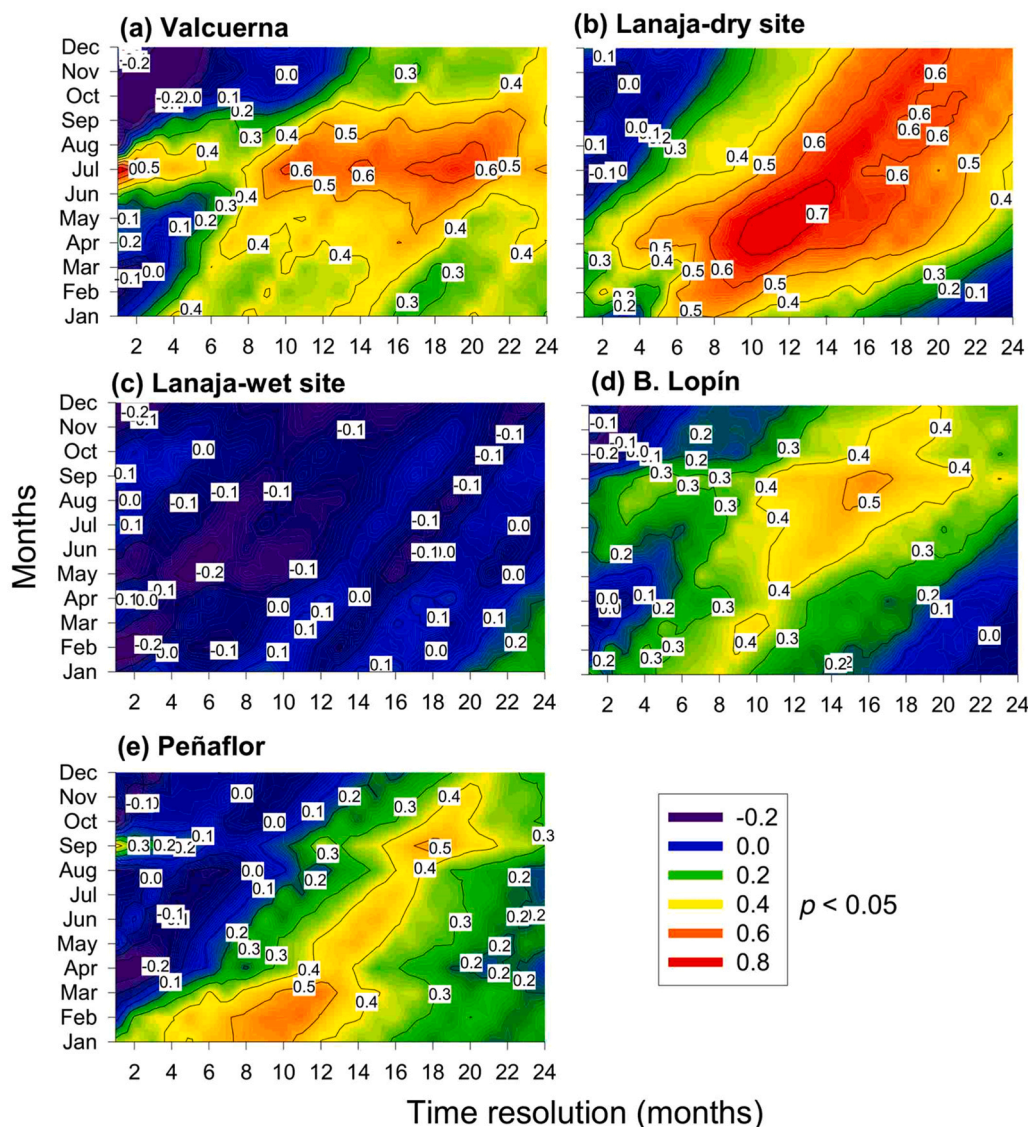
Fig. 4. Relationships (Pearson correlation coefficients) calculated between monthly SPEI data and the site series of ring-width indices. SPEIs were calculated from 1- to 24-month long scales (x axes). Correlation coefficients (colour scale) higher than 0.40 are significant ($p < 0.05$).

Valcuerna tree-ring width was higher in the 1990s than in the 2010s (Fig. 1). Lopín showed a very low AR1, whilst the MS was maximum in the Lanaja-wet site. Regarding relationships among individual series of ring-width indices within each site, the PC1, rbar and EPS showed maximum values in the Lanaja-dry site, suggesting high internal coherence, followed by Valcuerna, whereas the Lanaja-wet site showed the minimum values of these three statistics.

The Lanaja-dry and Peñaflor series of ring-width indices showed significant positive correlations with Lopín series indicating similar year-to-year growth variability (Table S1). This was confirmed by the PCA biplot where these three sites were closely grouped suggesting similar climate-growth relationships (Fig. 2).

3.2. Growth responses to climate and a drought index

The water-year precipitation was positively related to growth indices in the Lanaja-dry ($r = 0.50$, $p = 0.005$), Lopín ($r = 0.64$, $p = 0.0003$), and Peñaflor ($r = 0.39$, $p = 0.04$) sites, but also in the Valcuerna site ($r = 0.40$, $p = 0.03$; Fig. S3). Accordingly, the PC1 scores were positively correlated with water-year precipitation ($r = 0.51$, $p = 0.008$), i.e. the PC1 represented a wet-dry temporal gradient separating very wet (e.g.,

1997) and very dry (e.g., 2005) years (Fig. 2). These extreme years in precipitation terms led to regional and sharp growth increases and reductions in 1997 and 2005, respectively (Fig. 1). The PC2 scores were positively related to March mean maximum temperatures ($r = 0.38$, $p = 0.06$), indicating a higher responsiveness to warm spring conditions. This was evident in Valcuerna, Lanaja-wet and Lopín sites (Fig. 3).

In Valcuerna, growth was improved by warm March and cool-wet July conditions (Fig. 3). High flow levels in May-June and summer were also associated to improved growth in this site. In the Lanaja-dry site, high precipitation in spring (April) enhanced growth, whereas in the Lanaja-wet site high maximum and minimum temperatures in current March and May, respectively, did it. In Lopín warm March conditions, high precipitation in June and August and low maximum temperatures in July increased growth. Lastly, in Peñaflor, wet May conditions were related to high ring-width indices (Fig. 3).

The highest correlation between growth indices and the SPEI ($r = 0.78$) was found for the Lanaja-dry site, specifically considering 12-month May SPEI values (Fig. 4). This was followed by Valcuerna site, where the correlation coefficients peaked at short ($r = 0.77$, 1-month July SPEI) and long temporal scales ($r = 0.66$, 19-month July SPEI). Intermediate responses to drought intensity were found at mid ($r = 0.57$,

Table 3
Earlywood anatomy variables and statistics including vessel area, hydraulic diameter and potential hydraulic conductivity (*Kp*). Values are means ± SE. Different letters indicate significant (*p* < 0.05) differences in tree-ring width among sites according to Mann-Whitney tests.

Site	Vessel area (μm²)	*Dh*, hydraulic diameter (μm)	*Kp* (kg m⁻¹ MPa⁻¹ s⁻¹ 10⁻¹⁰)	PC1 (%)	rbar
Valcuerna	20436 ± 578b	175.3 ± 2.2b	8.3 ± 0.4b	41.4	0.32
Lanaja-dry site	9469 ± 169a	123.1 ± 1.1a	1.4 ± 0.1a	46.1	0.37

11-month February SPEI) to long (*r* = 0.54, 16-month September SPEI) temporal scales in Peñaflor and Lopín, respectively. Finally, no significant correlation was found in the Lanaja-wet site.

3.3. Earlywood anatomy

Both earlywood vessel area, hydraulic diameter and *Kp* were lower in the Lanaja-dry site than in Valcuerna (Table 3). In contrast, the PC1 and rbar values of these anatomical series were higher in the Lanaja-dry site albeit lower than in the case of series of ring-width indices. The mean series of hydraulic diameter of these two sites were not significantly correlated suggesting different responses to climate variability (Fig. S4).

In Valcuerna, a positive climate water balance in the prior November and current March and high flow in the prior December were positively related to earlywood hydraulic diameter (Fig. 5). In Lanaja-dry site, a positive climate water balance in the prior winter, particularly in December, and cool March conditions enhanced earlywood hydraulic diameter.

Overall, wet conditions during the water year improved radial growth of tamarisk in the driest Lanaja-dry site, whilst elevated flow during the water year increased the earlywood hydraulic diameter in the Valcuerna site (Fig. 6).

3.4. Sapwood element concentrations

We found higher sapwood concentrations in trees from the Lanaja-dry site as compared with trees from Valcuerna site in the case of Ca, Cu, K, Mn, Si, S and Ti (Table 4). However, C and N concentrations were significantly higher in Valcuerna than in the Lanaja-dry site.

4. Discussion

The contrasting growth patterns and responses to climate and the SPEI drought index of the compared tamarisk stands can be interpreted by the different habitats where they are found because permanent and temporary streams lead to different strategies of soil water use in the study semi-arid region. As expected, radial growth rates and earlywood vessel areas were lower in the driest Lanaja-dry site, where concentrations of nutrients related to drought and salinity tolerance (Ca, K, Mn) were higher. In contrast, growth rates increased in wetter sites (e.g., Lopín), probably with shallow soil water sources, or in sites located near a permanent stream (Valcuerna) with higher C and N wood concentrations. In the Lanaja-dry site, growth strongly depended on a high long-term (12-month) cumulative water balance, but this was also observed in Valcuerna where both long- and short-term droughts constrained growth. In the other extreme, growth did not respond to the SPEI drought index in the relatively flat Lanaja-wet site indicating a high soil water availability in spring. An analogous finding was observed for earlywood hydraulic diameter which depended on prior autumn-winter
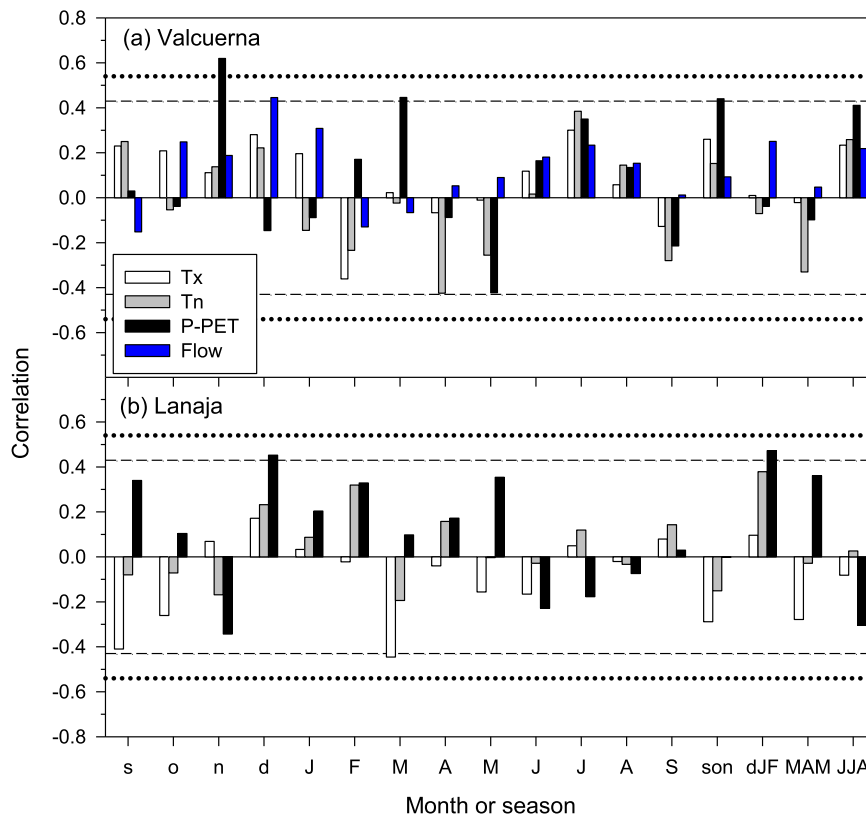
Fig. 5. Relationships (Pearson correlation coefficients) calculated between seasonal and monthly climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; P-PET, climate water balance) or flow and the site series of tamarisk earlywood hydraulic diameter in the (a) Valcuerna and (b) Lanaja-dry sites. Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. Correlations were calculated from September of the previous year (lowercase letters) up to September of the current year (uppercase letters).
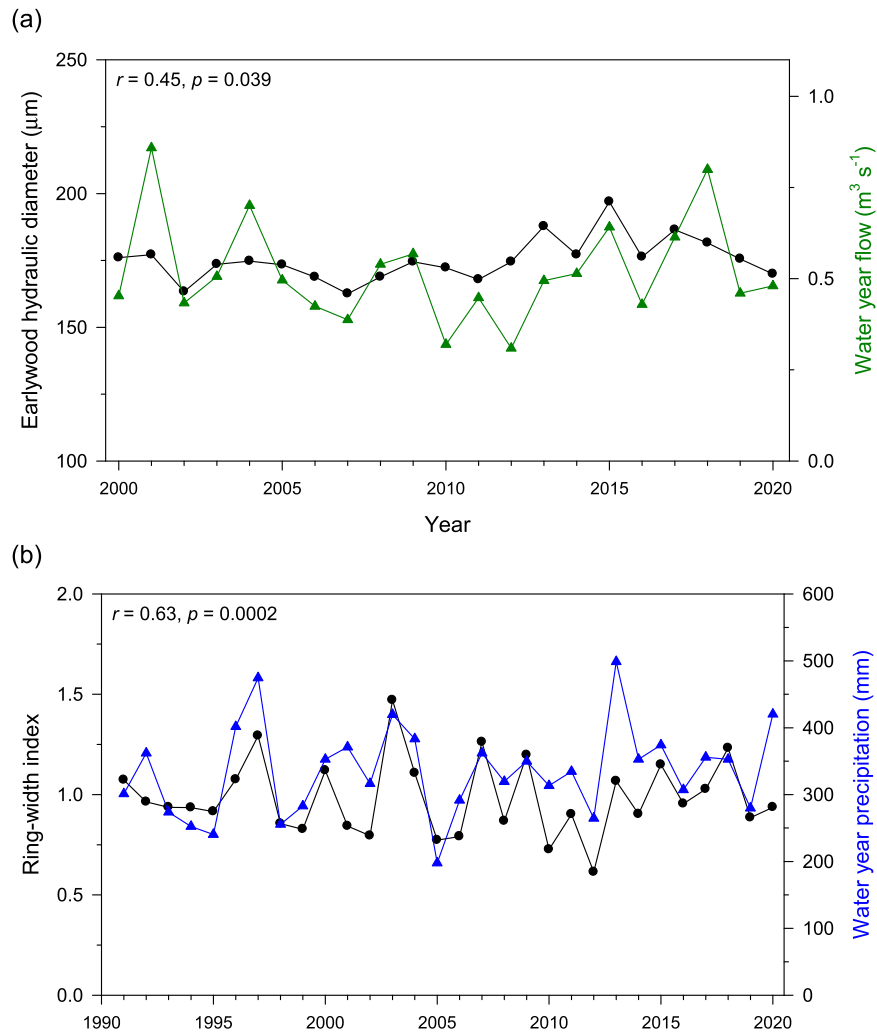
Fig. 6. Positive relationships found between (a) mean monthly flow during the water year (green symbols) and hydraulic diameter (black symbols) in the Valcuerna site, and (b) between water year precipitation (blue symbols) and tamarisk ring-width indices (black symbols) in the Lanaja-dry site. The Pearson coefficients and their significance levels are shown.

precipitation and flow in the Lanaja-dry and Valcuerna sites, respectively.

Few studies have applied dendrochronology to tamarisks due to their lobate stems, multi-stemmed growth form or rotten heartwood (Cooper et al., 2003). This could be the case because some tamarisks do not have recognizable tree-ring boundaries, probably according to the growing habitat, limiting their use in dendrochronology. We combined the study of cores and wood cross-sections to circumvent these problems and avoided sampling unstable terraces because stem burial due to sedimentation leads to sharp growth decreases (Friedman et al., 2005). Previous studies found a positive relationship between precipitation during the growing season and *T. ramosissima* radial growth emphasizing the role played by evaporative water demand when groundwater is deep (Xiao and Xiao, 2007). Others pinpointed the growing season (May–Jully) by intra-annual monitoring of xylem development (Xiao et al., 2014), confirming previous research on tamarisk species from Israel who found tamarisk radial growth started in spring and cambial activity either remained active throughout the year or showed lower activity in summer and winter (Fahn, 1958). In general, drought and a low availability of shallow soil water sources constrained tamarisk growth (Horton et al., 2001, Fang et al., 2021). This concurred with our findings in the Lanaja-dry and Peñaflor sites, where the highest correlations with the SPEI indicate a strong sensitivity to precipitation and a dependence on shallow soil water sources. The availability of soil water

explains the lack of response to the SPEI in the Lanaja-wet site. In Valcuerna and Lopín, trees are located near more lasting or permanent streams with major flows in summer due to irrigation surplus in the case of Valcuerna. This would explain tamarisk growth responsiveness to summer flow. In contrast, tamarisk growth in drier sites (Lanaja-dry site, Peñaflor) with less shallow soil water availability depends on a positive water balance in April-May. In these two sites, the relationships and dominant temporal scales of growth-SPEI associations indicate the aquifer and groundwater recharges during seasons with higher precipitation and low evapotranspiration rates, i.e. from prior autumn-winter to current spring. The inferred maximum growth rates peaked from April to June are coherent with climate-growth relationships and previous studies on wood phenology in Mediterranean tamarisks (Fahn, 1958).

Tamarisk growth depended on long periods (water year) of positive climate water balance whereas the potential hydraulic conductivity (*Kp*) depended on precipitation or flow from prior autumn to early spring, before earlywood formation (Xiao et al., 2014). Maximum transversal conduit diameters of nearly 130 µm were measured in *T. ramosissima*, similar to values presented here, which explains its high transpiration and hydraulic conductivity rates (Rzepecki et al., 2011). The calculated *Kp* values in the Lanaja-dry site were similar to those reported by these authors, but those obtained in Valcuerna were much higher confirming that tamarisks growing near permanent streams show high growth rates.

Table 4

Values of element concentrations in sapwood samples from Valcuerna and Lanaja-dry sites. All element concentrations are given as mg kg^{-1} excepting C, Ca, K, Mg, N, Na, P and S (%). Mean values were compared among sites using Mann-Whitney U tests. Significant U values are shown in bold characters.

Site	Variable	Al	B	C	Ca	Cr	Cu	Fe	K	Li	Mg	Mn	N	Na	Ni	Pb	P	S	Si	Sr	Ti	Zn
Valcuerna	Mean	24.64	8.26	43.47	1.17	3.92	3.80	50.22	0.37	1.26	0.23	21.64	1.49	0.17	7.26	1.33	0.11	1.46	57.21	200.57	1.36	8.00
	SE	4.32	0.80	0.24	0.14	0.64	0.24	5.66	0.03	0.30	0.02	1.14	0.18	0.03	3.18	0.52	0.02	0.09	18.55	20.84	0.35	0.85
Lanaja-dry site	Mean	32.15	7.45	42.05	1.93	7.62	4.84	65.83	0.47	1.07	0.26	26.05	1.07	0.21	4.88	0.87	0.07	2.18	97.78	224.21	3.85	9.64
	SE	4.35	0.31	0.18	0.17	2.14	0.25	8.42	0.03	0.14	0.01	1.22	0.10	0.02	1.22	0.12	0.01	0.17	31.75	27.33	0.99	1.06
	U	36	56	**29**	**23**	38	**23**	36	**28**	53	37	**25**	**28**	43	35	58	47	**25**	**22**	40	**25**	41
	P	0.12	0.82	0.05	0.01	0.15	0.01	0.12	0.03	0.64	0.14	0.02	0.03	0.27	0.11	0.92	0.42	0.02	0.01	0.20	0.02	0.23

The peak in the correlation between June-July SPEI and tamarisk growth in Valcuerna suggest the ability of the species to utilize pulse water from shallow sources when available.

In tamarisk, water and gas exchange depends on deep soil water sources, particularly during dry periods (Cao et al., 2020), because groundwater supplies approximately 84 % of the total transpiration (Wang et al., 2019). These authors calculated that tamarisks mainly consume soil moisture up to a 6-m depth from May to October, which causes the water table to decline and then groundwater recovery occurs in winter. Our results evidence that this period of soil water recharge is critical for earlywood development in tamarisks growing near ephemeral streams. Thus, earlywood conductivity depends on prior water availability rather than on soil salinity because irrigation with saline water did not affect xylem vessel area in *Tamarix africana* (Abou Jaoudé et al. 2012).

We found higher concentrations of some major (Ca, K and Mn) and minor (Cu, Si and Ti) elements in wood from the dry Lanaja-dry site, but lower C and N concentrations than in Valcuerna. Salt tolerance by plants depends on osmotic adjustments, including a high K/Na ratio to maintain an adequate cell turgor or mechanisms to avoid Na toxicity or repair damaged tissues (Shabala and Cuin, 2007). In plants, Ca and K are major osmolytes and Ca supply is linked to transpiration rates (Conn and Gilliham, 2010). The higher concentrations of Ca in wood could reflect a higher drought stress in the tamarisks from the Lanaja-dry site if Ca acted as a major osmoloyte. Analogously, drought-stressed conifers showed high Ca and Mn wood concentrations than heathy conspecifics (Hevia et al., 2019; González de Andrés et al., 2021, 2022). High leaf Mn concentrations have been linked to reduced photosynthesis rates and low growth rates due to metabolic interferences with other nutrients (St Clair et al., 2005).

In the case of Valcuerna, the much higher N wood concentration could come from agricultural sources because croplands in the Valcuerna basin are intensively fertilized and irrigated leading to stream eutrophication. Salt and nitrate leaching are common problems in some of these intensively irrigated and fertilized agricultural areas with saline soils (e.g., Merchán et al., 2015). Therefore, retrospective analyses of tamarisk tree-ring wood could be used in future studies to reconstruct N inputs in agricultural basins such as Valcuerna and to test if they are related to improved growth rates. In less disturbed areas such as the Taklamakan desert (northwestern China), tamarisks showed no N limitation because they developed efficient root systems to uptake enough nutrients from groundwater (Arndt et al., 2004).

Facultative phreatophytes such as tamarisks show a high root plasticity developing an efficient water-use strategy to survive on hyperarid to semiarid sites with different salinity levels (Arndt et al., 2004; Sun et al., 2016). Soil water potential influences the distribution of adventitious roots in tamarisk which show a huge year-to-year variability along the soil profile (Yu et al., 2013). Tamarisks form abundant lateral roots close to the water table exploiting deeper water sources during long dry periods (Xu et al., 2011; Wang et al., 2021). This could explain the different temporal patterns of growth reactions to drought, from responses to long spring droughts in the driest Lanaja-dry site, where precipitation is the main water source, to responses to both short and long summer droughts in the Valcuerna site near the permanent stream. In the last case, the different growth responses could reflect a shift in water sources from flow to precipitation, respectively. For instance, in the hyperarid Namib, *Tamarix usneoides* growing along ephemeral rivers relied on seasonally shifting shallow and deep soil water sources depending on aquifer recharge (Schachtschneider and February, 2010). During a record drought in Kansas (USA), invasive *T. ramosissima* were able to rapidly shift water sources (from groundwater to vadose-zone water) in response to declines in the water table (Nippert et al., 2010). This confirms that tamarisks may use multiple water sources to minimize leaf drought stress. However, in the Taklamakan desert, the growth rate of this species and groundwater depth were uncoupled which may be explained by its high tolerance of lower leaf water potentials through

osmotically active substances (Gries et al., 2003). According to this and other studies (Li et al., 2019), such less strict stomatal regulation and low belowground carbon costs would enhance growth regardless groundwater depth.

To conclude, tamarisk tree rings and earlywood anatomy offer valuable information on the growth responses to changes in precipitation and flow in the case of stands located near ephemeral or permanent streams, respectively. In the case of wood element concentrations, Ca abundance seems to be linked to drought stress whereas high N concentrations probably reflect eutrophication due to agricultural use. These ideas should be further tested in other semi-arid regions with other tamarisk species. In future studies, growth, earlywood anatomy, leaf and wood nutrient data could be compared to spatiotemporal changes in root distribution and changes in flow or groundwater depth. The different patterns in soil water sources of this facultative phreatophyte can be disentangled using wood (C, O) and water (O, H) isotopes, but this information should be linked to changes in radial growth and productivity, particularly during dry periods.

CRediT authorship contribution statement

Cristina Valeriano: Writing – review & editing, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Antonio Gazol:** Writing – review & editing, Visualization, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Michele Colangelo:** Writing – review & editing, Visualization, Supervision, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **J. Julio Camarero:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2024.126234.

References

Abou Jaoudé, R., de Dato, G., De Angelis, P., 2012. Photosynthetic and wood anatomical responses of *Tamarix africana* Poiret to water level reduction after short-term fresh- and saline-water flooding. Ecol. Res. 27, 857–866.

Araya, T., Mlahlwa, A.V., Abd Elbasit, M.A.M., Newete, S.W., 2022. The impact of *Tamarix* invasion on the soil physicochemical properties. Sci. Rep. 12, 5750. https://doi.org/10.1038/s41598-022-09797-3.

Arndt, S.K., Kahmen, A., Arampatsis, C., Popp, M., Adams, M., 2004. Nitrogen fixation and metabolism by groundwater-dependent perennial plants in a hyperarid desert. Oecologia 141, 385–394.

Baum, B.R., 1978. The Genus *Tamarix*. The Israel Academy of Sciences and Humanities. Jerusalem, Israel.

Berga Celma, A., 1993. Relaciones clima-agua-suelo-subsuelo en Monegros II. PhD Thesis, Univ. Lleida, Lleida, Spain.

Braun-Blanquet, J., Bolós, A., 1957. Les groupements végétaux du bassin moyen de l'Ebre et leur dynamisme. An. Est. Exp. Aula Dei 5, 1–266.

Briffa, K.R., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Kluwer, Dordrecht, pp. 137–152.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258.

Bunn, A.G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2023. dplR: Dendrochronology program library in R. R. Package Version, 1.7.6, https://CRAN.R-project.org/package=dplR.

Busch, D.E., Smith, S.D., 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwest U.S. Ecol. Monogr. 65, 347–370.

Busch, D.E., Ingraham, N.L., Smith, S.D., 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. Ecol. Appl. 2, 450–459. https://doi.org/10.2307/1941880.

Camarero, J.J., Colangelo, M., Rodríguez-González, P.M., 2023. Tree growth, wood anatomy and carbon and oxygen isotopes responses to drought in Mediterranean riparian forests. . Ecol. Manag. 529, 120710.

Cao, Q., Yang, B., Li, J., Wang, R., Liu, T., Xiao, H., 2020. Characteristics of soil water and salt associated with *Tamarix ramosissima* communities during normal and dry periods in a semi-arid saline environment. Catena 93, 104661.

Conn, S.J., Gilliham, M., 2010. Comparative physiology of elemental distributions in plants. Ann. Bot. 105, 1081–1102.

Cooper, D.J., Andersen, D.C., Chimner, R.A., 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. J. Ecol. 91, 182–196.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An ensemble version of the E-OBS temperature and precipitation data sets. J. Geophys. Res. Atm. 123, 9391–9409. https://doi.org/10.1029/2017JD028200.

Devitt, D.A., Piorkowski, J.M., Smith, S.D., Cleverly, J.R., Sala, A., 1997. Plant water relations of *Tamarix ramosissima* in response to the imposition and alleviation of soil moisture stress. J. Arid Environ. 36, 527–540.

Di Tomaso, J.M., 1998. Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. Weed Technol. 12, 326–336.

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. Oecologia 88, 430–434.

Fahn, A., 1958. Xylem structure and annual rhythm of development in trees and shrubs of the desert. 1. Tamarix aphylla T. Jordan. Var. negevensis T. Gall. Var. maris-Mortu. Trop. Woods 109, 81–94.

Fang, O.-Y., Zhang, Y., Zhang, Q., Jia, H.-F., 2021. Growth responses of *Tamarix austromongolica* to extreme drought and flood in the upper Yellow River basin. Chin. J. Plant Ecol. 45, 641–649. https://doi.org/10.17521/cjpe.2021.0020.

Fernández-González, F., Molina, A., Loidi, J., 1990. Los tarayales de la depresión del Ebro. Acta Bot. Malacit 15, 311–322.

Friedman, J.M., Vincent, K.R., Shafroth, P.B., 2005. Dating floodplain sediments using tree-ring response to burial. Earth Surf. Proc. Landf. 30, 1077–1091.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London.

Gärtner, H., Nievergelt, D., 2010. The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia 28, 85–92. https://doi.org/10.1016/j.dendro.2009.09.002.

Glenn, E., Tanner, R., Mendez, S., Kehret, T., Moore, D., Garcia, J., Valdes, C., 1998. Growth rates, salt tolerance characteristics of native and invasive riparian plants from the delta of Colorado River, Mexico. J. Arid Environ. 40, 271–294.

González de Andrés, E., Suárez, M.L., Querejeta, J.I., Camarero, J.J., 2021. Chronically low nutrient concentrations in tree rings are linked to greater tree vulnerability to drought in *Nothofagus dombeyi*. Forests 12, 1180. https://doi.org/10.3390/f12091180.

González de Andrés, E., Gazol, A., Querejeta, J.I., Igual, J.M., Colangelo, M., Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., 2022. The role of nutritional impairment in drought-induced dieback of Pyrenean silver fir forests. Glob. Ch. Biol. 14, 4439–4458.

Gries, D., Zeng, F., Foetzki, A., Arndt, S.K., Bruelheide, H., Thomas, F.M., Zhang, X., Runge, M., 2003. Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table. Plant, Cell Env. 26, 725–736.

Hargreaves, G.H., Samani, Z., 1985. Reference crop evapotranspiration from temperature. Appl. Eng. Agric. 1, 96–99. https://doi.org/10.13031/2013.26773.

Hevia, A., Sánchez-Salguero, R., Camarero, J.J., Querejeta, J.I., Sangüesa-Barreda, G., Gazol, A., 2019. Long-term nutrient imbalances linked to drought-triggered forest dieback. Sci. Tot. Env. 690, 1254–1267. https://doi.org/10.1016/j.scitotenv.2019.06.515.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull. 43, 69–78.

Horton, J.L., Kolb, T.E., Hart, S.C., 2001. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. Plant, Cell Environ. 24, 293–304.

Horton, J.L., Hart, S.C., Kolb, T.E., 2003. Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. Isot. Environ. Health Stud. 39, 69–82. https://doi.org/10.1080/1025601031000096772.

Larsson L.A., Larsson P.O. 2022. CDendro and CooRecorder (v. 9.8.1). Cybis Elektronik and Data AB. Saltsjöbaden, Sweden.

Li, E., Tong, Y., Huang, Y., Li, X., Wang, P., Chen, H., Yang, C., 2019. Responses of two desert riparian species to fluctuating groundwater depths in hyperarid areas of Northwest China. Ecohydrology 12, e2078.

Merchán, J., Causapé, J., Abrahão, R., García-Garizábal, I., 2015. Assessment of a newly implemented irrigated area (Lerma Basin, Spain) over a 10-year period. II: salts and nitrate exported. Agric. Water Manag. 158, 288–296.

Moreno-Gutiérrez, C., Dawson, T.E., Nicolas, E., Querejeta, J.I., 2012. Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. N. Phytol. 196, 489–496. https://doi.org/10.1111/j.1469-8137.2012.04276.x.

Newete, S.W., Allem, S.M., Venter, N., Byrne, M.J., 2019. *Tamarix* efficiency in salt excretion and physiological tolerance to salt-induced stress in South Africa. Int. J. Phytorem. 22, 3–9.

Newete, S.W., Abd Elbasit, M.A.M., Araya, T., 2020. Soil salinity and moisture content under non-native *Tamarix* species. Int. J. Phytorem. 22, 931–938. https://doi.org/10.1080/15226514.2020.1774503.

Nippert, J.B., Butler, J.J., Kluitenberg, G.J., Whittemore, D.O., Arnold, D., Spal, S.E., Ward, J.K., 2010. Patterns of *Tamarix* water use during a record drought. Oecologia 162, 283–292. https://doi.org/10.1007/s00442-009-1455-1.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., et al., 2024. vegan: community ecology package. R. Package Version 2, 6-5, https://github.com/vegandevs/vegan.

Pedrocchi C. 2000. Historia Natural de Los Monegros. Instituto de Estudios de Los Monegros, Grañén, Huesca, Spain.

Querejeta, J.I., Ren, W., Prieto, I., 2021. Vertical decoupling of soil nutrients and water under climate warming reduces plant cumulative nutrient uptake, water-use efficiency and productivity. New Phytol. 230, 1378–1393.

R Development Core Team. 2023. R: A language and environment for statistical computing. R version 4.2.3, R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rzepecki, A., Zeng, F., Thomas, F.M., 2011. Xylem anatomy and hydraulic conductivity of three co-occurring desert phreatophytes. J. Arid Environ. 75, 338–345.

Sala, A., Smith, S.D., Devitt, D.A., 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. Ecol. Appl. 6, 888–898.

Schachtschneider, K., February, E.C., 2010. The relationship between fog, floods, groundwater and tree growth along the lower Kuiseb River in the hyperarid Namib. J. Arid Environ. 74, 1632–1637.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ, 25 years of image analysis. Nat. Methods 9, 671–675.

Shabala, S., Cuin, T.A., 2007. Potassium transport and plant salt tolerance. Physiol. Plant. 133, 651–669.

Silvertown, J., Araya, Y., Gowing, D., 2015. Hydrological niches in terrestrial plant communities: a review. J. Ecol. 103, 93–108.

Smith, S.D., Devitt, D.A., Sala, A., Cleverly, J.A., Busch, D.E., 1998. Water relations of riparian plants from warm desert regions. Wetlands 18, 687–696.

Sookbirsingh, R., Karina, C., Thomas, E.G., Rusell, R.C., 2010. Salt separation processes in the saltcedar *Tamarix ramosissima* (Lebed.). Comm. Soil Sci. Plant. Anal. 41, 1271–1281.

Sperry, J.S., Nichols, K.L., Sullivan JEM, Eastlack, S.E., 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75, 1736–1752.

St. Clair, S.B., Carlson, J.E., Lynch, J.P., 2005. Evidence for oxidative stress in sugar maple stands growing on acidic, nutrient imbalanced forest soils. Oecologia 145, 258–269. https://doi.org/10.1007/s00442-005-0121-5.

Sun, Z., Long, X., Ma, R., 2016. Water uptake by saltcedar (*Tamarix ramosissima*) in a desert riparian forest: responses to intra-annual water table fluctuation. Hydrol. Proc. 30, 1388–1402.

Thomas, F.M., 2014. Ecology of phreatophytes. Prog. Bot. 335–375. https://doi.org/10.1007/978-3-642-38797-5_11.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119, 345–360.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718.

Villar, J.L., Alonso, M.Á., Crespo, M.B., 2022. Synopsis of the genus *Tamarix* (Tamaricaceae) in the Iberian Peninsula and Balearic Islands. Anales del Jardín Botánico de Madrid 79, e132. https://doi.org/10.3989/ajbm.2639.

Wang, T.-Y., Yu, J.J., Wang, P., Min, L., Pozdniakov, S.P., Yuan, G.-F., 2019. Estimating groundwater evapotranspiration by phreatophytes using combined water level and soil moisture observations. Ecohydrology 12, e2092.

Wang, T.-Y., Wang, P., Wang, Z.-L., Niu, G.-Y., Yu, J.-J., Ma, N., Wu, Z.-N., Pozdniakov, S.P., Yan, D.-H., 2021. Drought adaptability of phreatophytes: insight from vertical root distribution in drylands of China. J. Plant Ecol. 14, 1128–1142. https://doi.org/10.1093/jpe/rtab059.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201–213.

Willms, J., Rood, S.R., Willms, W., Tyree, M., 1998. Branch growth of riparian cottonwoods: a hydrologically sensitive dendrochronological tool. Trees Struct. Funct. 12, 215–223. https://doi.org/10.1007/s004680050143.

Xiao, S.C., Xiao, H.L., 2007. Radial growth of *Tamarix ramosissima* responds to changes in the water regime in an extremely arid region of northwestern China. Environ. Geol. 53, 543–551. https://doi.org/10.1007/s00254-007-0666-1.

Xiao, S.C., Xiao, H.L., Peng, X.M., Tian, Q.Y., 2014. Intra-annual stem diameter growth of *Tamarix ramosissima* and association with hydroclimatic factors in the lower reaches of China's Heihe River. J. Arid Land 6, 498–510.

Xu, G.Q., Li, Y., Xu, H., 2011. Seasonal variation in plant hydraulic traits of two co-occurring desert shrubs, *Tamarix ramosissima* and *Haloxylon ammodendron*, with different rooting patterns. Ecol. Res. 26, 1071–1080.

Yin, C.H., Feng, G.U., Zhang, F., Tian, C.Y., Tang, C., 2010. Enrichment of soil fertility and salinity by tamarisk in saline soils on the northern edge of the Taklamakan Desert. Agric. Water Manag. 9, 1978–1986.

Yu, T., Feng, Q., Si, J., Xi, H., Li, W., 2013. Patterns, magnitude, and controlling factors of hydraulic redistribution of soil water by *Tamarix ramosissima* roots. J. Arid Land 5, 396–407. https://doi.org/10.1007/s40333-013-0173-z.

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436.

Zepner, L., Karrasch, P., Wiemann, F., Bernard, L., 2021. ClimateCharts.net – an interactive climate analysis web platform. Int. J. Digit. Earth. 14, 338–356.

Zhang, L.H., Chen, P.H., Li, J., Chen, X.B., Feng, Y., 2016. Distribution of soil salt ions around *Tamarix chinensis* individuals in the Yellow River Delta. Acta Ecol. Sin. 36, 5741–5749.

Zohary, M., 1987. *Tamarix* L. In: Zohary, M. (Ed.), Flora palaestina 2. Academy of Sciences and Humanities. Jerusalem, Israel, pp. 350–362.