



Dendrochronological assessment of drought resilience in Mediterranean shrub species near their xeric limits in Spain

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ARTICLE INFO

Keywords:

Berberis vulgaris
Dendroecology
Mediterranean scrubland
Retama sphaerocarpa
Rhamnus species

ABSTRACT

Climate warming, drought stress and aridification impact shrub radial growth in drylands, but our knowledge on climate-growth relationships of these species is limited. To fill this research gap, we studied the age, growth patterns and year-to-year variability of five shrub species (*Rhamnus alaternus*, *Rhamnus lycioides*, *Rhamnus saxatilis*, *Berberis vulgaris*, and *Retama sphaerocarpa*) under semi-arid Mediterranean conditions in nine sites, located near the xeric distribution limits of the study species in Spain. Shrubs showed short (*R. sphaerocarpa* and *B. vulgaris*, 14–20 years) to intermediate lifespans (*Rhamnus* species, 25–46 years), albeit a *R. lycioides* individual reached an age of 144 years. Accordingly, ring-widths varied from 2.02 mm in *R. sphaerocarpa* to 0.40 mm in *R. lycioides*. Both *R. alaternus* and *R. lycioides* showed negative growth-lifespan trade-offs. The ring-width series showed common growth variability between coexisting species (*R. alaternus* and *R. lycioides*) and also between sites for the same species (*R. sphaerocarpa*, *B. vulgaris*). Growth was constrained by elevated temperatures in early spring and summer, and enhanced by wet winter-to-spring conditions. A negative water balance from the previous October up to July limited growth. Growth-drought correlations peaked in the most arid site. Resilience indices varied between species and years. In general, shrubs showed good post-drought recovery. Our findings indicate favorable prospects for the study shrubs under more arid climate scenarios.

1. Introduction

Climate warming and associated aridification are negatively impacting forests and even scrublands under semi-arid climate conditions leading to severe dieback and mortality events (Liu et al., 2013; Xu et al., 2017; Camarero et al., 2020; Kannenberg et al., 2021). This is the case of Mediterranean forests and scrublands, which are considered particularly vulnerable to water shortage, warmer conditions and increased evaporative demand (Camarero et al., 2015; Gazol et al., 2017; Férriz et al., 2021). However, different successional dynamics have been observed in these drought-prone regions (Doblas-Miranda et al., 2017). On one hand, drought-induced tree mortality has triggered shifts from forests to scrublands dominated by drought-tolerant shrub species (Batllori et al., 2020). On the other hand, shrub encroachment linked to the cessation of livestock grazing is occurring in many Mediterranean areas despite ongoing aridification (Buitenwerf et al., 2018).

The different scrubland dynamics in semi-arid Mediterranean regions are mediated by the contrasting responses of shrub radial growth to climate conditions, particularly drought stress (Gazol and Camarero, 2012; Camarero et al., 2021; Gazol et al., 2025). However, we still lack quantitative characterizations of climate-growth relationships in most shrub species from drylands (but see Oladi et al., 2017; Melián et al., 2024). In addition, post-drought growth recovery has been assessed only in a few shrub species of semi-arid regions (Gazol et al., 2017; Tamudo et al., 2024), although resilience indices allow measuring such recovery capacity (e.g., Gao et al., 2025). Moreover, growth-lifespan trade-offs, characterized by higher (lower) growth rates for individuals with shorter (longer) lifespans, have been widely documented for trees (Brienen et al., 2020; Liu et al., 2025). However, they have not been investigated in shrubs despite these trade-offs could also explain the different performance of shrub species in drought-prone regions. For instance, slow-growing shrub species with lower vulnerability to

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<https://doi.org/10.1016/j.dendro.2026.126503>

Received 13 December 2025; Received in revised form 8 February 2026; Accepted 10 March 2026

Available online 11 March 2026

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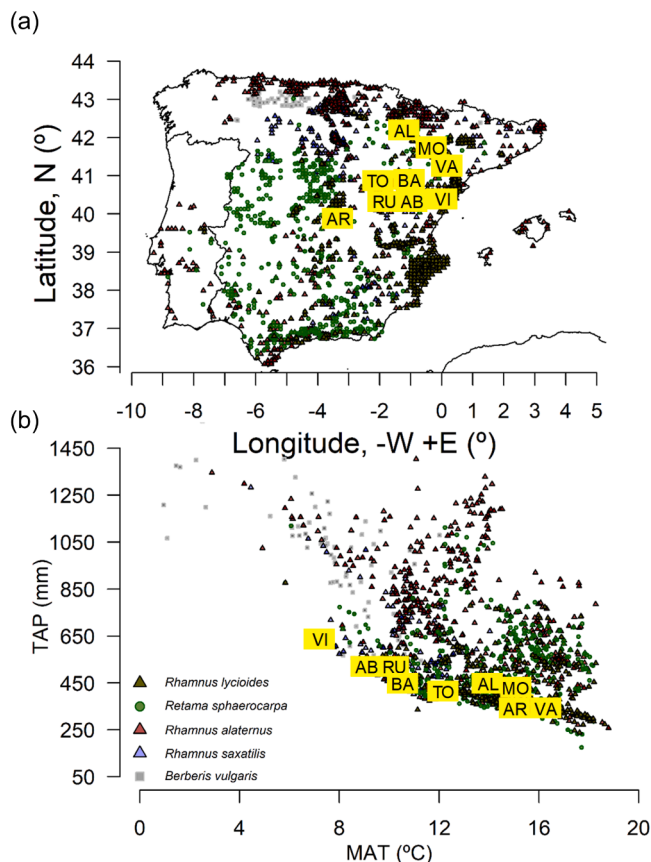


Fig. 1. (a) Distribution of the five studied shrub species and approximate location of sites (yellow labels) sampled in Spain. (b) Distribution of the study species and sites across bioclimatic gradients (MAT, mean annual temperature; TAP, total annual precipitation). Note that most sites are near the xeric distribution limits of the study species.

cavitation than trees (Maherali et al., 2004), long lifespan, dense wood and a high capacity to recover after droughts could better tolerate water deficit and become more dominant (Götmark et al., 2016). To address these issues, the radial growth patterns and variability of five shrub species (*Rhamnus alaternus*, *Rhamnus lycioides*, *Rhamnus saxatilis*, *Berberis vulgaris*, and *Retama sphaerocarpa*) showing different life habits and wood types and occurring in semi-arid Mediterranean sites were investigated by using dendrochronological methods (Fritts, 1976).

The general objective of this study is to search for drought-resilient shrub species which could be better adapted to tolerate warmer and more arid conditions in the future. The specific objectives of the study are: (i) to quantify age, radial growth rates and common year-to-year growth variability in the five studied shrub species, (ii) to assess climate-growth relationships focusing on drought impacts, and (iii) to calculate resilience indices during different droughts. We expect that the

shrub species from the most arid sites will show lower growth rates, higher responsiveness to climate and resilience. We also expect that shrub species will respond to water availability during the previous autumn and winter because these are the seasons when soil recharge occurs in the study sites (Pasho et al., 2012), and because shrubs usually show an earlier radial growth phenology and use upper soil-water pools than coexisting trees (Lipshitz and Lev-Yadun, 1986; Camarero et al., 2013; Gazol and Camarero, 2012; Moreno-Gutiérrez et al., 2012; Illuminati et al., 2022; Muñoz-Gálvez et al., 2025).

2. Materials and methods

2.1. Study sites and species

Sampled sites were located in north-eastern and central Spain (longitude -3.63° W– 0.09° E; latitude 40.01° – 41.82° N, elevation range 260–1702 m a.s.l.), on relatively undisturbed sites with basic soils. The selected sites were located near the xeric distribution limits of the study species (Fig. 1). We selected five shrub species native to the western Mediterranean Basin and showing contrasting bioclimatic conditions (Table 1). We also considered species with different leaf phenology and wood type, two traits which can be related to drought tolerance (e.g., Serra-Maluquer et al., 2022).

First, we sampled two semi-arid steppe sites (Aranjuez, Monegros-Lanaja) of *Retama sphaerocarpa* (L.) Boiss (Fabaceae), a 2–4 m tall, pioneer shrub forming diffuse-porous wood. This species has developed ephemeral leaves and performs most of its photosynthesis through its green stems (cladodes). Second, three *Rhamnus* species (Rhamnaceae) were sampled because they showed different leaf habit and two of them coexisted. *Rhamnus alaternus* L. is an evergreen shrub species, 1–5 m tall, forming diffuse to semi-ring-porous wood and located in Mediterranean scrublands. *Rhamnus lycioides* L. is a deciduous or semi-deciduous shrub species, 1–4 m tall, forming diffuse to semi-ring-porous wood and co-occurring with *R. alaternus*. These two *Rhamnus* species were sampled in two semi-arid sites dominated by scrublands and open woodlands (Alcubierre, Valcuerna). In addition, *Rhamnus saxatilis* Jacq., a deciduous shrub forming diffuse to semi-ring-porous wood was sampled in one location characterized by open woodlands (Bañón), under more continental conditions. Third, *Berberis vulgaris* (Berberidaceae), a small (usually 0.5–2.0 m tall) deciduous shrub forming semi-ring porous, was sampled in four locations under continental conditions and corresponding to open holly oak (*Quercus ilex* L.) and Scots pine (*Pinus sylvestris* L.) woodlands and forest edges (Allepuz, Rubielos de la Cérda, Torrijo del Campo, and Villarroja de los Pinares). Comparatively, the *R. sphaerocarpa* and *R. alaternus*–*R. lycioides* individuals were sampled in the most arid sites, whereas the *B. vulgaris* individuals were sampled in the coldest sites (Table 1, Fig. 1).

2.2. Climate data

To assess the geographical and climate distribution of the study species across the Iberian Peninsula we checked the ANTHOS

Table 1

Geographic and climatic characteristics of the study sites and shrub species. Abbreviations of climate variables: MAT, mean annual temperature; TAP, total annual precipitation; AI, aridity index.

Site (code)	Species (code)	Latitude (°N)	Longitude (°-W, +E)	Elevation (m a.s.l.)	MAT (°C)	TAP (mm)	AI
Alcubierre (AL)	<i>R. alaternus</i> (Ra), <i>R. lycioides</i> (Rl)	41.818	-0.507	599	13.8	457	0.290
Valcuerna (VA)	<i>R. alaternus</i> (Ra), <i>R. lycioides</i> (Rl)	41.426	0.088	260	15.6	377	0.232
Bañón (BA)	<i>R. saxatilis</i> (Rs)	40.836	-1.190	1183	10.6	465	0.357
Allepuz (AB)	<i>B. vulgaris</i> (Bv)	40.500	-0.748	1348	9.1	521	0.361
Rubielos de la Cérda (RU)		40.736	-1.218	1381	9.7	512	0.363
Torrijo del Campo (TO)		40.825	-1.394	996	11.7	431	0.333
Villarroja de los Pinares (VI)		40.507	-0.617	1702	7.1	641	0.409
Monegros-Lanaja (MO)	<i>R. sphaerocarpa</i> (Rp)	41.738	-0.340	414	14.6	436	0.273
Aranjuez (AR)		40.008	-3.627	523	15.0	383	0.167

Information System (available at www.anthos.es), which contains presence data on vascular plants provided by the Real Jardín Botánico of the Spanish National Research Council (CSIC). Then, to define the species' bioclimatic space, we used 1-km gridded climate data from the WorldClim database (Fick and Hijmans, 2017) for those locations where any of the study species occurred. Mean annual temperature and total annual precipitation were obtained for those locations and for the period 1970–2000.

Site aridity was determined using the annual Aridity Index (AI), gridded at a 30 arc-seconds spatial resolution, considering the period 1980–2023 (Zomer et al., 2022). The AI is defined as the ratio between precipitation and potential evapotranspiration, with $0.50 \geq AI > 0.20$ values corresponding to semi-arid climate conditions.

To calculate climate-growth relationships by avoiding problems with gaps or heterogeneous data detected in local climate series, we used the 0.1°-gridded EOBS climate dataset (ver. 31.0e; Cornes et al., 2018). We obtained monthly data of mean maximum (Tmax) and minimum (Tmin) temperatures and summed precipitation (Prec) for the period 1980–2023. To assess drought severity and duration, we used monthly and weekly, 1-km gridded data of the Standardized Precipitation Evapotranspiration Index (SPEI), available at the webpage <http://monitordesequia.csic.es/>. We considered again the period 1980–2023. The SPEI is a multi-scalar drought index based on cumulative climate water balances which depend on temperature and precipitation (Vicente-Serrano et al., 2010, 2017). We considered 1- to 24-month-long SPEI temporal scales in further analyses.

2.3. Assessing intra-annual growth

To better understand how climate drives growth, we monitored intra-annual growth rates of the widely distributed *R. alaternus* (Fig. 1) in the Alcubierre study site, which represented average climate conditions of the study region (Table 1). Five mature individuals of similar basal diameter (10–15 cm) and height (1.7–2.0 m) were selected and two shoots per individual were tagged in the sunny, south-oriented side of their upper crowns. Then, the longitudinal growth was measured monthly from November 2019 to July 2021. We considered 2020 (total annual precipitation of 409 mm) and 2021 (total annual precipitation of 297 mm) as average (“normal”) and “dry” years, respectively. We also installed manual point dendrometers (Agricultural Electronics Corp., Tucson, USA) in the major stem of each individual at 1.0 m after carefully removing dead bark and recorded monthly radial increments during the same period.

2.4. Ring widths: growth-lifespan trade-off, climate-growth correlations, and resilience

In each site, from 14 to 22 mature individuals of each species were sampled across a ca. 1-ha-large area as a function of species' abundance. Basal cross-sections were taken with hand or machine saws. These samples were air dried and carefully sanded with sandpaper of different grits until annual rings were clearly distinguishable. The year of formation was assigned to each annual ring through visual cross-dating of the samples under the stereomicroscope (Fritts, 1976). Then, samples were scanned with 1200 dpi resolution (Epson Expression 10000 XL, Seiko, Japan). Ring widths were measured with a 0.01 mm resolution along two opposite radii of each cross-section using the CDendro-CooRecorder software (Maxwell and Larsson, 2021). The visual cross-dating was checked using the COFECHA software, which calculates moving correlations between individual ring-width series and the mean site series (Holmes, 1983).

Age was estimated by counting the number of annual rings from the bark to the pith. To assess the relationships between lifespan and growth rate, early growth rate was calculated as the mean ring width over the first 10 years (Brienen et al., 2020; Liu et al., 2025). This was only done for the two shrub species (*R. alaternus*, *R. lycioides*) showing a wide

enough range of ages (Fig. S1).

To assess climate-growth relationships, ring-width series were detrended by fitting selected cubic smoothing splines with a length of 0.67 of the series and a 0.5 response cut-off (Fritts, 1976). Then, ring widths were divided by fitted values to obtain series of ring-width indices (RWIs), which were subjected to pre-whitening to remove temporal autocorrelation. The individual series of indices were averaged using bi-weight robust means to build mean series of growth indices (chronology) for each species within each site. To characterize the ring-width series, we calculated the mean ring width and first-order autocorrelation (AC1) of ring-width series, and the mean correlation (Rbar) between individual RWIs of the same species in each site (Briffa and Jones, 1990).

To evaluate post-drought recovery, the resilience indices proposed by Lloret et al. (2011) were calculated. This was done for selected drought years (2005, 2012 and 2022), for the common period (2000–2023) and corresponding to 12-month September SPEI values lower than -1.5 (Fig. S2). The resilience indices were calculated on standardized RWIs, prior to removing first-order autocorrelation, and considering 3-year periods before and after the selected drought years. The calculated resilience indices were: (1) resistance (Rt), the ratio between growth indices during the drought year (D) and the previous 3-year mean (μ_{t-3}); (2) recovery (Rc), the ratio between the following 3-year mean (μ_{t+3}) growth indices and that of the drought year; and (3) Rs, resilience, the ratio between post-drought and pre-drought 3-year means of growth indices. Therefore, indices were computed as:

$$R_t = D / \mu_{t-3} \quad (1)$$

$$R_c = \mu_{t+3} / D \quad (2)$$

$$R_s = \mu_{t+3} / \mu_{t-3} = R_t \times R_c \quad (3)$$

The R_t and R_c indices describe, respectively, the ability to withstand the drought impacts and to recover. Values of R_t or $R_c \geq 1$ indicate good performance, while R_t or $R_c < 1$ reflect poor performance relative to baseline conditions (pre-drought for R_t , and drought for R_c).

2.5. Statistical analyses

In sites where two species co-occur or in those species sampled in several sites, the age distributions were compared using χ^2 tests after applying Yates's correction. To compare resilience indices between sites, species or years we used Mann-Whitney U tests. ANCOVAs were used to compare slopes between sites or periods of age-growth rate and SPEI-growth linear regressions, respectively.

To summarize the similarity in growth variability between species and sites, Pearson correlations were calculated between the series of ring-width indices, and a Principal Component Analysis (PCA) was calculated on the variance-covariance matrix of these series. Both analyses were done for the common period 2000–2023. The first four principal components (PC1, PC2, PC3 and PC4) were kept because each one accounted for more than 5% of the common variability.

Pearson correlations between monthly climate variables (Tmax, Tmin, Prec) and series of ring-width indices were calculated from the previous September to the current (year of growth) September. Correlations were calculated for the best-replicated period (2000–2023) and the number of significant ($p < 0.05$) correlations were counted to summarize the results. In the exceptional case of long ring-width series (*R. lycioides* in the Valcuerna site, VA), running correlations between selected climate variables and the ring-width series were calculated considering 20-year moving intervals. Analyses were performed in the R environment for statistical computing (R Core Team, 2024) and also using the PAST software ver. 5.2 (Hammer et al., 2001). The package dplR (Bunn, 2010; Bunn et al., 2025) was used to detrend and analyze ring-width series. WorldClim climate data (mean annual temperature, total annual precipitation) were downloaded and plotted using the

Table 2
Statistics of the ring-width series measured for the five study shrub species. Sites' and species' codes are as in Table 1. Abbreviations: AC1, first-order autocorrelation of ring-width data; Rbar, mean correlation between indexed ring-width series. Values are means ± SD.

Site	Species	No. individuals (No. radii)	Timespan	Age (years)	Ring width (mm)	AC1	Rbar
MO	Rp	22 (42)	2001 – 2021	14 ± 2	2.02 ± 0.56	0.13 ± 0.37	0.38 ± 0.30
AR	Rp	18 (34)	1991 – 2024	15 ± 7	1.05 ± 0.36	0.06 ± 0.35	0.43 ± 0.32
AL	Ra	21 (43)	1969 – 2023	31 ± 13	0.65 ± 0.22	0.17 ± 0.22	0.31 ± 0.19
AL	Rl	18 (35)	1944 – 2023	39 ± 20	0.60 ± 0.32	0.26 ± 0.24	0.29 ± 0.19
VA	Ra	17 (34)	1979 – 2023	25 ± 6	0.76 ± 0.29	0.13 ± 0.24	0.33 ± 0.28
VA	Rl	24 (47)	1882 – 2023	46 ± 35	0.40 ± 0.14	0.24 ± 0.24	0.32 ± 0.18
BA	Rs	14 (28)	1974 – 2023	37 ± 11	0.68 ± 0.18	0.34 ± 0.26	0.28 ± 0.26
AB	Bv	15 (28)	2002 – 2024	15 ± 4	0.95 ± 0.29	0.24 ± 0.26	0.42 ± 0.24
RU	Bv	14 (26)	2003 – 2024	15 ± 3	0.54 ± 0.14	0.23 ± 0.24	0.48 ± 0.29
TO	Bv	15 (30)	2000 – 2024	20 ± 2	0.59 ± 0.10	0.21 ± 0.27	0.42 ± 0.22
VI	Bv	21 (40)	1988 – 2020	18 ± 5	0.49 ± 0.13	0.30 ± 0.22	0.42 ± 0.22

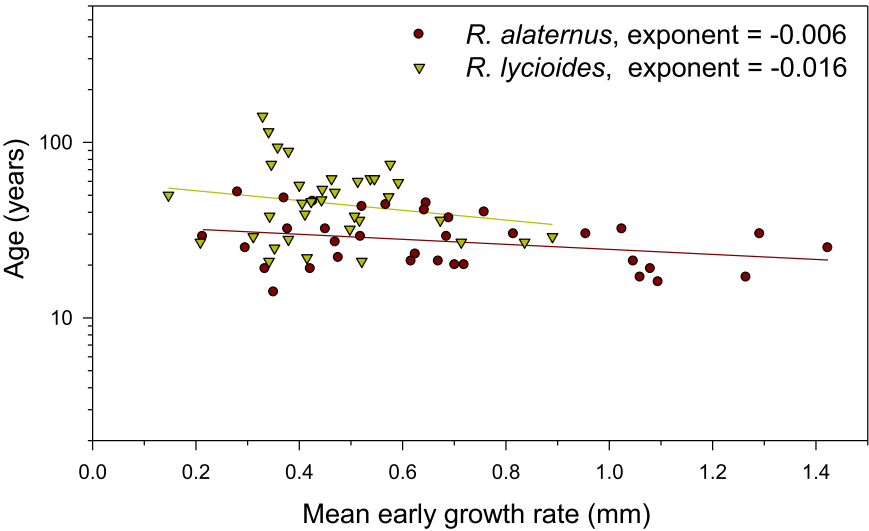


Fig. 2. Negative relationship between mean early growth rate (mean ring width over first 10 years) and age in *R. alaternus* and *R. lycioides*. The numbers show the exponents for fitted negative exponential curves. Note the logarithmic scale of age.

geodata and raster R packages, respectively (Hijmans, 2005a, 2005b). The PCA was calculated using the vegan R package (Oksanen et al., 2025). Climate-growth correlations were calculated using the treeclim package (Zang and Biondi, 2015).

3. Results

3.1. Age and growth patterns and growth-lifespan trade-off

Mean ages varied from *R. sphaerocarpa* and *B. vulgaris* (14 – 20 years) to *Rhamnus* species (25 – 46 years, Table 2). Mean ring-widths varied accordingly from 2.02 mm in *R. sphaerocarpa* (site MO) to 0.40 mm in *R. lycioides* (site VA). In the second site, a *R. lycioides* individual reached an age of 144 years. In the case of age distributions, a significant difference was found when comparing *R. alaternus* and *R. lycioides* in site VA ($\chi^2 = 18.783, p = 0.018$). Different age distributions were also found between sites for *B. vulgaris* ($\chi^2 = 32.140, p = 0.045$) and *R. sphaerocarpa* ($\chi^2 = 13.523, p = 0.012$). The first-order autocorrelation reached maximum values in *R. saxatilis* (0.34) and *B. vulgaris* (0.30, site VI), and the lowest ones in *R. sphaerocarpa* (0.06, site AR), whereas mean correlation values showed maximum values in *B. vulgaris* (0.48, site RU) and *R. sphaerocarpa* (0.43, site AR; Table 2). The growth-lifespan trade-offs showed negative but not significant relationships in *R. alaternus* ($r = -0.286, p = 0.096$) and *R. lycioides* ($r = -0.238, p = 0.168$; Fig. 2). *R. alaternus* showed a less negative exponent (-0.006; 95% confidence intervals, -0.012, 19.04) for the

fitted negative exponential curve than *R. lycioides* (-0.016; 95% confidence intervals, -0.020, 44.90), indicating a slower reduction in growth rate as shrubs age in the former species. Indeed, *R. lycioides* showed a higher mean age than *R. alaternus* ($U = 261, p = 0.0001$), whereas *R. alaternus* showed higher growth rates than *R. lycioides* ($U = 349, p = 0.0015$), being this difference particularly notable in site VA (Table 2). However, the slopes of linear regressions fitted to growth rate vs. $\log_{10}$ (age) values did not differ between *R. alaternus* and *R. lycioides* (ANCOVA, $F = 1.778, p = 0.187$), indicating similar growth-lifespan trade-offs.

3.2. Shared year-to-year growth variability

The ring-width series showed common growth variability between coexisting species (*R. alaternus* and *R. lycioides*) and also between sites for the same species in the case of *R. sphaerocarpa* and *B. vulgaris* (Figs. 3 and 4). Drops in the growth index corresponded to droughts such as 1986, 1994, 2005, 2012 and 2022, whereas high growth rates were observed in wet years (e.g. 1996 – 1997 in sites AL and VA). The highest positive correlations between indexed ring-width series corresponded to the two *R. lycioides* sites, followed by *R. alaternus* and *R. lycioides* from sites AL and VA, and *R. alaternus* in those two sites (Fig. 4). Only *B. vulgaris* in sites TO and RU showed a significant ($p < 0.05$) positive correlation, whilst *B. vulgaris* from site RU showed significant positive correlations with all *R. alaternus* and *R. lycioides* series of growth indices, and *B. vulgaris* from site TO showed it with those of site VA. The *R. alaternus* series from site AL, the *B. vulgaris* series

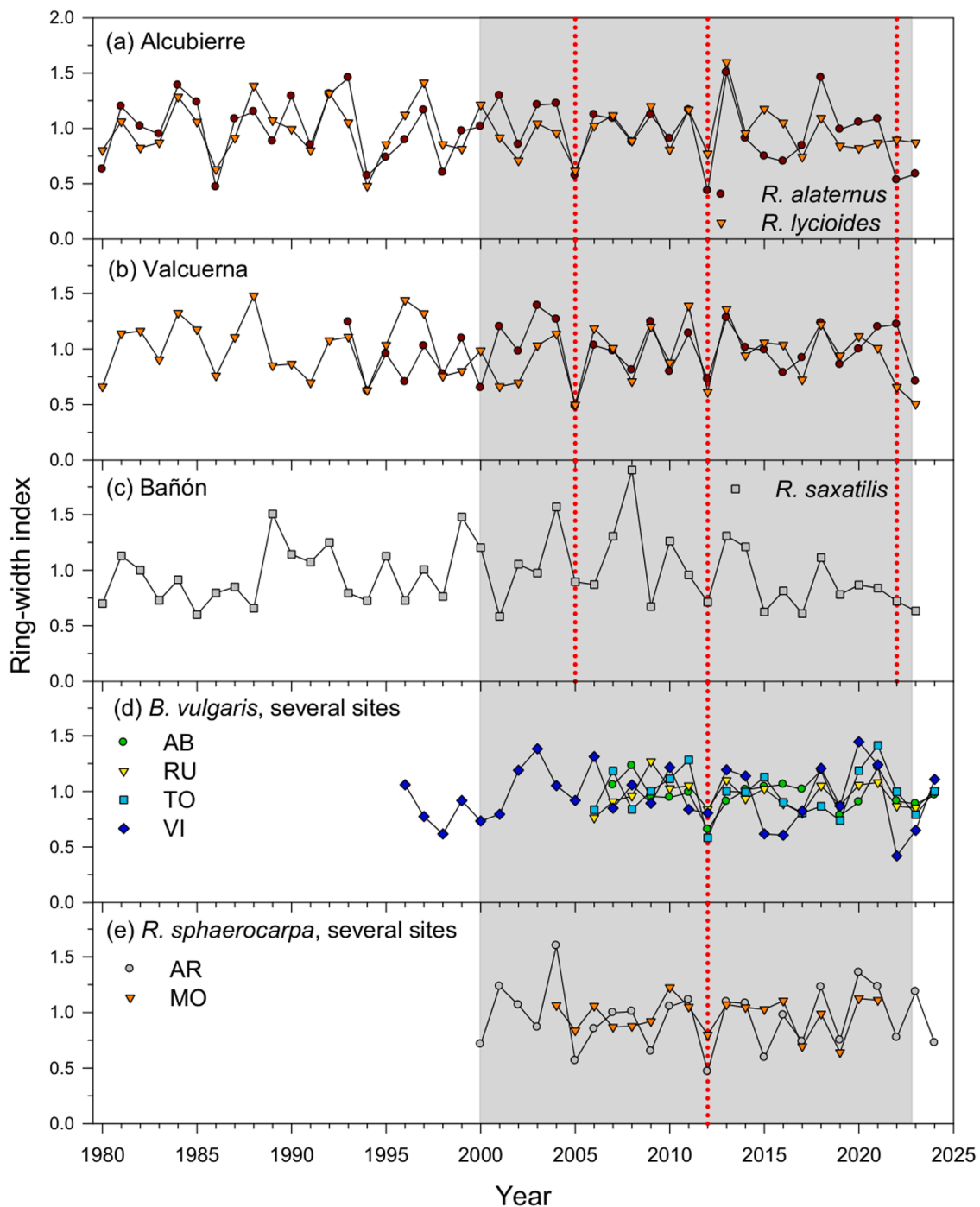


Fig. 3. Series of ring-width indices calculated for the best-replicated period of each species in each site. The grey box shows the common period (2000 –2023). The vertical dotted lines indicate the study droughts (2005, 2012, and 2022).

from site VI and that of *R. sphaerocarpa* from site AR were also positively correlated. In contrast, the series of *R. sphaerocarpa* from site MO was not significantly correlated with any other series of growth indices.

The PC1, PC2, PC3 and PC4 of the series of ring-width indices accounted for 42.5%, 18.9%, 12.5%, and 8.7% of the common variability, respectively (Table S1; Fig. S3). The *R. alaternus* series from site AL and that of *B. vulgaris* from site VI showed the highest loadings in the PC1, whereas that of *R. sphaerocarpa* from site AR showed the lowest ones. In the PC2, *R. lycioides* from site VA and *R. saxatilis* from site BA showed the highest and lowest loadings, respectively. In the PC3, *R. saxatilis* presented the highest loadings and *B. vulgaris* from VI the

lowest ones. Lastly, in the PC4, *R. sphaerocarpa* from site MO showed the highest loadings and, again, *B. vulgaris* from VI the lowest ones.

3.3. Growth responses to climate variables and the drought index

The assessment of intra-annual growth patterns in *R. alaternus* showed that both longitudinal and radial growth peaked from April to June, and maximum radial-growth rates were more than twice the average ($0.013 \text{ mm day}^{-1}$) than the dry year ($0.006 \text{ mm day}^{-1}$; Fig. S4). In addition, a second growth peak was observed in October during the average year. The growth of *Rhamnus* species was mainly constrained by

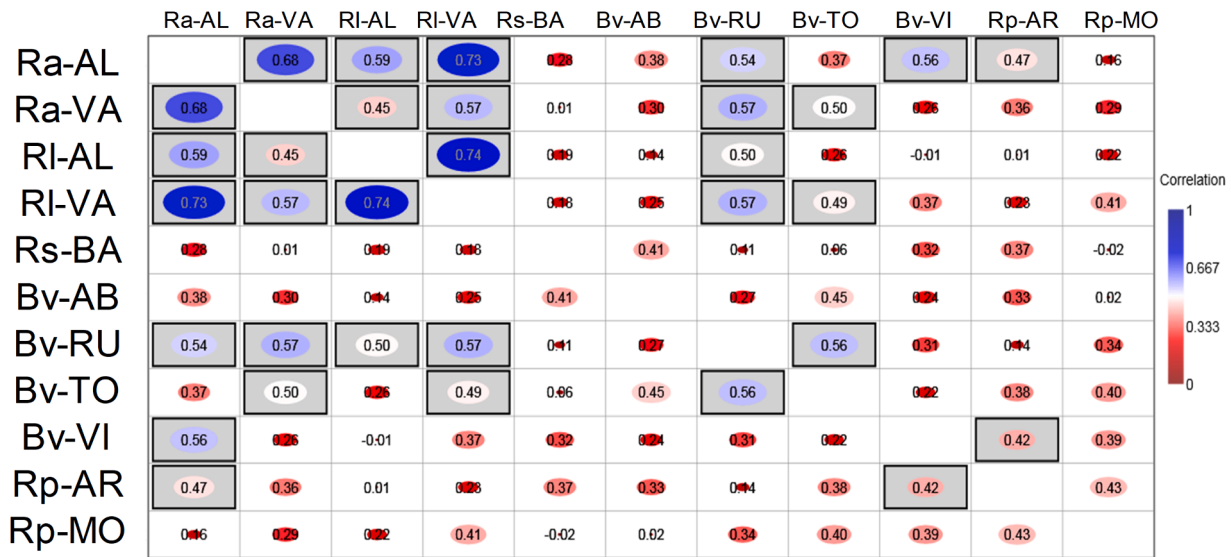


Fig. 4. Correlation matrix calculated between the site series of ring-width indices (period 2000–2023). Values outlined with boxes are significant Pearson correlation coefficients ($p < 0.05$). Note that most coefficients were positive. Species' and sites' codes are as in Table 1.

elevated temperatures in March, June, and July, and enhanced by wet conditions in January, April, and June (Fig. 5). In the case of *B. vulgaris*, elevated temperatures in June, and also in the previous September, were also negatively correlated with growth indices, whilst high precipitations in January–February showed positive correlations. In *R. sphaerocarpa*, warm March conditions constrained growth and wet January and spring conditions improved it.

Growth indices showed maximum correlations with weekly SPEI values from February to October and at scales of 3 (*R. sphaerocarpa*) to 12 (*R. alaternus*, *R. lycioides*) months (Table 4, Figs. S5 and S6). The maximum correlation was achieved by *R. sphaerocarpa* in the most arid AR site, followed by *R. sphaerocarpa* in the site MO, *R. lycioides* in site AL, and *B. vulgaris* in site RU. *R. alaternus* in site AL and *R. saxatilis* showed the lowest SPEI-growth correlation coefficients.

Considering the common growth variability accounted for the PC1 scores, the maximum correlation ($r = 0.846$, $p < 0.0001$) was found for July SPEI values calculated at 10-month-long scales, i.e. for the cumulative water balance from the previous October up to July (Fig. 6). A similar association was found for the PC1 scores of *Rhamnus* growth indices ($r = 0.670$, $p = 0.0001$; period 1980–2023) for 10-month June SPEI values (Fig. S7).

In the case of the longest chronology corresponding to *R. lycioides* from site VA, a strong correlation ($r = 0.552$, $p < 0.0001$; period 1960–2023) was also found with January precipitation (Fig. S8). This correlation peaked in the period 1986–2005.

3.4. Resilience indices

In coexisting *R. alaternus* and *R. lycioides*, Rt and Rs values tended to be higher in the second species, whereas Rc values were higher in *R. alaternus*, particularly in site AL (Fig. 7). In *R. saxatilis*, Rs was higher in 2005 than in 2012. Overall, *Rhamnus* species showed a good recovery capacity with most Rc values being greater than 1. In fact, considering the relationships between the PC1 scores of *Rhamnus* indexed ring-width series and SPEI during drought and post-drought years, we found similar slopes and correlation coefficients for both types of years confirming a high resilience for these species (Fig. S9). In the case of *B. vulgaris*, the VI site showed higher Rt and Rs and lower Rc values during the 2012 drought than the other sites, whereas the TO site showed lower Rt and Rs and higher Rc values. In *R. sphaerocarpa*, Rc values were higher in the driest site AR as compared with site MO during the 2012 drought.

4. Discussion

The five studied shrub species showed variables ages and growth rates, and their growth was limited by dry conditions from the previous October up to July under semi-arid Mediterranean conditions (Fig. 6). The two coexisting *Rhamnus* species showed the highest growth similarity, as expected, but they were also coupled with some *B. vulgaris* population (RU, TO) growing under similar dry conditions (Fig. 4). This coherence in growth variability among dry but distant sites may correspond to regional climate influences, illustrated by the severe droughts impacting several species and sites as in 2005 and 2012 (Fig. 3). Therefore, despite being coupled to local microclimate conditions (Pellizzari et al., 2017), shrubs also respond to climate regional variability as trees do (Gazol and Camarero, 2012). This means that shrubs are also vulnerable to hotter droughts as has been observed in some of the study sites (e.g., VA; cf. Gazol et al., 2017; Tamudo et al., 2024). Such vulnerability should correspond to fast-growing shrubs with lower wood density and more prone to xylem cavitation (Maherali et al., 2004; Götmark et al., 2016; Martínez-Cabrera et al., 2011).

Rhamnus species were particularly sensitive to elevated spring temperatures (Fig. 5), which favor an excessive water loss through stomata and may reduce the turgor and division rate of cambium cells (Altieri et al., 2015). This sensitivity to warmer spring conditions is in agreement with the intra-annual growth pattern of *R. alaternus* characterized by a major peak in spring (see also Liphshitz and Lev-Yadun, 1986). Nevertheless, this species showed a high post-drought recovery capacity (Fig. 7), suggesting it is able to use shallow water sources and present high growth rates (Fig. 2) under wetter winter-spring conditions (Muñoz-Gálvez et al., 2025). In contrast, *R. lycioides* attained higher ages and showed lower growth rates. This led to negative growth-lifespan trade-offs, which were not significant and would require further sampling of sites and shrub species to test whether they hold as they do in trees (Brienen et al., 2020; Liu et al., 2025). This highlights that the variability in growth rates and lifespan between shrub species, which could be related with their multi-stemmed growth form, deserves further attention when assessing drought resilience and functional traits (Götmark et al., 2016). Furthermore, the high inter-specific variability in age could influence drought resilience (Table 2).

As expected, the shrub species from the most arid site (*R. sphaerocarpa*) presented the strongest drought-growth coupling, confirming the importance of local climate conditions, despite common

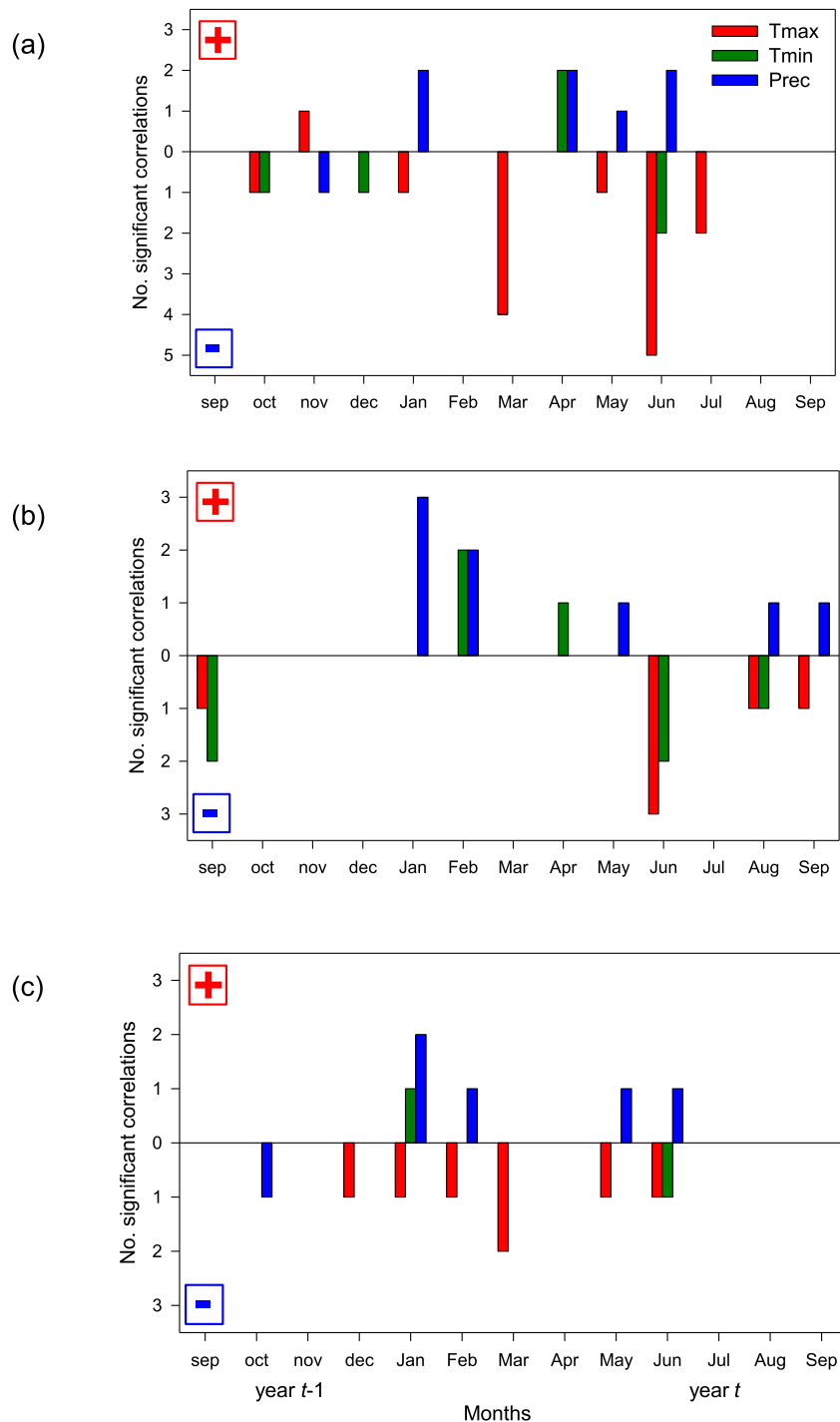


Fig. 5. Number of sites showing positive (symbol “+”) and negative (symbol “–”) significant ($p < 0.05$) climate-growth correlations found in (a) *Rhamnus* species, (b) *B. vulgaris*, and (c) *R. sphaerocarpa*. Monthly climate variables are: Tmax, mean maximum temperature (red bars); Tmin, mean minimum temperature (green bars); and Prec, precipitation (blue bars).

regional drought signals, for shrub growth. In most cases, shrub growth not only depended on growing-season water availability, but also on prior autumn and winter precipitation (Table 4). In these Mediterranean sites, these two seasons are critical for the recharge of soil water pools often exhausted during the warm and dry summer (Pasho et al., 2012). Nevertheless, some of the study species may be also able to exploit and use deeper water sources under dry conditions (Muñoz-Gálvez et al., 2025), buffering drought stress and promoting post-drought recovery. A research field that requires further attention is the understanding of

relationships between shrub resilience and the plasticity to obtain water from different soil depths.

Interestingly, shrub populations from the arid sites of each species showed high Rc indices indicating recovery capacity and how intense was the growth drop due to drought stress. For instance, both *R. sphaerocarpa* and *B. vulgaris* showed the highest Rc index in their driest study sites (AR, TO; Fig. 7). This result highlights a high adaptive capacity to tolerate water shortage. It could be investigated whether this tolerance is mediated by different growth phenology of the same species

Table 4
Summary of the SPEI-growth correlations (see also Figs. S5 and S6). Sites' and species' codes are as in Table 1.

Site (code)	Species	Timespan	Maximum correlation coefficient	SPEI scale of the max. correlation (months)	Period when max. correlation was found
Monegros-Lanaja (MO)	<i>R. sphaerocarpa</i>	2001 –2021	0.739	3	Mid-March
Aranjuez (AR)		1991 –2024	0.799	3	Mid-June
Alcubierre (AL)	<i>R. alaternus</i>	1980 –2023	0.435	9	Late June
Valcuerna (VA)		1980 –2023	0.675	12	Late July
Alcubierre (AL)	<i>R. lycioides</i>	1980 –2023	0.694	12	Mid-August
Valcuerna (VA)		1980 –2023	0.597	9	Early June
Bañón (BA)	<i>R. saxatilis</i>	1980 –2023	0.575	9	Mid-October
Allepuz (AB)	<i>B. vulgaris</i>	2002 –2023	0.664	6	Mid-October
Rubielos de la Cérda (RU)		2003 –2023	0.685	9	Early June
Torrijo del Campo (TO)		2000 –2023	0.661	6	Early May
Villarroya de los Pinares (VI)		1988 –2020	0.638	3	Late February

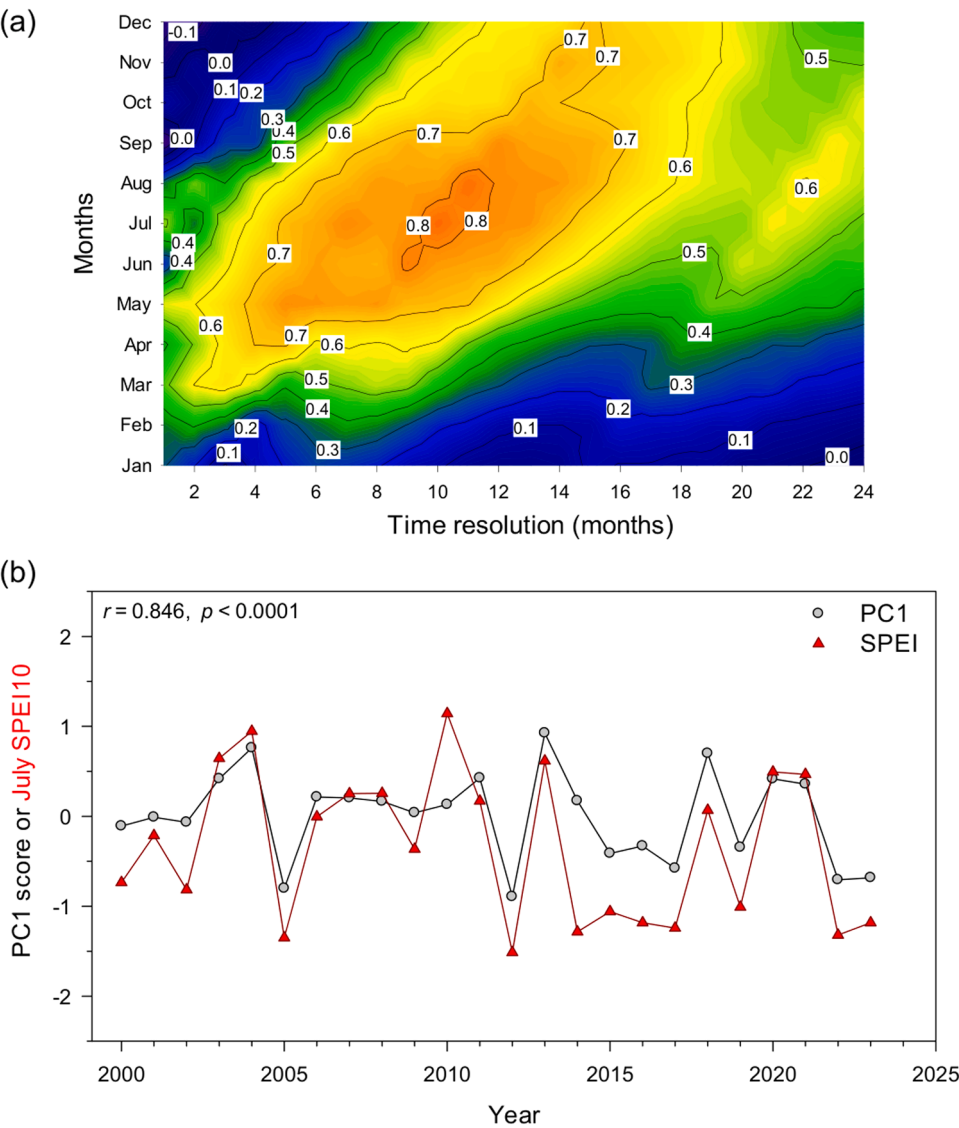


Fig. 6. (a) Correlation coefficients (color scale) calculated by relating the PC1 scores of shrub growth indices (period 2000 –2023) and the monthly SPEI (mean of all sites' SPEI series) calculated at 1- to 24-month-long timescales (x axis). (b) The PC1 scores (grey circles) are positively correlated with the July SPEI calculated at 10-month-long scales (red triangles).

as a function of climate conditions. For instance, the highest resistance to drought of *B. vulgaris* in its coolest and wettest site (VI; Fig. 7) could be linked to buffered water shortage or a delayed cambial resumption (Fig. 5). In other cold, high-elevation sites of this species (e.g., AB), the

highest response to SPEI in autumn (Table 4) could reflect a shorter growing season or a delayed end of the growing season (Camarero et al., 2013), thus avoiding the dry summer. Finally, we acknowledge that the lack of sites along the studied ecological gradient, where at least three of

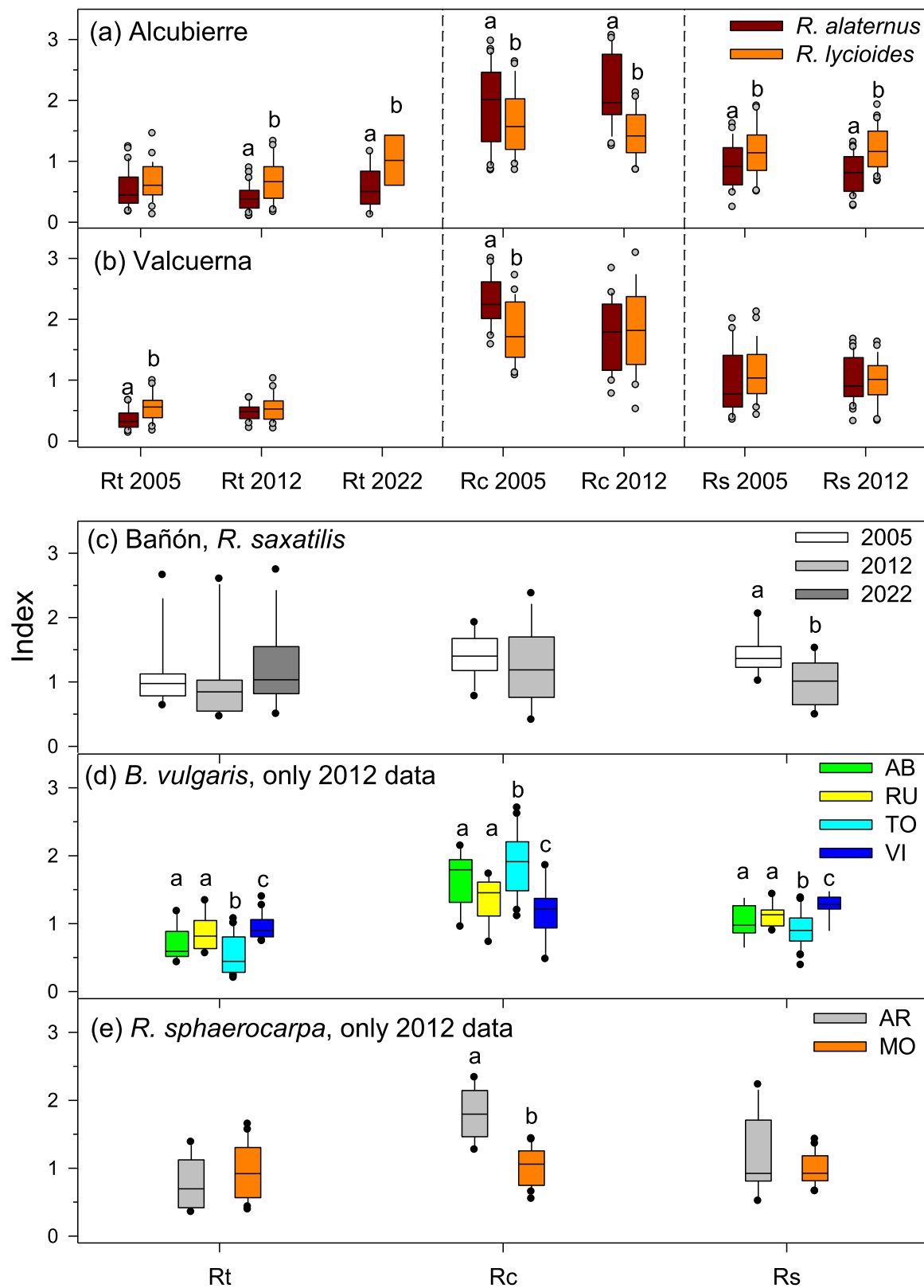


Fig. 7. Resilience indices (Rt, resistance; Rc, recovery; Rs, resilience) calculated for the study shrub species: *R. alaternus* and *R. lycioides* in Valcuerna (a) and Alcubierre (b) sites; (c) *R. saxatilis* in Bañón; (d) *B. vulgaris* in four study sites (AB, RU, TO, VI); and *R. sphaerocarpa* in two study sites (AR, MO). Resilience indices were calculated for the 2005, 2012 and 2022 droughts (plots (a), (b) and (c)) or only for the 2012 drought (plots (d) and (e)). Different letters indicate significant ($p < 0.05$) differences.

the selected species coexist, makes cross-species ranking, in terms of drought resilience, potentially confounded by different site conditions including climate, topography, soil features, and ecological contexts (but see Tamudo et al., 2024).

5. Conclusions

Under semi-arid conditions and in sites situated near the xeric distribution limits of the study species, the five shrubs showed wide ranges of ages and growth rates. Common year-to-year growth patterns when coexisting (*R. alaternus*, *R. lycioides*) or in the case of several sites of the same species (*R. sphaerocarpa*, *B. vulgaris*) were also found. Elevated temperatures in early spring limited shrub growth, whereas wet conditions in the prior winter and spring enhanced it. The radial growth of Mediterranean shrubs was constrained by 3-to-12-month long droughts starting in the previous autumn, and even in summer, and ending in autumn. Such long response periods and the dependence of shrub growth on precipitation from the prior autumn to the current spring are coherent with an early start of the growing season and the sustained use of shallow soil water sources when climate conditions are mild and wet. Further research on shrub growth phenology and soil water-use combining, for instance, water isotopes and dendrometers would help testing these ideas. Under the forecasted warmer and more arid conditions, the study species are expected to show a good post-drought recovery capacity. However, elevated temperatures in spring and summer would reduce growth rates of *Rhamnus* species and *B. vulgaris*, respectively.

CRediT authorship contribution statement

José Antonio Sánchez-Sancho: Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Álvaro Rubio-Cuadrado:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **J. Julio Camarero:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Antonio Gazol:** Writing – review & editing, Visualization, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Elisa Tamudo:** Writing – review & editing, Visualization, Software, Resources, Methodology, Investigation, 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.

Acknowledgments

This study was funded by projects PID2021–123675OB-C43 and TED2021–129770B-C21 (Spanish Ministry of Science and Innovation). We thank C. Valeriano for her help during sample processing and measuring.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2026.126503](https://doi.org/10.1016/j.dendro.2026.126503).

Data Availability

Data will be made available on request.

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