



Mediterranean service trees respond less to drought than oaks

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ABSTRACT

Some widely distributed timber species, such as oaks, are vulnerable to low soil water availability and drought. Therefore, selecting broadleaved minor species with lower sensitivity to drought could be an alternative in seasonally dry areas. However, the growth performance of these minor hardwood species is unknown, particularly under warm and dry conditions at the southern limit of their distribution range. We assessed the radial growth response to drought by correlating tree-ring and climate data in coexisting service trees (*Sorbus domestica*) and two oak species (*Quercus faginea*, *Quercus pyrenaica*). Trees were sampled in three Mediterranean sites located in Spain with different precipitation patterns. We used the Vaganov–Shashkin (VS) growth model to infer the main climate constraints of growth. To ascertain whether climate is changing tree phenology, we also simulated changes in xylem onset and cessation timings and compared them with leaf falling dates in service trees. Service trees showed a trend towards advancing leaf fall, but this was not related to xylem growth. Oaks responded more to a drought index than service trees. The strongest responses corresponded to droughts peaking from spring to summer, but oaks tended to respond to longer droughts (9–13 months) than service trees (2–7 months). These different responses are due to the positive responses of all species to high precipitation in the growing season, but the sensitivity of oak growth to warm summer conditions and increased atmospheric water demand. The VS model indicated a more bimodal growth pattern in service trees than in oaks, which could allow the former to recover better after a dry summer. Service trees could be more widely used as a source of valuable timber wood under Mediterranean continental conditions.

1. Introduction

Drought is becoming a major constraint of forest growth worldwide (Babst et al., 2019). Climate models forecast longer and more severe droughts in response to warming scenarios by the late 21st century (Cook et al., 2014), particularly in drought hotspots such as the Iberian Peninsula (García-Valdecasas Ojeda et al., 2021). In southern Europe, some major timber species such as European beech (*Fagus sylvatica* L.) and several oak species respond negatively to low soil water levels and are vulnerable to drought (Corcuera et al., 2006; Serra-Maluquer et al., 2019; Camarero et al., 2021), which has increased the interest in broadleaf minor timber species with assumed higher drought tolerance under warmer climate scenarios (Kunz et al., 2018; Fuchs et al., 2021). Rare, hardwood, noble tree species with high-quality timber could represent a promising alternative for rural development in seasonally

dry areas through well managed pure or mixed plantations (Loewe-Muñoz et al., 2020).

The service tree (*Sorbus domestica* L.) is a hardwood, winter-deciduous species, widely distributed across Europe, where it appears as scattered individuals or forming small stands linked to the dispersal of its seeds by frugivorous animals (Rotach, 2003). In central and northern Europe, under mesic or cold climate conditions, it is regarded as more drought-resistant than the European beech, but less resistant than the sessile oak (*Quercus petraea* [Matt.] Liebl.) (Hemery et al., 2010; Kunz et al., 2018). Tree-ring data have allowed quantifying the tolerance to drought of broadleaved minor species in temperate central Europe (Fuchs et al., 2021). However, these comparisons have not been done yet at the southern margin (rear edge) of its distribution area in southern Europe and under Mediterranean continental conditions, where trees have to withstand a double climate stress characterized by cold winters

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and dry summers (Mitrakos, 1980). Furthermore, to adequately quantify drought tolerance the growth recovery after dry years should be considered selecting suitable dry years and using appropriate resilience metrics (Schwarz et al., 2020).

Service trees perform best on sites with deep fertile soils and good water supply, but theoretically can tolerate dry and sunlight conditions better than other coexisting tree species such as oaks (Paganová, 2007, 2008). It has been shown that low water availability and high temperature can reduce the radial growth of service trees in mesic sites (Rasmussen, 2007). However, how service trees respond to water deficit and recover after drought in comparison with co-occurring, widely distributed hardwood tree species such as oaks is poorly studied in drier regions. Therefore, we need a better understanding of how severe and successive droughts, as those frequently affecting the Mediterranean Basin, impact service tree growth. In addition, drought timing is also a relevant factor determining drought recovery so gaining knowledge on tree phenology would improve our knowledge on post-drought resilience (Gazol et al., 2018; Bose et al., 2021). To fill this knowledge gap on drought tolerance of this minor broadleaf timber species in southern Europe, we studied the growth patterns and their responses to climate and a drought index, including post-drought recovery, of the service tree as compared with two coexisting Mediterranean oaks (*Quercus pyrenaica* Willd., *Quercus faginea* Lam.). These two shade-tolerant oaks form pure and mixed forests in sites with relatively wet soils and are more widely distributed and considered to tolerate drought better than the service tree. In addition, these oak species are resilient in response to disturbances through vigorous resprouting and have been well studied from dendroecological and ecophysiological points of view (Corcuera et al., 2006; Alla and Camarero, 2012; Peguero-Pina et al., 2015; Vieira et al., 2022).

To frame the climatic limitations of growth in service trees and oaks we used the process-based Vaganov–Shashkin growth model (hereafter VS model; Vaganov et al., 2006). The use of the VS model is justified because it simulates ring-width indices as a function of meteorological data by explicitly considering non-linear relationships between radial growth rates and climatic limitations such as low soil moisture. Furthermore, this model allows simulating the dates of xylem growth onset and cessation. To determine whether climate warming has affected service tree phenology and their growth capacity we compared the simulated xylem onset and cessation timings with a phenological series of leaf fall date obtained near one of the study sites. Our specific aims are: (i) to quantify the growth rate and patterns of service trees and coexisting oaks using tree-ring width data, (ii) to assess the growth responses to climate and a drought index of these three species under Mediterranean continental conditions, and (iii) to infer the intra-annual growth rates and meteorological limitations using the VS model.

2. Materials and methods

2.1. Study sites and tree species

We selected three study sites located in northeastern Spain and subjected to continental Mediterranean climate conditions characterized by cold winters and dry summers: southwestern Soria (hereafter Soria), Bañón and Utrillas (Fig. S1, Table 1). According to climate data from the Iberian Digital Climate Atlas (Ninyerola et al., 2005), Soria is the wettest site, whereas Utrillas is the driest site (see Table 1). The lowest mean minimum temperatures range from -2.1°C in Soria to

-2.7°C in Bañón, and the highest mean maximum temperatures range from 29.2°C in Soria to 29.7°C in Utrillas.

Slopes are steeper in Utrillas than in the other two sites. Soils are basic and deep in all sites, excepting Utrillas where they are shallow and rocky. Service trees were often planted or managed for fruit or timber production, but the depopulation of rural areas in Spain, which accelerated in the 1960s, has triggered the abandonment of their traditional management. Nowadays, trees in Soria and Bañón present a good vitality and health status, whereas several old individuals from Utrillas (20% of sampled trees) show canopy dieback. Sampled service trees were mature and neither severely pruned nor coppiced in the past. They were found near tree species including: *Juglans regia* L., *Crataegus monogyna* Jacq. and *Populus nigra* L.

The service tree distribution includes the Mediterranean Basin and central Europe (Fig. 1a), but its natural distribution is unknown since it has spread through cultivation since the times of the Roman Empire and man has contributed to its dispersal and widespread distribution (Rotach, 2003). It can be found in relatively dry sites with poor soils, reaching 15–20 m in height, albeit on deep, fresh soils and near water sources (creeks, irrigation ditches) it can outgrow other species and become a tall tree (25–30 m high) reaching stem diameters of up to 60 cm (Rotach, 2003). This shade-intolerant species produces a semi-ring-porous, dense, tough wood of high economic value with distinct annual rings. It produces edible fruits whose seeds are dispersed by birds and mammals, although regeneration from seed is scarce. It is usually out-competed by more shade-tolerant species such as oaks. Service trees are valued for their high quality timber production and ability to improve the productivity and timber quality of mixed forests (Quevedo et al., 2007). There has been a renewed interest in service trees' fruits due to changes in consumer tastes, which are returning to fruits with traditional flavours and high nutritional value (Sottile et al., 2017).

All sampled trees and stands were apparently healthy and did not present any indication of drought-induced dieback (abundant dead leaves and shoots, epicormic shoots). Nevertheless, *Q. faginea* has showed drought-induced dieback in sites drier than the study sites (e.g., Camarero et al., 2016). In the case of service trees, most sampled individuals were isolated or forming small stands.

The two study oaks (*Quercus pyrenaica* Willd. in Soria, *Quercus faginea* Lam. in Bañón and Utrillas) are mainly distributed in the western Mediterranean Basin (Fig. S1). These are winter deciduous species forming ring-porous wood with *Q. pyrenaica* predominantly found on acid soils and cool-wet sites, and *Q. faginea* growing on basic soils and warmer and drier sites than *Q. pyrenaica*. All sampled oak stands were naturally growing, formerly coppiced for timber and charcoal production. They had basal areas ranging from 15.1 (*Q. faginea* in Bañón) to 27.0 (*Q. pyrenaica* in Soria) $\text{m}^2 \text{ha}^{-1}$ and stem density ranging between 1200 (*Q. faginea* in Bañón) to 3845 (*Q. pyrenaica* in Soria) stems ha^{-1} . In Soria, oaks were sampled in sites with deep, acid soils located in the northwestern part of the province (41.848°N , 2.662°W , 1117 m a.s.l.).

2.2. Leaf falling phenology, climate data and drought index

Leaf fall dates (start of leaf falling in autumn) specific to service tree were obtained from the Galve meteorological station (40.655°N , 0.882°W , 1188 m a.s.l.), located at 32 and 15 km SW from Bañón and Utrillas study sites, respectively, and subjected to similar climate conditions (data from the Phenology Network of the Spanish Meteorological Agency –AEMET). They were observational data taken in situ from 1995

Table 1

Geographical and climatic features of the three study sites. Abbreviations: MAT, mean annual temperature; TAP, total annual precipitation.

Site (code)	Latitude N ($^{\circ}$)	Longitude W ($^{\circ}$)	Elevation (m)	Slope ($^{\circ}$)	Aspect	MAT ($^{\circ}\text{C}$)	TAP (mm)
Soria (S)	41.415	3.084	1005	5–10	N–NE	10.5	619
Bañón (B)	40.837	1.191	1108	0–10	NE–NW	10.4	485
Utrillas (U)	40.788	0.828	1083	10–15	NE–NW	10.6	460

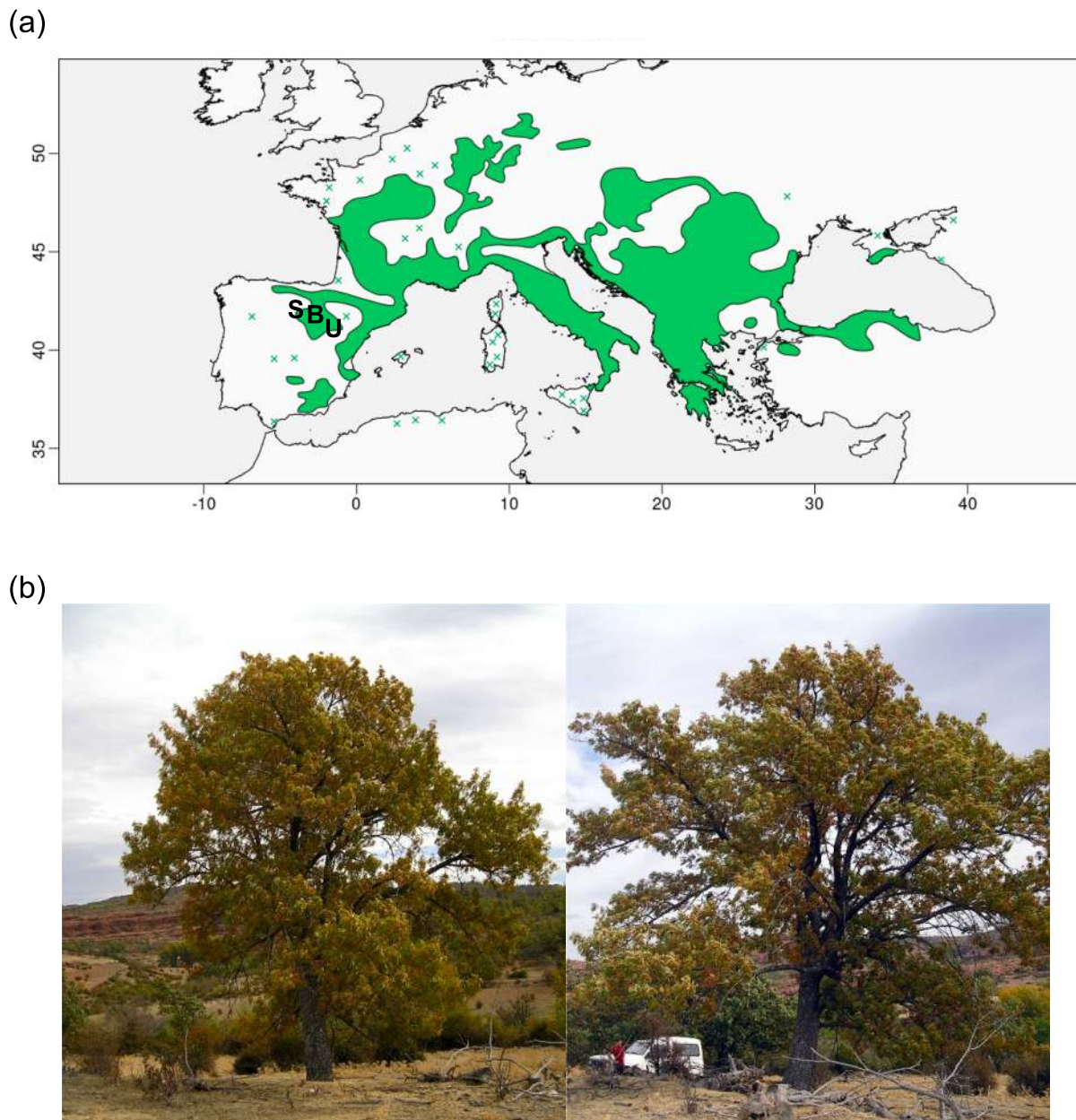


Fig. 1. (a) Distribution map of *Sorbus domestica* in Europe and situation of study sites in northern Spain (S, Soria; B, Bañón; U, Utrillas). The map was modified from Caudullo et al. (2017). (b) Views of two monumental service trees located near the Soria study site.

to 2021.

To avoid problems with gaps in climate data or heterogeneous series, we used the 0.1°-gridded EOBS climate dataset (v25.0e; Cornes et al., 2018). We obtained monthly data of mean maximum (Tx) and minimum (Tn) temperatures and total precipitation (Pr) for the 1965–2021 period. To emphasize year-to-year climate variability, climate variables were detrended using linear regressions. The resulting climate residuals (differences between observed and fitted values) were used to calculate climate-growth relationships.

To assess drought severity and duration we used monthly, 0.1°-gridded data of the Standardized Precipitation Evapotranspiration Index (SPEI) in the same period (Fig. S2). The SPEI is a multi-scalar drought index computed from monthly rainfall, temperature and potential evapotranspiration showing cumulative water surplus or deficit (Vice-Serrano et al., 2010). We considered 1- to 24-month long SPEI temporal scales. Linear regressions showed significant negative trends of the SPEI in all sites, i.e. increasing aridification due to warmer

conditions (Fig. S2). The major recent droughts affecting all sites occurred in 1994–1995, 2005 and 2012. These years of drought were selected because (i) they showed SPEI values lower than -1.5 in at least two of the study sites, and (ii) they corresponded to major drops in forest growth and productivity across Spain (cf. Gazol et al., 2018, 2022).

2.3. Sample collection and tree-ring processing

From late autumn to winter 2022, from 15 to 25 dominant trees were sampled at breast height (1.3 m) in each site using a 5-mm Pressler increment borer. Two cores per tree were taken. In the case of service trees, sampled trees were usually isolated and they were located ca. 20 to 150 m apart within a ca. 5 ha large area. In the case of oaks, they were located ca. 10 to 20 m apart within a ca. 2 ha large area. Cores were sanded with progressively finer grain sandpaper until tree-ring limits were clearly identified under a binocular microscope. Tree-ring widths were visually cross-dated using standard dendrochronology methods

(Stokes and Smiley, 1996) and then measured to the nearest 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany).

Cross-dating quality check and chronology building were done using the dplR (Bunn, 2008) and detrendR packages (Campelo et al., 2012). To show growth trends we converted the individual ring-width series into mean basal area increment (BAI) series for each site and species assuming a concentric stem growth. We calculated the ratio between the mean BAI value during the three years after selected droughts (1994–1995, 2005 and 2012) and the BAI value during the dry year to assess post-drought growth recovery (Gazol et al., 2018). Using 2- and 4-year long windows for calculating post-drought recovery led to similar results as those based on 3-year long windows (*data not shown*). In cores without pith, we corrected the BAI by estimating the length of the missing radius using a graphical method based on the convergence of rays at the pith (Rozas, 2003).

To calculate climate- and drought- growth relationships each tree-ring series was detrended by fitting 32-year cubic smoothing splines with a 50 % frequency response cut-off to individual ring-width series. In this way, we obtained ring-width indices by dividing observed by fitted values. Growth persistence in detrended ring-index series was removed by autoregressive modeling, and the pre-whitened residual series of ring-width indices (TRWi) were averaged using a biweight robust mean to produce residual chronologies for the three sites. The quality of the chronologies was assessed by calculating several dendrochronological statistics (Fritts, 1976): mean sensitivity (MSx), first-order autocorrelation of raw data (AR1), mean correlation between series (Rbar), and expressed population signal (EPS). Tree age at 1.3 m was estimated based on the oldest, cross-dated core per tree after correcting the missing innermost rings using a graphical method (Rozas, 2003). All tree-ring analyses were carried out using the R statistical software (R Development Core Team, 2022).

2.4. Vaganov-Shashkin process-based model of tree-growth

The VS model was used to estimate intra-annual growth rates and to infer the main climate variables constraining radial growth. The daily growth rates simulated by the VS model were used to estimate phenological growth events including the dates of xylem growth onset, growth peak and growth cessation (presented as DOY, day of the year). In each site, the residual ring-width (TRWi) chronology of each tree species was used to fit the VS model. The VS model simulates TRWi as a function of daily temperature and precipitation, based on the principle of limiting factors (Vaganov et al., 2006). The radial growth rate is a function of three partial growth rates that depend on daily temperature, soil water content, and photoperiod which does not change among years. Therefore, the VS model calculates daily growth rates (Gr) considering limitations due to temperature (GrT) and soil moisture (GrW). Lower GrT or GrW values indicate growth is more constrained by low temperatures or low soil moisture, respectively. The influence of radiation on growth (photoperiod) is considered fixed for each site as a function of site latitude. For each site, the daily precipitation and mean daily temperatures from the closest grid of the E-OBS 0.1°-gridded dataset were downloaded. The best-replicated common period (1965–2021) was used for fitting the VS model. A simple optimization algorithm was applied for tuning 17 parameters, while the remaining parameters of the VS model were kept constant (Table S1). Due to the short best-replicated period, no validation analysis was performed on an independent period. For that reason and to avoid model over-fitting, a restricted and realistic range of values for each parameter was defined (Table S1). To ensure that all models were tuned under similar conditions, the initial parameter values, the random seed (999) and the number of iterations (999) were the same for all models. In addition, only a single parameter was adjusted at a time, while the remaining parameters assumed the previously optimized values.

2.5. Statistical analyses

We used the Kendall τ to assess the trends in leaf phenology data. The Spearman correlation coefficient (r_s) was used to compare the phenology series with the ring-width residual chronologies (TRWi). The Pearson correlation coefficients (r) was calculated between observed and simulated chronologies to assess the reliability of the VS model simulations. BAI ratios were compared among species using t tests.

For each site and tree species, the residual chronology was used to investigate the climatic signal considering the period 1965–2021. Pearson correlations were calculated between the species or sites chronologies to assess their similarity. Pearson correlations were also calculated between the TRWi series and the residuals of monthly climatic variables (mean maximum and minimum temperatures, precipitation) considering the window from previous October to current September. In the case of the SPEI, correlations were also calculated between the chronologies and the monthly values of SPEI. Lastly, 20-year moving correlations were calculated between the chronologies and the SPEI data after selecting the SPEI temporal resolutions and months showing the highest correlations in previous analyses. Climate- and SPEI-growth correlations were calculated using the treeclim R package (Zang and Biondi, 2015).

3. Results

3.1. Leaf phenology

There was a significant negative trend in the date when leaf falling started ($\tau = -0.55$, $p = 0.003$, Fig. 2). These dates were negatively related to August minimum temperatures ($r = -0.55$, $p = 0.005$). We only found a negative, but not significant, correlation between leaf falling dates and the Utrillas BAI series of service trees ($r_s = -0.30$, $p = 0.26$).

3.2. Size, age and growth trends

The oldest service trees (at least 116 years old) were sampled in Soria and Utrillas, whereas the oldest service tree sampled in Bañón was at least 102 years old. In Soria, big, monumental individuals were found with a maximum diameter of 51.6 cm (Fig. 1b). In comparison, the biggest stems of service trees sampled in Bañón and Utrillas were 43.0 and 41.1 cm thick, respectively. We found significant and positive associations between dbh and age in service trees in Soria and Bañón, but not in Utrillas (Table S2), where the lowest growth rates were found (Table 2, Fig. S3). The oldest sampled stem oaks were located in Utrillas (at least 107 years old), followed by Bañón (at least 87 years old) and Soria (at least 74 years old).

In Soria, service trees had thicker stems and presented higher growth rates (both tree-ring width and BAI) than oaks, whereas service trees had lower BAI than oaks in the other two sites (Table 2, Fig. 3). Regarding the other tree-ring statistics, few differences were found between service trees and oaks, excepting mean sensitivity in Bañón which was higher in service trees than in oaks. The highest first-order autocorrelation and mean correlation between series were found in Utrillas.

Overall, service trees presented a higher mean post-drought recovery (ratio between BAI of the three years after drought and the BAI of the dry year) than oaks (mean $\pm$ SE, 1.27 ± 0.08 vs. 1.01 ± 0.08 , $t = 2.21$, $p = 0.04$). The post-drought recovery was much higher in service trees than in oaks considering only the Soria and Bañón sites (service trees 1.95 ± 0.17 , oaks 1.42 ± 0.06 , $t = 2.98$, $p = 0.003$). The lowest and highest post-drought recovery values were observed in the 2005 drought and corresponded to Utrillas (0.54) and Soria (1.60) oaks, respectively. In service trees, the lowest (0.84) and highest (1.75) post-drought recovery values corresponded to the 2005 and 1995 droughts in Soria and Bañón, respectively.

Considering the best-replicated period (1965–2021), the Bañón and Utrillas service trees chronologies were significantly correlated ($r =$

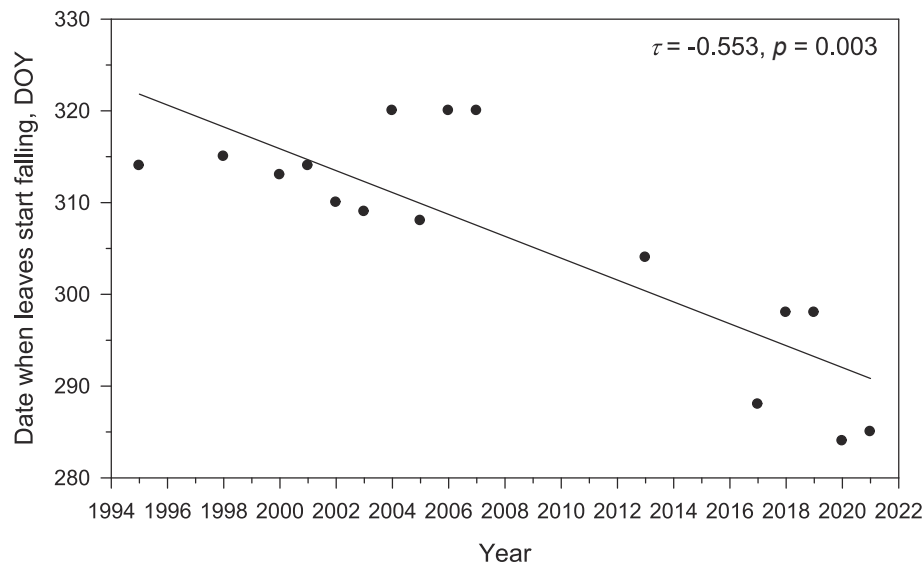


Fig. 2. Trend (Kendall tau, τ) of the start of leaf falling dates of service trees in Galve, near the Utrillas study site. DOY is the date of the year.

Table 2

Diameter at breast height (dbh), tree-ring width data and statistics (TRW, BAI, AR1, MSx, Rbar) calculated for the best-replicated period (1965–2021) in the three study sites (S, Soria; B, Bañón; U, Utrillas). Abbreviations. TRW, tree-ring width; BAI, basal area increment; AR1, first-order autocorrelation; MSx, mean sensitivity; Rbar, mean correlation among series. Values are means $\pm$ SE. Different letters indicate significant ($p < 0.05$) differences between species within the same site (Mann-Whitney tests).

Site	Tree species	Dbh (cm)	No. trees (No. cores)	Age at 1.3 m (years)	TRW (mm)	BAI (cm ²)	AR1	MSx	Rbar
S	<i>S. domestica</i>	28.3 $\pm$ 3.6b	15 (22)	55 $\pm$ 6	1.81 $\pm$ 0.17b	6.84 $\pm$ 0.54b	0.45 $\pm$ 0.10	0.41 $\pm$ 0.03	0.49 $\pm$ 0.11
	<i>Q. pyrenaica</i>	22.5 $\pm$ 2.0a	20 (40)	61 $\pm$ 2	1.20 $\pm$ 0.32a	3.19 $\pm$ 0.22a	0.45 $\pm$ 0.09	0.47 $\pm$ 0.05	0.47 $\pm$ 0.13
B	<i>S. domestica</i>	23.9 $\pm$ 2.9	25 (38)	51 $\pm$ 5	1.27 $\pm$ 0.26	3.76 $\pm$ 0.32a	0.48 $\pm$ 0.05	0.52 $\pm$ 0.05b	0.48 $\pm$ 0.10
	<i>Q. faginea</i>	25.2 $\pm$ 3.5	25 (42)	56 $\pm$ 3	1.37 $\pm$ 0.15	4.44 $\pm$ 0.23b	0.57 $\pm$ 0.06	0.33 $\pm$ 0.03a	0.59 $\pm$ 0.11
U	<i>S. domestica</i>	28.5 $\pm$ 3.7	15 (30)	59 $\pm$ 4	0.93 $\pm$ 0.21	2.15 $\pm$ 0.09a	0.63 $\pm$ 0.06	0.36 $\pm$ 0.02	0.65 $\pm$ 0.09
	<i>Q. faginea</i>	25.4 $\pm$ 4.1	18 (36)	66 $\pm$ 4	1.09 $\pm$ 0.20	2.83 $\pm$ 0.14b	0.64 $\pm$ 0.09	0.34 $\pm$ 0.02	0.76 $\pm$ 0.07

0.65, $p < 0.001$) followed by the Soria and Utrillas chronologies ($r = 0.31$, $p = 0.012$) (Figs. S3 and S4). In the case of oaks, all series were significant and positively correlated, with the highest correlations found for Bañón vs. Utrillas ($r = 0.65$, $p < 0.001$) and Soria vs. Utrillas ($r = 0.33$, $p = 0.006$). When comparing the chronologies of coexisting service trees and oaks, we only found a significant positive correlation in Bañón ($r = 0.62$, $p < 0.001$).

3.3. Climate- and drought-growth relationships

All species positively reacted to high precipitation in spring and summer, but only oaks showed significant negative responses ($p < 0.05$) of radial growth to summer temperature (Figs. 4 and 5). For service trees, the highest correlations between growth and climatic variables were found for April precipitation in Bañón ($r = 0.53$) and Utrillas ($r = 0.53$), while in Soria the highest correlation was found for minimum temperature. The highest correlations between minimum temperature and service tree growth were found in January (Soria) and April (Utrillas), whereas in Bañón no significant correlations were found with any temperature variable (Fig. 4).

In all sites, the highest correlations between oak growth and climate variables were found for precipitation: June in Soria ($r = 0.43$) and Utrillas ($r = 0.41$), and April in the case of Bañón ($r = 0.57$). Oak growth showed positive and negative correlations with minimum and maximum temperatures, respectively (Fig. 5). Positive correlations were found between oak growth and minimum temperature in January (Soria and Bañón), February (Soria) and April (Bañón), whereas in Utrillas no significant correlations were found for minimum temperature. At each site, the strongest correlation between oak growth and maximum

temperature occurred in different months: March in Bañón ($r = -0.31$), June in Utrillas ($r = -0.39$), and July in Soria ($r = -0.42$).

Overall, oak series presented higher correlations with the SPEI than service trees series (Fig. 6). The highest correlations found between oak and SPEI series corresponded to (in decreasing order): Utrillas ($r = 0.68$; SPEI 11, June), Soria ($r = 0.63$; SPEI 13, July), and Bañón ($r = 0.60$; SPEI 9, April). In contrast, the highest correlations found between service trees and SPEI series corresponded to: Bañón ($r = 0.49$; SPEI 7, July), Soria ($r = 0.37$; SPEI 6, March) and Utrillas ($r = 0.27$; SPEI 2, April).

In Bañón and Utrillas, moving correlations between selected SPEI variables and growth in oaks and service trees were significant and stable over the study period. Correlations were higher in service trees than in *Q. faginea*, particularly in Utrillas after the 2000s, when the growth in *Q. faginea* turned increasingly limited by drought (SPEI 11 in June; Fig. 7). In contrast, in Soria the moving correlations between service trees growth and March SPEI 6 were unstable, becoming only significant after the 1990s. In Soria, the moving correlations for *Q. pyrenaica* were always significant for the studied period and the influence of July SPEI 13 on oak growth increased since the 1990s; but this increase was smaller than in service trees (Fig. 7).

3.4. Growth variability simulated by the Vaganov-Shashkin model

The VS model accurately simulated the year-to-year tree growth variability of the three tree species (Figs. 8 and S4, Table 3). The intra-annual growth pattern was characterized by a main growth peak around June, but this pattern and the length of the growing season showed a high inter-annual variability (Figs. S5, S6, S7 and S8). Tree growth was limited by low temperatures at the onset and end of the growing season,

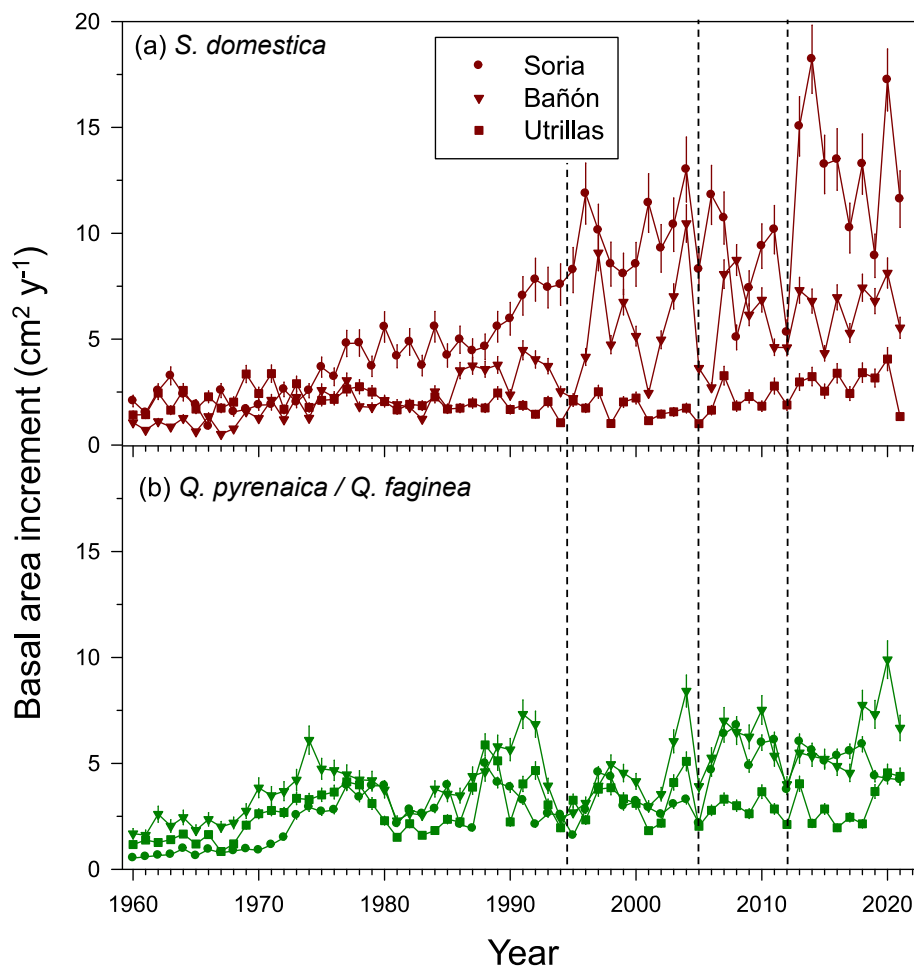


Fig. 3. Growth data (basal area increment) of the study species and sites considering the period 1960–2021. The vertical dashed lines indicate the study droughts (1994–1995, 2005 and 2012). Values are means $\pm$ SE.

and by low soil moisture availability from spring to autumn and also by high summer temperatures.

The daily growth responses to temperature were more stable for service trees than for oaks (Figs. S6 and S7), in particular during the start and end of the growing season, whereas in oaks the high variability observed, particularly in spring, suggests that other clues than temperature should be involved in triggering the start of growth. Service trees showed a bimodal pattern of favorable conditions for growth, with a first peak around June and a minor peak around September–October (ca. 20% of annual growth), whereas in oaks the favorable period for growth was unimodal, peaking in June–July (Fig. 8). Oaks showed a more limited growth after the summer as compared with service trees due to water shortage. In fact, the relevance of reduced soil moisture in late summer as a major constraint of growth increased in all study sites and tree species, but it was more evident for oaks from Utrillas and Soria (Fig. 9). In contrast, the estimated period with growth limitations due to low temperatures decreased and this trend is more evident in spring than in autumn (Fig. S6).

Regarding growth phenological events (xylem onset and cessation dates) inferred from the VS-model simulations, service trees and *Q. faginea* showed trends towards an earlier start of the growing season, whereas a later growth cessation was observed in *Q. pyrenaica* from Soria, in both species from Bañón and in service trees from Utrillas (Fig. S9). Finally, we found positive correlations, albeit not significant, between the date of leaf falling start of service trees and the simulated date of xylem onset of Bañón service trees ($r_s = 0.42$, $p = 0.10$).

4. Discussion

Oaks responded more strongly to drought than service trees, as the former are more sensitive to increased summer temperatures, and therefore increased atmospheric water demand, than the latter. Oaks tend to exhibit anisohydric ('water-spending') behavior, maintaining high transpiration and stomatal conductance rates under moderate drought conditions by uptaking water from deep soil water pools (Klein, 2014; Ripullone et al., 2020). For instance, stem water content peaked in late spring in *Q. pyrenaica* when water availability was the highest, whereas during the dry summer water was extracted from deep soil layers (Hernández-Santana et al., 2008).

In the case of *Sorbus* species, rowan (*Sorbus aucuparia* L.) showed a high resistance to drought-induced xylem embolism (Vogt, 2001). The anisohydric *Sorbus alnifolia* (Sieb. & Zucc.) C. Koch exhibited a high resistance to drought-induced dieback, and neither growth nor mortality were affected by experimentally reduced precipitation (Chen et al., 2019). This low responsiveness to drought of *S. alnifolia* was associated to an increase in non-structural carbohydrates, which could act as osmolytes or be used to resume growth once water stress is alleviated (Woodruff et al., 2015). In seedling experiments, service trees showed a remarkable ability to recover after drought stress, possibly because they lost part of the whole stem hydraulic conductivity (Kunz et al., 2016). This recovery ability makes this species suitable for sites where seasonal precipitation results in recurrent and less intense droughts, such as Mediterranean forests.

Service trees showed a high water-use efficiency and a constant

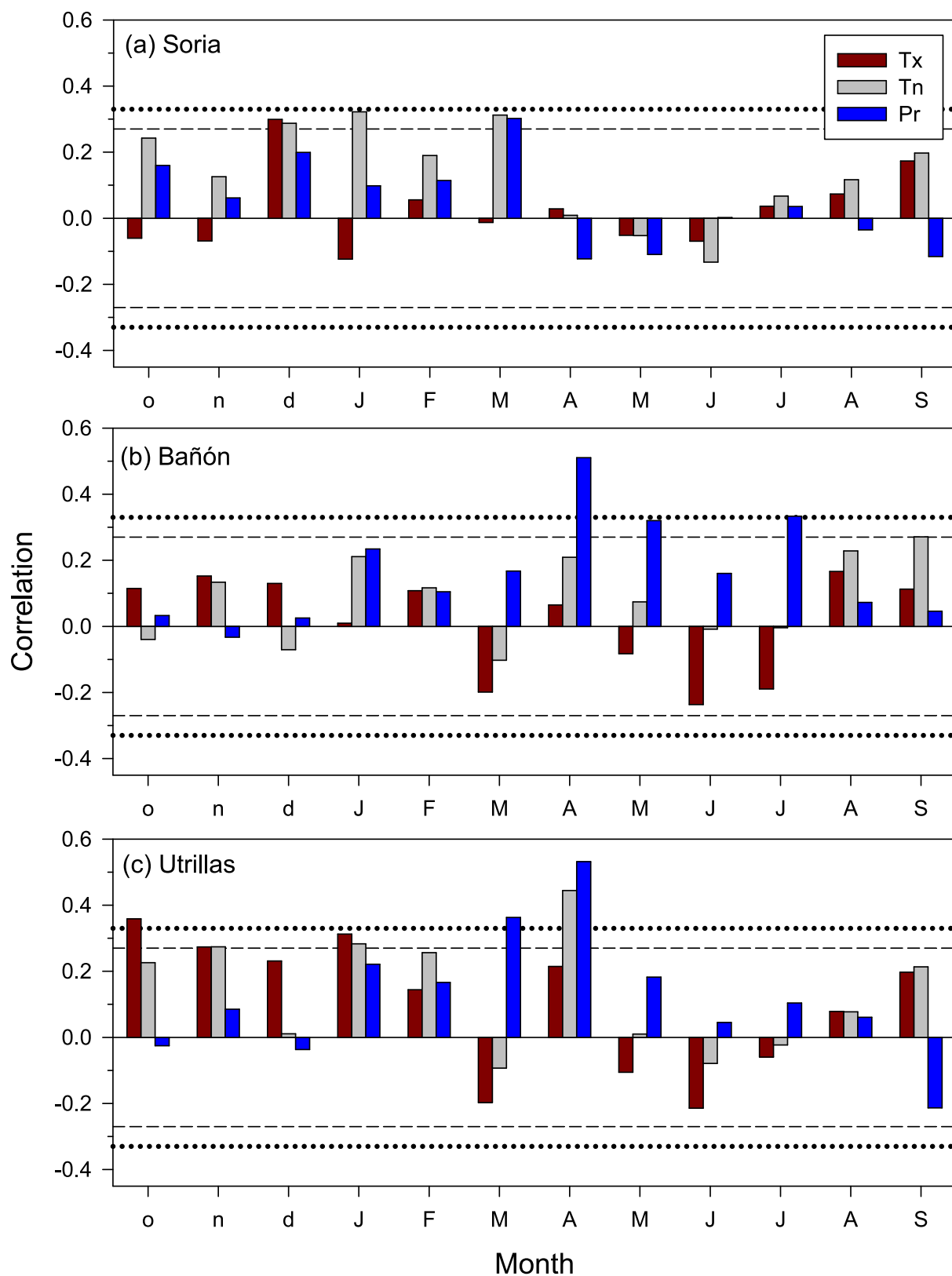


Fig. 4. Climate-growth relationships of the service tree based on Pearson correlations (bars) calculated relating site series of ring-width indices and monthly climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; Pr, total precipitation) in the three study sites: (a) Soria, (b) Bañón, and (c) Utrillas. Correlations were calculated from October of the prior year (months abbreviated by lowercase letters) to September of the current year (months abbreviated by uppercase letters). Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

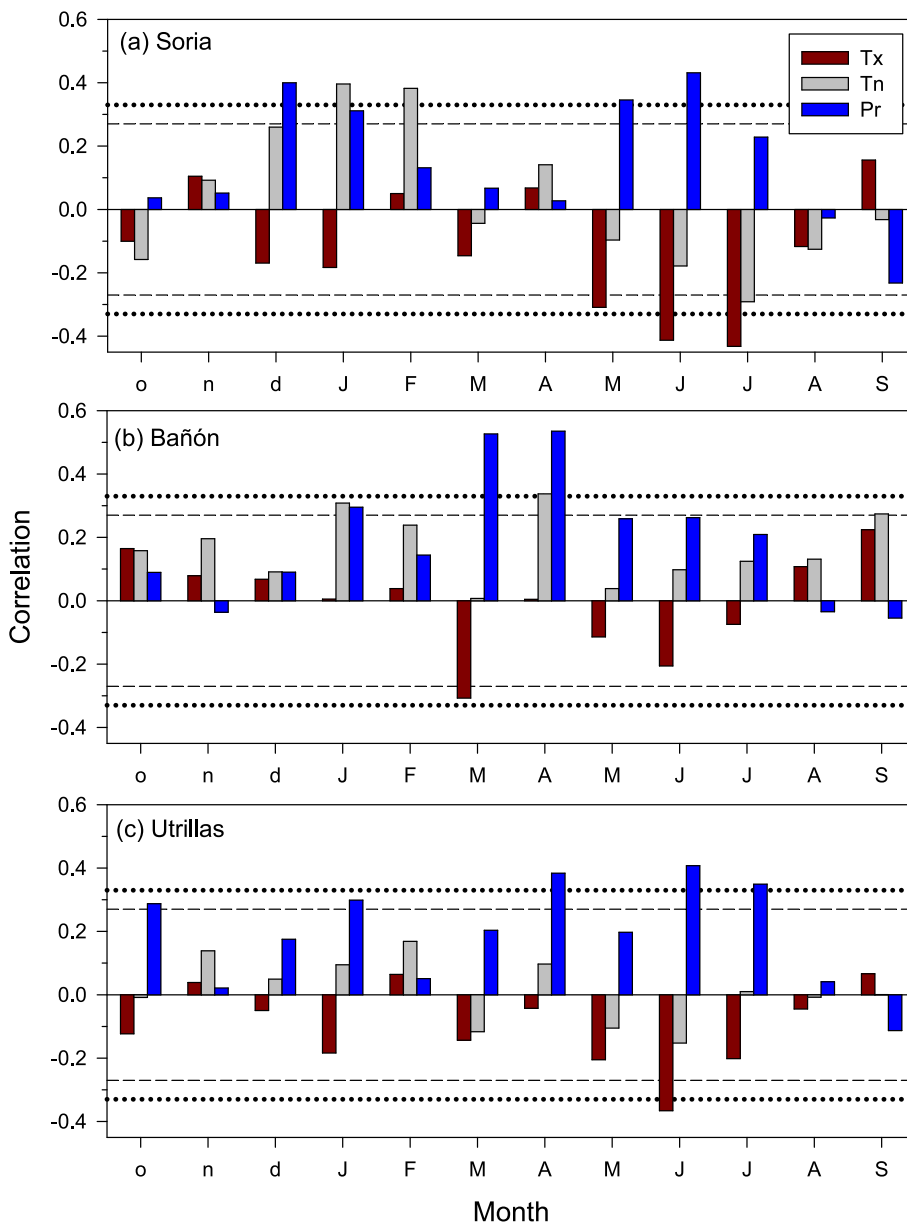


Fig. 5. Climate-growth relationships of the study oak species based on Pearson correlations (bars) calculated relating site series of ring-width indices and monthly climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; Pr, total precipitation) in the three study sites: (a) Soria, (b) Bañón, and (c) Utrillas. Correlations were calculated from October of the prior year (months abbreviated by lowercase letters) to September of the current year (months abbreviated by uppercase letters). Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

reduction in stomatal conductance rates as drought intensified (Kunz et al., 2016) suggesting a more isohydric behavior than the wild service tree (*Sorbus torminalis* L.), which showed a high vulnerability to xylem embolism in the field (Martínez-Vilalta et al., 2002). Overall, these ecophysiological studies confirm that *Sorbus* species, and particularly service trees, are drought-tolerant hardwood species that frequently regenerate through root sprouts (Biedenkopf et al., 2007) and have a high resilience capacity (Paganová, 2008). Moreover, such recovery ability is also observed after other disturbances such as fire because service trees show rapid growth rates and high resprouting ability which could allow them to become dominant in burned areas (Quevedo et al., 2007). These data agree with our findings based on tree rings which showed a better post-growth growth recovery in service trees than in oaks.

In northern and central Europe, the radial growth of the wild service tree is limited by summer drought but enhanced by cool, humid and cloudy conditions during the growing season and in the prior winter (Rasmussen, 2007; Pyttel et al., 2013; Cedro and Cedro, 2015; Cedro, 2016). In the Spanish study sites, the growth of service trees was constrained by dry spring conditions, particularly in the dry sites, and also

by cool conditions. For instance, the responsiveness of service tree growth to March–April precipitation observed in Bañón and Utrillas, but not in Soria, may be explained by the warmer and drier conditions of the first two sites. Sampled service tree individuals were usually found in habitats with deep soils, excepting Utrillas where rocky soils probably contributed to exacerbate drought stress, and they were not intensively managed in the past. The oaks were more responsive to the SPEI drought index and this association seems to be strengthening in Soria and Utrillas, where aridification trends were more marked. This is probably related to the negative effects of warmer spring-to-summer conditions on oak growth which may revert the positive effects of increased spring rainfall (Alla and Camarero, 2012).

The VS-model identified low levels of soil moisture in late summer as the main constraints of oak growth which concurs with its responses to long droughts (9–13 months) peaking in spring–summer. In contrast, service trees were less responsive to drought and mainly responded to shorter droughts (2–7 months). Both the SPEI-growth correlations and the VS-model simulations forecast a major relevance of drought stress as driver of oak growth in Soria and Utrillas, whereas the relatively low growth rates and canopy dieback of service trees in Utrillas suggest some

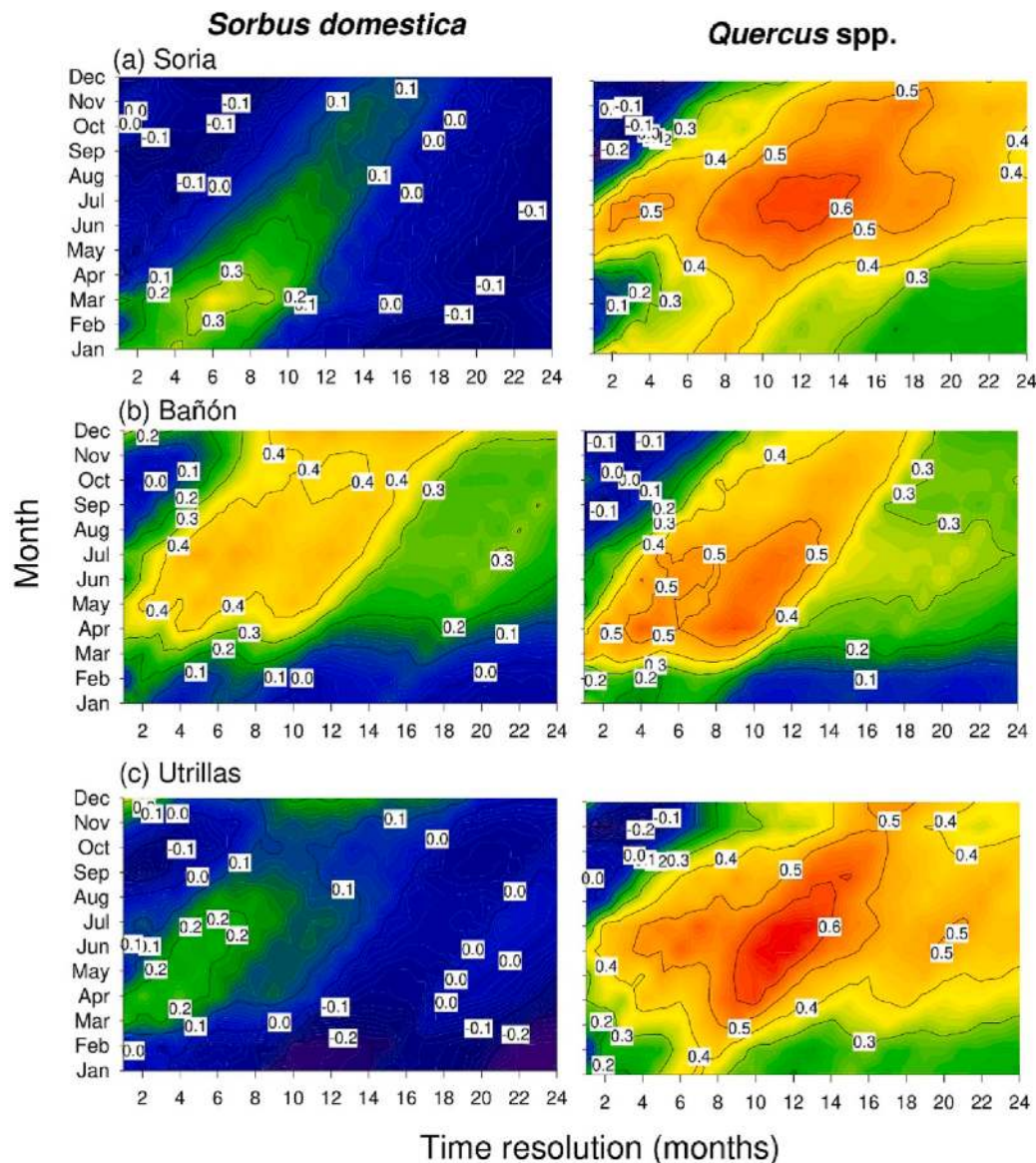


Fig. 6. Correlations obtained by relating the mean site series of ring-width indices of service trees (left column) and oaks (right column) and the SPEI drought index in the three study sites: (a) Soria, (b) Bañón, and (c) Utrillas. Pearson correlations were calculated for 1- to 24-month long temporal scales (x axes) and from January to December (y axes).

of them could die in the short term. In contrast, several monumental trees from Soria, showing remarkable sizes and high growth rates, should be further catalogued and preserved.

Unexpectedly, service trees showed earlier dates of leaf falling in autumn near Utrillas as August minimum temperatures rose, but this advance of autumn phenology did not affect the annual growth, as observed in conifers (Camarero et al., 2022). Warmer temperatures can lead to drier conditions, albeit correlations between leaf falling dates were marginally significant with prior-winter moisture conditions (January SPEI 3, $r = -0.47$, $p = 0.06$). This finding does not agree with the delayed leaf colouring observed in deciduous species, including the rowan, across Switzerland and linked to drier conditions (Meier et al., 2021). Warmer and drier summer conditions may cause premature leaf colouring and fall (Gallinat et al., 2015; Xie et al., 2018), which could explain the advancement of leaf falling. Longer phenological series of service trees would be required to test this idea.

Our findings support previous research showing that temperature rather than photoperiod controls growth cessation in *Sorbus* species (Heide, 2011). The VS-model simulations suggest that the mechanism

involved in growth onset in oaks should be different from the one followed by the service tree, which is able to growth after summer. The potential bimodal behavior of service trees could be assessed using dendrometers and could also explain its better post-drought recovery as compared with unimodal oaks (Camarero et al., 2010; Vieira et al., 2022), and the lower correlations found between observed and simulated ring-width chronologies in service trees. Other factors affecting growth, such as masting, could also be involved and should be investigated in the future. However, in the rowan the flowering intensity and radial growth were not related (Kobro et al., 2003). Nevertheless, the VS model should be further refined to better integrate photoperiod cues so as to improve growth simulations and xylem onset and cessation dates. For instance, Gauzere et al. (2017) found that in photosensitive species such as European beech and the sessile oak, budburst dates could be better simulated using models integrating a compensatory effect of long photoperiod on chilling deficiency.

Our results suggest that in the Iberian Peninsula, service trees may replace some oak species with higher sensitivity to drought due to climate change (Paganová, 2007), and the southern edge range of the

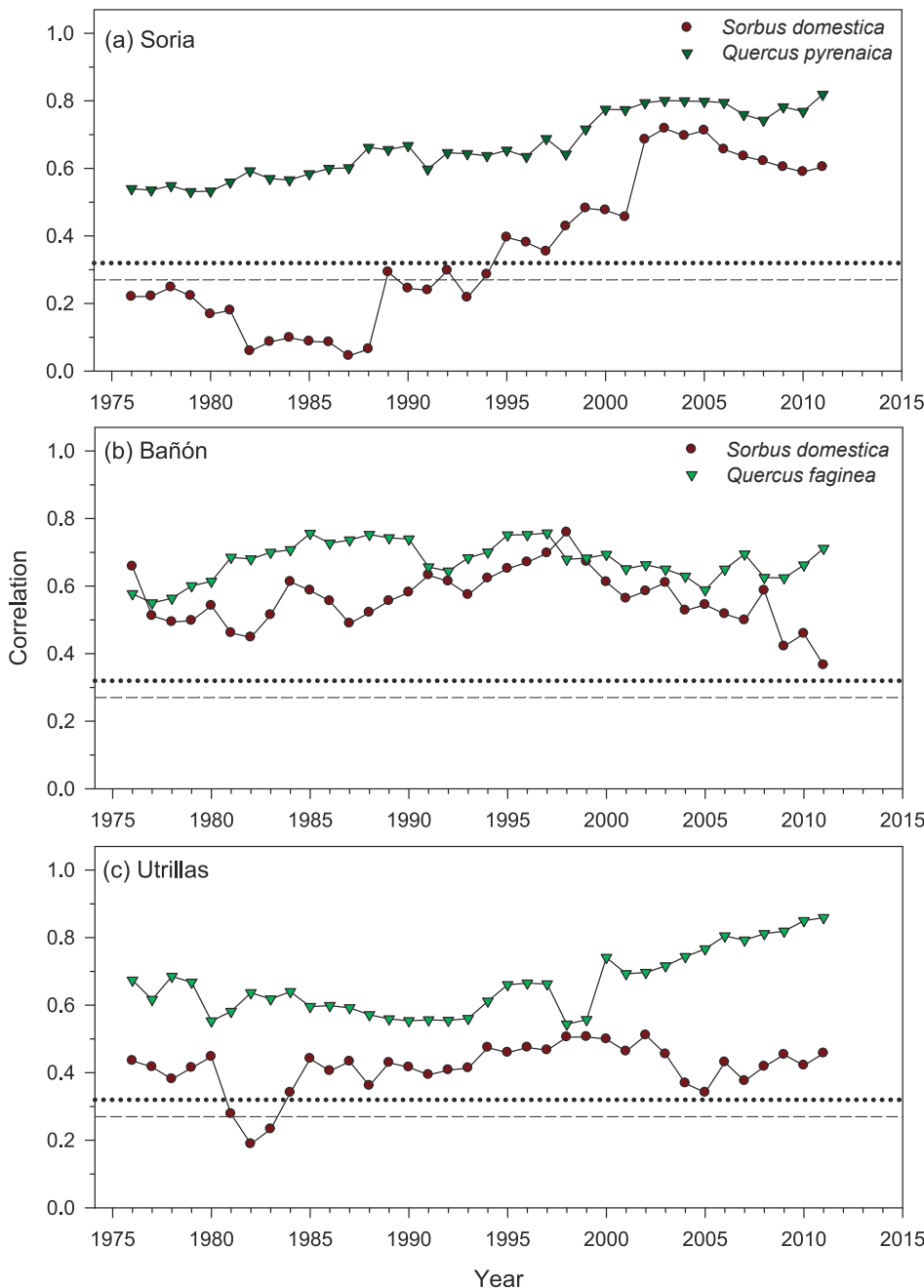


Fig. 7. Moving correlations calculated using 20-year moving intervals and relating series of ring-width indices of *S. domestica* (brown symbols) and co-occurring oaks (green symbols) and SPEI. The selected SPEI temporal resolutions are months corresponding to those showing the highest correlations (see Fig. 6). The horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

studied species is expected to shift northwards, as predicted for temperate broadleaved species (Thuiller et al., 2006). However, the natural spread of service trees may be limited by several factors, including their scattered distribution due to secular human use, poor sexual regeneration, low seed dispersal, vulnerability to drought stress, and low competition with other species, which together may reduce their ability to adapt to climate change (Rasmussen and Kollmann, 2004a, 2004b; Hemery et al., 2010; Kunz et al., 2016).

The natural dispersal of service trees should be assisted by humans through selection of adequate provenances and high-quality seeds from stands with a high number of trees to prevent low genetic variation in progeny (Biedenkopf et al., 2007) and to avoid range reductions due to climate warming and habitat fragmentation. Local expansion into suitable sites with fertile, deep soils or stable water supply (e.g., near rivers or former cropland) may also be necessary (Paganová, 2008). Overall, human-assisted migration of service trees may be necessary to facilitate

their spread to more suitable sites and ensure their survival under climate change. Forest managers must pay particular attention to species that, despite their current scattered distribution, have a high potential to enhance drought-prone forests under both current and expected climate scenarios.

5. Conclusions

Service trees were less responsive to warmer spring-summer conditions and drought severity than coexisting oaks. Service trees showed a better post-drought recover at inter- and intra-annual scales than oaks, which were more sensitive to late-summer drought stress and showed limited growth rates in autumn. In the driest sites, old, senescent service trees are threatened by both lack of management and aridification, as indicated by their low growth rates. However, monumental service trees in colder sites show a high growth potential and should be considered a

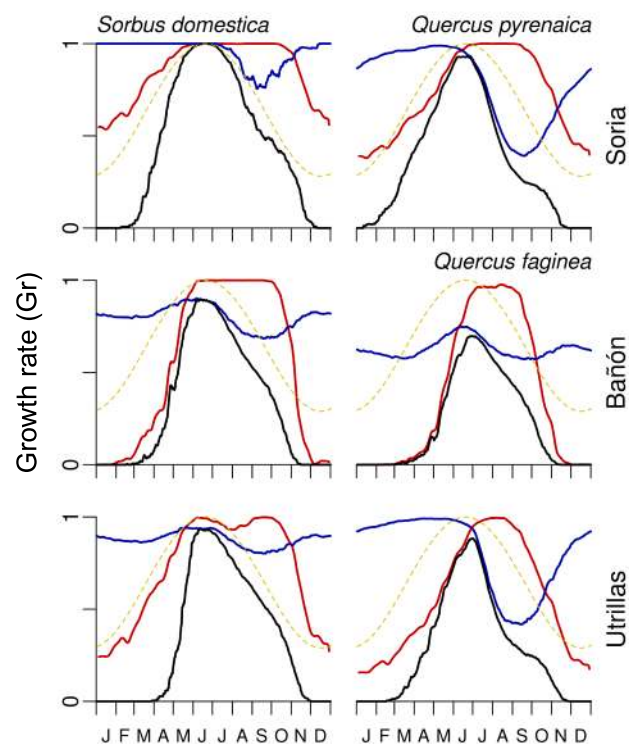


Fig. 8. Daily mean growth response curves (black lines) or growth rates (Gr) considering temperature (GrT, red lines) and soil moisture (GrW, blue lines) limitations based on the Vaganov-Shashkin model for the six chronologies and for the best-replicated common period (1965–2021). The dashed lines show the estimated influence of radiation on growth rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Vaganov-Shashkin parameters estimated automatically for each chronology and for the best-replicated common period (1965–2021). The last line shows the Pearson correlation coefficients (r) between observed and simulated chronologies which were significant ($p < 0.05$) for all chronologies. The description of each parameter is given in Table S1.

Variable (units)	Service trees			Oaks		
	Soria	Bañón	Utrillas	Soria	Bañón	Utrillas
T1 (°C)	−4.9	6.5	−1	−4.6	8	−1.3
T2 (°C)	10	10.2	10.2	15.6	16.6	17.7
T3 (°C)	24.7	24.6	19.6	26.9	20.9	28.8
T4 (°C)	44.9	39.2	35.2	36.9	40.3	37.9
M1 (v/v)	0.069	0.062	0.064	0.021	0.062	0.07
M2 (v/v)	0.101	0.246	0.158	0.239	0.249	0.216
M3 (v/v)	0.8	0.8	0.8	0.8	0.8	0.8
M4(v/v)	0.95	0.95	0.95	0.95	0.95	0.95
M0 (v/v)	0.562	0.301	0.303	0.33	0.307	0.312
Mmin (v/v)	0.049	0.046	0.041	0.065	0.054	0.035
Mmax (v/v)	0.572	0.44	0.362	0.427	0.374	0.667
rootD (mm)	435	795	1475	550	1305	520
Rated	0.0041	0.0046	0.0037	0.0013	0.0044	0.0010
Pmax (mm / day)	68	65	79	48	73	61
k1	0.860	0.860	0.778	0.608	0.95	0.551
k2 (mm / day)	0.333	0.310	0.201	0.229	0.227	0.342
k3 (mm / day)	0.076	0.052	0.05	0.117	0.052	0.114
Tbeg (°C)	8.2	7.9	10.0	6.0	6.5	7.2
Tend (°C)	8.9	12.0	8.8	11.4	12.3	9.4
r	0.54	0.64	0.58	0.71	0.77	0.70

priority for conservation. These trees represent legacies of past intensive management in drought-prone agroforestry systems across southern Europe. Our correlational and modeling approach could be further

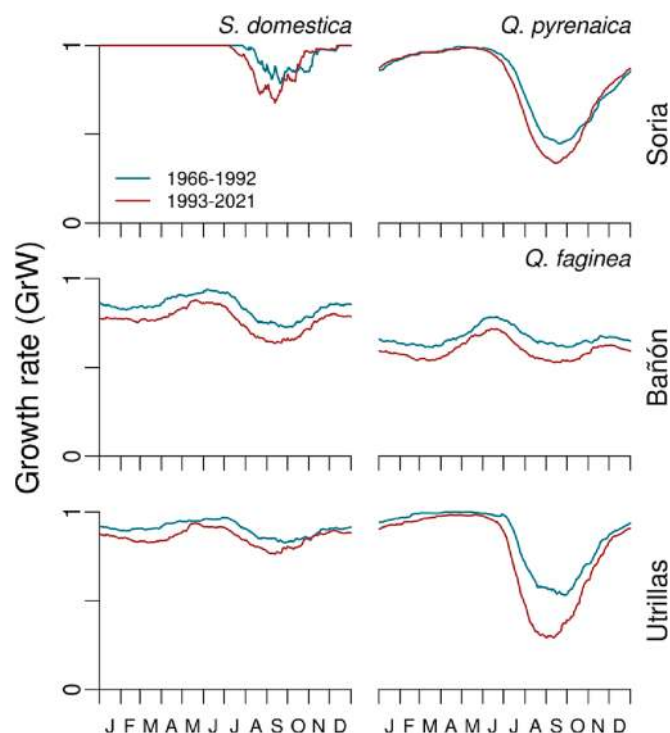


Fig. 9. Temporal variation of relative growth response to soil moisture (GrW) in the periods 1966–1992 (blue lines) and 1993–2021 (red lines). Note that lower GrW values indicate growth is more constrained by low soil moisture. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extended to evaluate and forecast growth responses to warmer climate conditions in drought-prone sites. Under continental Mediterranean conditions minor broadleaved timber tree species such as service trees show a good potential to enrich drought-prone, multifunctional forests.

Within the current frame of climate change, especially regarding the Mediterranean continental inland areas, service trees represent an interesting alternative to the other valued European species used in plantations for high-quality timber purposes such as walnut and cherry trees. Walnut trees find serious handicaps to withstand spring droughts and frosts and they require fertile soils, whereas cherries cannot withstand severe drought or very basic soils. On the contrary, service trees are very well adapted to tolerate these adverse circumstances. Furthermore, service trees provide not only high quality timber, but also fruits with potential for the food industry, so they can be considered a double attitude forest species, valid either for afforestation or production purposes. This encourages its use in future forestry projects in Mediterranean areas.

CRediT authorship contribution statement

J. Julio Camarero: Conceptualization, Data curation, Writing – original draft. **Filipe Campelo:** Data curation, Formal analysis, Funding acquisition, Investigation. **José Antonio Sánchez-Sancho:** Data curation, Writing – review & editing. **José Carlos Santana:** Data curation, Methodology.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121070>.

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