



Growth phenology adjusts to seasonal changes in water availability in coexisting evergreen and deciduous mediterranean oaks



Filipe Campelo^a, Álvaro Rubio-Cuadrado^{b,c}, Fernando Montes^d, Michele Colangelo^{c,e}, Cristina Valeriano^c, J. Julio Camarero^{c,*}

^a Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, Coimbra, 3000-456, Portugal

^b Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y Del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria S/n, 28040, Madrid, Spain

^c Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, E-50192, Zaragoza, Spain

^d Departamento de Dinámica y Gestión Forestal, Instituto de Ciencias Forestales (ICIFOR-INIA-CSIC), Ctra. La Coruña Km 7.5, 28040, Madrid, Spain

^e Scuola di Scienze Agrarie, Forestali, Alimentari e Ambientali, Università Della Basilicata, Viale Dell'Ateneo Lucano 10, 85100, Potenza, Italy

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ABSTRACT

Different leaf (evergreen vs. deciduous habit) and xylem (diffuse-vs. ring-porous wood) traits represent contrasting strategies to face seasonal changes in water availability and temperature. However, how contrasting leaf and xylem habits of coexisting tree species affect stem wood formation and tree-ring development remains poorly understood. Here, we investigated the spatio-temporal patterns of wood formation in two deciduous oaks (*Quercus faginea* and *Quercus petraea*) and two evergreen oaks (*Quercus ilex* and *Quercus suber*) coexisting in seasonally dry Mediterranean forests along an aridity gradient in Spain. We hypothesized that growth responses to drought and intra- and inter-annual growth patterns would differ between functional groups. We simulated intra- and inter-annual growth using a modified version of the Vaganov-Shashkin (VS) process-based, growth model. The VS model simulations were used to estimate growth changes under a high emission scenario (RCP 8.5) for the current distribution of the study oak species and to forecast their future performance under warm (4.8 °C) conditions in the Iberian Peninsula. Our simulations indicate that climate warming would induce a shortening of the ring-growth season and a reduction of radial growth in evergreen and deciduous Mediterranean oaks, particularly in dry sites from southern and eastern Iberia currently occupied by *Q. ilex* and *Q. faginea*. Evergreen oaks may better recover after dry periods than deciduous oaks by resuming growth after the summer drought. Low soil water availability in spring would be more detrimental to growth of deciduous oaks. Process-based growth models should be refined and validated to better forecast changes in tree growth as a function of climate.

1. Introduction

The Mediterranean Basin is a climate-change hotspot, where evident trends of warming and aridification have reduced soil moisture and increased drought stress in the last decades (Giorgi, 2006). Drought-triggered forest dieback has been observed in many Mediterranean forests, where tree growth and forest productivity are mainly driven by seasonal changes in water availability (Camarero et al., 2015a, 2015b; Gentilesca et al., 2017; Valeriano et al., 2021). Indeed, this region is at risk of experiencing strong alterations in forest ecosystem structure and composition due to their vulnerability to climate extremes such as droughts and heat waves (Cramer et al., 2018). Therefore, improving our

knowledge of tree growth responses to climate is a top priority in the Mediterranean region.

Tree species in Mediterranean forests face two potential stress periods: cold in winter and water shortage during the summer due to low precipitation and high evapotranspiration rates (Castro-Díez and Montserrat-Martí, 1998; Lempereur et al., 2016). To overcome the summer water deficit, trees change their morphological and/or physiological traits to minimize water loss (Vieira et al., 2013). Grouping trees into functional groups based on their morphological and physiological traits, such as leaf and xylem habits, can help to better understand how they cope with seasonal water deficit (Pacheco et al., 2015; Huang et al., 2020).

* Corresponding author.

E-mail address: jjcamarero@ipe.csic.es (J.J. Camarero).

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Deciduous and evergreen Mediterranean oaks constitute two clearly differentiated functional groups in terms of their carbon and water economies, despite co-existing in a wide range of environments (Sheshtakova et al., 2014; Guan et al., 2023). The coexistence of deciduous and evergreen oak species in this region, where they can reach their southernmost distribution limits (Camarero et al., 2021a), can be partially attributed to their different functional strategies for coping with summer drought, i.e. due to temporal niche differences (Baldochi et al., 2010). Deciduous oaks have “cheap” tissue investment and fast returns, making them advantageous in environments with high intra-annual variation in temperature or precipitation, and in sites with higher soil moisture and nutrients (Guan et al., 2023). In contrast, evergreen oaks have “expensive” tissue investment and slower returns, making them better adapted to sites with low climatic seasonality or limited resource availability. The conservative strategy of evergreen oaks allows them to assimilate carbon over extended growing seasons, compensating for low photosynthetic rates in summer and winter, and conferring a competitive advantage in xeric sites (Alonso-Forn et al., 2020). Deciduous oaks may lose abundant shoots and leaves during drought (Camarero et al., 2016), whereas evergreen oaks show high resistance to xylem embolism and effective photoprotection, allowing their leaves to function during drought and keeping living buds for longer lifespans (Alla et al., 2013).

Differences in leaf-habit can also be reflected in the intra-annual wood formation pattern (García-Cervigón et al., 2020). In some evergreen oaks, such as *Quercus ilex*, a second period of wood formation can occur after summer under favorable conditions (Lempereur et al., 2016), resulting in the formation of a false ring (Campelo et al., 2007). This second peak of growth (bimodality) is thought to be an adaptation of evergreen species to take advantage of the autumn rains and mild temperatures in the Mediterranean climate (Camarero et al., 2010, 2021b; Campelo et al., 2018; Garcia-Fornier et al., 2019). A prolongation of the vegetative period in autumn was also reported in *Quercus faginea* in sites where temperatures and water availability are favorable (Mediavilla and Escudero, 2003).

The aim of this study is to investigate the potential differential impacts of future climate change on coexisting oaks with different leaf habits (evergreen vs. deciduous) and wood types (diffuse-vs. ring-porous) using a process-based model of tree growth (Vaganov-Shashkin model—hereafter VS model; see Vaganov et al., 2006; Tychkov et al., 2019). The VS tree-ring growth model is a process-based model that describes tree-ring formation as a function of local climate conditions (e.g., temperature, soil moisture) and solar radiation (Anchukaitis et al., 2020). This model was first introduced for conifers and has recently been successfully applied to hardwood species including oaks (Campelo et al., 2018; Tumajer et al., 2022), ash (Campelo et al., 2022) and services trees (Camarero et al., 2023). Unlike models accounting for carbon allocation (Li et al., 2014), the VS-model cannot simulate absolute growth values (i.e., basal area increment). However, the VS-model can accurately simulate inter- and intra-annual growth patterns and phenological events of wood formation (xylogenesis). Here, we propose a new approach to use VS-model simulations to investigate growth changes under future climate scenarios. This approach consists of averaging annual integrals of daily growth rates simulated by the VS-model for recent and future periods, and then calculate the ratio between future and recent periods to forecast changes in the growing season length in response to predicted climate scenarios.

Our initial hypothesis considers that deciduous oaks start to grow earlier and have a larger spring growth peak than evergreen oaks. We also expect a more pronounced bimodality in evergreen oaks, as they seem to better resume growth after the dry summer than deciduous oaks (cf. Montserrat-Martí et al., 2009). Lastly, we expect oak growth to be severely reduced by climate warming in xeric sites near the southernmost distribution limit of some species.

2. Material and methods

2.1. Study species

In the Iberian Peninsula, oaks are economically and ecologically important tree species. In the Mediterranean areas of the Iberian Peninsula, drought-resistant evergreen oak species (e.g., *Quercus ilex* L. and *Quercus suber* L.) are widely distributed in warmer sites in the south and south-west. These evergreen oaks are gradually replaced by deciduous oak species in more mesic sites as moving northwards (Benito Garzón et al., 2008). This geographic distribution seems to reflect the higher drought resistance of species such as *Q. ilex* (David et al., 2007), although the distribution of Mediterranean oak is highly shaped by historical human disturbances including logging, agricultural uses, pollarding and coppicing (Camarero and Valeriano, 2023).

Quercus ilex (Holm oak) is an evergreen tree with a wide distribution in the Mediterranean Basin (Fig. S1), and a wood anatomy that varies from semi-porous to diffuse porous (Campelo et al., 2010). Holm oak is a drought-tolerant species, able to withstand both winter frost and summer water stress (Nardini et al., 2000). Cork oak (*Q. suber*) is an evergreen Mediterranean tree with diffuse-porous wood that is widespread throughout the western Mediterranean Basin (Fig. S1), occurring in areas with an average annual rainfall of 400–1,000 mm and a mean annual temperature of 13–20 °C. Although both evergreen oak species often coexist, *Q. ilex* occurs mainly in the drier, inland regions on basic and acid soils, whereas *Q. suber* dominates in the wetter, western coastal areas on sites with acid soils (Vaz et al., 2010). According to David et al. (2007), the higher water status and more effective drought tolerance of *Q. ilex* is probably related to its deeper root systems compared to *Q. suber*.

Quercus faginea Lam., the Portuguese oak, is a winter deciduous tree with a ring-porous wood and restricted distribution to the Iberian Peninsula and Northern Africa, preferentially on basic soils (Loidi and Herrera, 1990) (Fig. S2). This is an anisohydric species adapted to the Mediterranean climate, though its “water-spending” strategy (Peguero-Pina et al., 2015). This species often shows reduced growth due to summer soil water shortage and its distribution could decrease due to increasing aridity as a result of global warming (Sánchez de Dios et al., 2009). *Quercus petraea* (Matt.) Liebl., the sessile oak, is a broad-leaved deciduous species with a ring-porous wood and it is widespread in temperate and sub-Mediterranean areas of Europe, with its southernmost limit of distribution reaching the northern Iberian Peninsula (Figs. 1 and S2). This temperate oak species requires relatively high air humidity and also high soil moisture, and at least 120 mm rainfall over the growing season (Bertini et al., 2011). *Quercus petraea* is phylogenetically closely related to *Q. faginea* (Hipp et al., 2019).

Both evergreen oaks (*Q. ilex* and *Q. suber*) exhibit a water-saving (isohydric) strategy that could be related to the evergreen trait to prevent irreversible foliage damage during the summer drought and preserve leaf functionality longer (Pinto et al., 2012). Although evergreen oaks are considered to be better adapted to the Mediterranean climate, as they occur in relatively warmer and drier areas compared to deciduous oaks, the coexistence of both functional groups can occur at intermediate soil water contents (Di Paola et al., 2017), whereas deciduous oaks tend to occur more frequently in habitats where water and nutrient availability is higher (Urbieta et al., 2008). The coexistence of evergreen and deciduous oaks can also be influenced by past forest management practices (Urbieta et al., 2008).

2.2. Study sites

Three sites (Agüero, Sestrica and Monfragüe) located in W and NE Spain where deciduous and evergreen oaks coexisted were selected along a gradient of summer aridity (Fig. 1 and Table 1). The three sites are

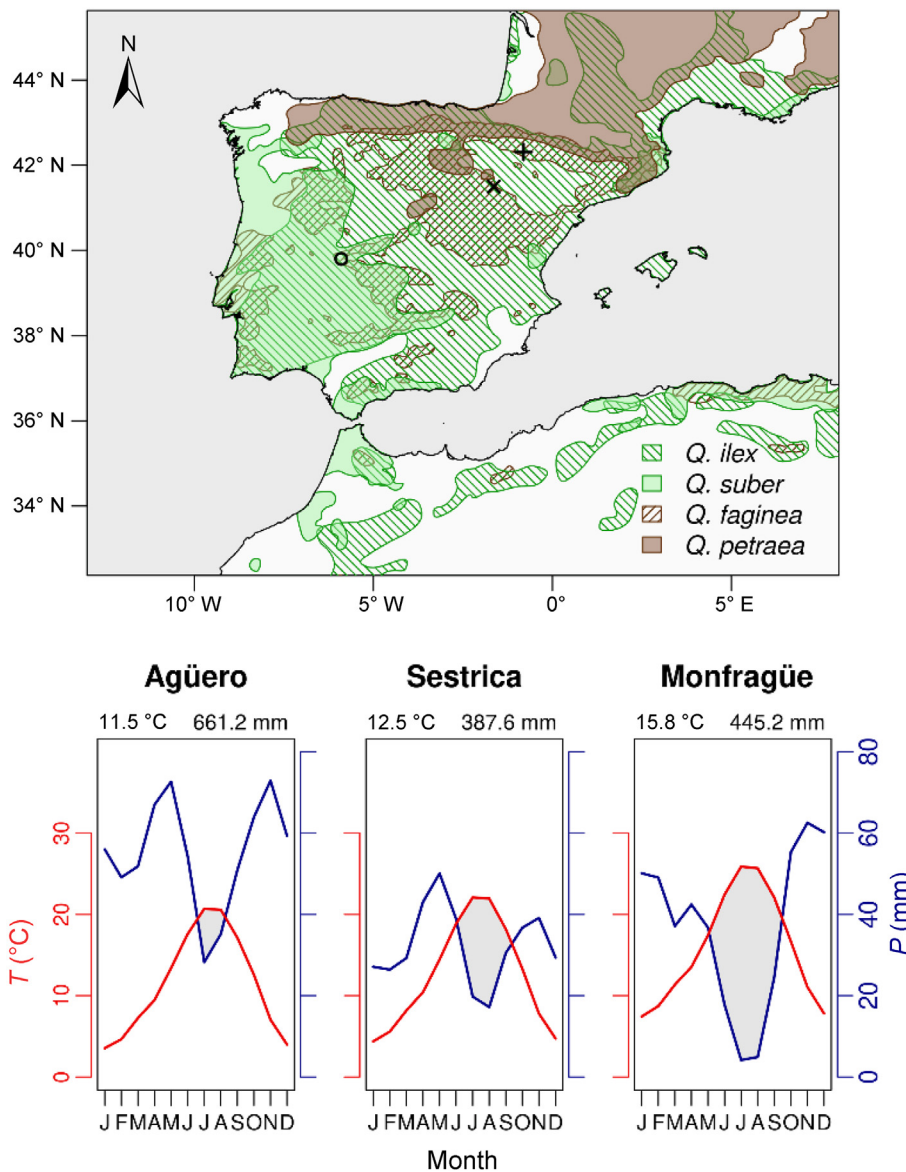


Fig. 1. Location of the three study sites in Spain (Agüero (+), Sestrica (×), and Monfragüe (○)), and climatic diagrams for the period 1962–2014 at the three sites; blue lines indicate precipitation (right y-axis), red lines indicate temperature (left y-axis), and the grey area indicates the theoretical dry period ($P < 2T$). Distribution of the study evergreen (*Quercus ilex* and *Q. suber*) and deciduous oak species (*Q. faginea* and *Q. petraea*) in northern Spain (adapted from Caudullo et al., 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Location of the two study sites.

Site	Latitude (° N)	Longitude (° W)	Elevation (m a.s.l.)	Slope (°)	Aspect	MAT (°C)	TAP (mm)
Agüero	42.3	0.8	750	5	W	11.5	661
Sestrica	41.5	1.6	865	10	E	12.5	388
Monfragüe	39.8	5.9	300	22	N	15.8	445

Mean annual temperature (MAT) and total annual precipitation (TAP) for the common period 1962–2014.

subjected to Mediterranean climatic conditions (summer drought, low annual precipitation with high year-to-year variability) and showed a summer dry period, that increases in intensity from Agüero to Monfragüe. Mean annual precipitation ranged from 388 (Sestrica) to 661 (Agüero) mm, and mean annual temperature varied from 11.5 to 15.8 °C. In Agüero, a mixed *Q. ilex* and *Q. faginea* stand was selected; here, the soil is calcareous, basic and poor. In Sestrica, a forest where *Q. suber* and *Q. petraea* coexisted was selected. In Monfragüe, the selected stand was dominated by *Q. suber* and *Q. faginea*. In these last two sites soils were acid and sandy. In the sites where *Q. suber* was present, cork extraction had been performed about 20 years ago. In all sites, coppicing was common until the 1960s, particularly in the case of *Q. ilex*, *Q. suber* and

Q. petraea. The mean diameter at breast height of sampled trees ranged between 18.0 (*Q. ilex* in Agüero) to 31.5 cm (*Q. suber* in Sestrica). According to data from nearby plots of the Spanish National Forest Inventory (Alberdi et al., 2017), basal area ranged between 3.1 (*Q. petraea* in Sestrica) to 15.2 (*Q. suber* in Sestrica) m².ha⁻¹.

2.3. Climate data

Due to the lack of local weather stations at each site, daily climatic data (precipitation and minimum and maximum temperature) were downloaded from the closest grid point from the E-OBS gridded (0.1° spatial resolution) climate dataset (v27.0e; Cornes et al., 2018). Daily

climatic data were obtained for the period between January 1, 1962 and December 31, 2014. The daily climatic was used to estimate monthly climatic data (minimum, mean and maximum temperatures, and precipitation).

2.4. Field sampling and dendrochronological data

In each site, between 12 and 21 mature and dominant trees were selected per tree species (Table 2). Two increment cores were taken with a 5-mm Pressler increment borer at 1.3 m per tree. Cores were air dried, glued on wooden sample supports and carefully sanded with progressively finer sandpaper. Tree rings were visually cross-dated and tree-ring widths were measured to the nearest 0.01 mm using a stereo-microscope and the LINTAB measuring table device connected to a computer running TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating quality of tree-ring series was evaluated using the COFECHA program (Holmes, 1983). To remove age-related growth trends and competition effects, a one-step detrending was applied to each tree-ring width series, using the R (R Core Team, 2022) packages *dplR* (Bunn, 2008) and *detrendeR* (Campelo et al., 2012). Cubic smoothing splines with 50% frequency-response cutoff equal to 30 years were applied to remove low-to medium-frequency signals and enhance the year-to-year signal. First-order autocorrelation was then removed by fitting autoregressive models. Lastly, ring-width chronologies were obtained for each site by averaging the resulting residual series of ring-width indices using a bi-weight robust estimate of the mean to reduce outliers' effects.

The statistical quality of each chronology was evaluated using the following variables: first-order autocorrelation (AR1), mean sensitivity (MS), mean correlation between series (Rbar) and Expressed Population Signal (EPS) (Fritts, 1976). The EPS defines how well the developed chronologies represent a theoretical, infinitely replicated chronology (Wigley et al., 1984). Following these authors, we used a threshold of EPS > 0.85 to determine the best-replicated period for each chronology and to define the reliable common-period for all chronologies. Mean annual tree-ring width, MS and AR1 were calculated on raw data, whereas indexed-series were used to calculate Rbar and EPS (Table 2).

2.5. Vaganov-Shashkin process-based model of radial growth

The Vaganov-Shashkin (VS) model of tree-ring formation was used to simulate daily growth variability for each site and species for the best-replicated common period (1962–2014). For each site, the residual ring-width (TRWi) chronology of each tree species was used to adjust the VS model. The VS model was applied to simulate TRWi as a function of daily temperature (GrT) and precipitation or soil moisture (GrW), based on the principle of limiting factors (Vaganov et al., 2006). A simple optimization algorithm was used to adjust six parameters, while the remaining parameters of the VS model were kept constant (Table S1). Due to the short best-replicated common period ($n = 53$ years), no validation analysis was performed on an independent period. Therefore, a restricted range of values was defined for each parameter to limit model over-fitting (Table S1). Differences in radial growth phenology and root system depth among species were taken into account by defining species-specific parameters used by the model. To ensure that all models

were fitted under similar conditions, both the random seed (999) and the initial values were the same. In addition, each parameter was optimized one by one, while the remaining parameters were kept constant at their previously optimized values. The daily growth rates simulated by the VS model were used to estimate phenological growth events including the dates of growth onset, growth peak and growth cessation (denoted as DOY, day of the year).

2.6. Analyses of climate-growth relationships

Climate-growth associations were investigated by calculating Pearson correlations between series of ring-width indices (residual chronologies) and monthly climatic variables (minimum, mean and maximum temperatures, precipitation) from January to September of the year of tree-ring formation and also considering seasonal variables during the growing season (March–July, May–July).

2.7. Projecting growth variations in response to climate scenarios

To forecast variations in annual tree growth due to climate change in the Iberian Peninsula, we used climate data projected for the 21st century –model EC-Earth3 (European EC-Earth Consortium; Döscher et al., 2021) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2015, 2016). We used data from the SSP5-8.5 (Shared Socio-economic Pathway 5 and the Representative Concentration Pathway 8.5) scenario, which is an updated version of the previous CMIP5 RCP 8.5 scenario and tracks historical emissions (Lelieveld et al., 2016). This business-as-usual or fuel fossil-based development scenario assumes that radiative forcing increases to reach $8.5 \text{ W}\cdot\text{m}^{-2}$ in 2100, resulting in $4.8 \text{ }^\circ\text{C}$ warming relative to the late-20th-century baseline.

For each oak species, the best-fitted VS-model (i.e., the model with the highest correlation between observed and estimated tree-growth) was used to forecast growth for the period 1950–2099. To avoid extrapolation bias, only grid-points within the distribution of each oak species, obtained from Caudullo et al. (2017), were considered. The mean annual growth estimated by the VS-model for the period 1950–1999 ($\text{Gr}_{1950-1999}$) was used as a reference and compared with the value forecasted for the period 2050–2099 ($\text{Gr}_{2050-2099}$). The ratio ($\text{Gr}_{2050-2099}/\text{Gr}_{1950-1999}$) was calculated for each grid-point. For a given grid-point, a ratio higher (lower) than 1 is observed if the mean annual relative growth is expected to increase (decrease) in the future compared to the recent period, and this change is attributed to climate warming.

3. Results

3.1. Tree-ring width data

The mean tree-ring width of deciduous oaks varied from 1.13 to 1.61 mm, with *Q. petraea* in Sestrica showing the narrowest rings and the lowest standard deviation (Table 2, Fig. S3). For evergreen oaks, mean tree-ring width varied from 1.08 to 2.27 mm, with *Q. suber* in Monfragüe showing the widest tree rings. At each site, mean first-order autocorrelation (AR1) values were higher in deciduous oaks than in evergreen oaks. Mean sensitivity was higher in evergreen than in deciduous oaks

Table 2
Number of trees and dendrochronological statistics of oaks species at the three studied sites.

Site	Oak species	No. Trees	No. Cores	Tree-ring width (mm)	AR1	MS	Rbar	EPS
Agüero	<i>Q. ilex</i>	20	24	1.08 ± 0.56	0.54 ± 0.16	0.42 ± 0.07	0.66 ± 0.15	0.84
	<i>Q. faginea</i>	15	30	1.61 ± 0.50	0.63 ± 0.20	0.28 ± 0.04	0.77 ± 0.13	0.90
Sestrica	<i>Q. suber</i>	15	28	1.75 ± 0.63	0.61 ± 0.19	0.41 ± 0.06	0.78 ± 0.11	0.86
	<i>Q. petraea</i>	21	41	1.13 ± 0.23	0.72 ± 0.08	0.33 ± 0.03	0.88 ± 0.07	0.98
Monfragüe	<i>Q. suber</i>	12	18	2.27 ± 0.56	0.44 ± 0.17	0.50 ± 0.07	0.65 ± 0.21	0.91
	<i>Q. faginea</i>	14	26	1.36 ± 0.52	0.47 ± 0.19	0.37 ± 0.07	0.47 ± 0.19	0.91

Abbreviations: TRW, tree-ring width; AR1, first-order autocorrelation; MS, mean sensitivity; Rbar, mean inter-series correlation; EPS, Expressed Population Signal. The Rbar and the EPS values were calculated using residual ring-width series for the best-replicated period (1962–2014).

(Table 2). The mean correlation between individual tree-ring width series (R_{bar}) ranged from 0.47 to 0.88, while the EPS varied from 0.84 to 0.98, suggesting a high year-to-year growth variation shared among conspecific individuals.

3.2. Tree-ring climatic signals

In the three sites, March–July and May–July precipitation promoted tree growth in the four oak species, with *Q. petraea* showing the highest correlation ($r = 0.68$) (Table 3). The highest growth-precipitation correlations were found for March–July, except for *Q. ilex* in Agüero, which showed the highest correlation in January ($r = 0.50$). In the warmest Monfragüe site, growth of *Q. suber* and *Q. faginea* was positively correlated to minimum temperature in January and February and negatively in June. In the three sites, tree growth of evergreen and deciduous oaks was negatively correlated with maximum temperature in June (Table 3). Most of the autumn climate-growth correlations were not significant for both temperature and precipitation, with the exception of positive correlations between tree growth and mean and maximum temperatures in September at Monfragüe for *Q. suber* and *Q. faginea*.

3.3. Fitting the Vaganov-Shashkin model

The fitted parameters of the VS-model for each site and oak species are shown in Table 4. In the three sites, tree-ring width chronologies simulated by the VS-model were highly correlated with observed chronologies ($r = 0.50–0.83$; $p < 0.05$; Fig. 2), with the highest correlation being found for *Q. petraea* in the Sestrica site. These correlations were similar for evergreen and deciduous oaks in the mesic (Agüero; 0.50–0.53) and warmest (Monfragüe; 0.79–0.80) sites, whereas in the driest Sestrica site the correlations were higher for deciduous species (*Q. petraea*; 0.83) than for evergreen species (*Q. suber*; 0.52).

3.4. Intra-annual growth patterns simulated by the Vaganov-Shashkin model

Intra-annual growth patterns simulated by the VS model for evergreen and deciduous oaks differed (Fig. 3), and these differences were explained in part by variations in the limiting climatic factors throughout

Table 3

Pearson's correlation coefficients between residual chronologies and monthly climate data (T_{min} , minimum temperature; T_{mean} , mean temperature; T_{max} , maximum temperature; Pre, total precipitation) for the best-replicated period 1962–2014.

			JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	MAR-JUL	MAY-JUL
T_{min}	Agüero	<i>Q. ilex</i>	0.08	0.16	-0.22	0.23	-0.23	-0.26	-0.23	-0.19	-0.02	-0.20	-0.30*
		<i>Q. faginea</i>	0.25	0.22	-0.10	0.22	-0.07	-0.14	-0.16	-0.12	0.03	-0.07	-0.15
	Sestrica	<i>Q. suber</i>	0.22	0.15	-0.01	0.26	0.05	-0.07	-0.02	0.16	0.04	0.06	-0.02
		<i>Q. petraea</i>	0.35*	0.36**	-0.07	0.21	-0.06	-0.11	-0.31*	-0.02	-0.02	-0.13	-0.21
	Monfragüe	<i>Q. suber</i>	0.35**	0.47***	-0.03	0.18	-0.31*	-0.43**	-0.28*	-0.15	0.29*	-0.31*	-0.47***
		<i>Q. faginea</i>	0.42**	0.36**	-0.07	0.21	-0.21	-0.38**	-0.08	-0.04	0.22	-0.20	-0.32*
T_{mean}	Agüero	<i>Q. ilex</i>	-0.05	0.11	-0.33*	0.26	-0.27*	-0.39**	-0.29*	-0.19	0.12	-0.36**	-0.45***
		<i>Q. faginea</i>	0.20	0.13	-0.19	0.15	-0.17	-0.26	-0.20	-0.11	0.10	-0.24	-0.29*
	Sestrica	<i>Q. suber</i>	0.15	0.10	-0.11	0.25	0	-0.21	-0.02	0.11	-0.02	-0.04	-0.11
		<i>Q. petraea</i>	0.28*	0.26	-0.11	0.12	-0.18	-0.28*	-0.35*	0.02	0.04	-0.26	-0.34*
	Monfragüe	<i>Q. suber</i>	0.13	0.33*	-0.11	0.11	-0.32*	-0.36**	-0.26	-0.08	0.32*	-0.32*	-0.42**
		<i>Q. faginea</i>	0.20	0.28*	-0.18	0.08	-0.28*	-0.36**	-0.07	0.04	0.30*	-0.29*	-0.34*
T_{max}	Agüero	<i>Q. ilex</i>	-0.22	0.05	-0.38**	0.25	-0.27*	-0.45***	-0.29*	-0.15	0.20	-0.46***	-0.49***
		<i>Q. faginea</i>	0.09	0.04	-0.24	0.06	-0.23	-0.33*	-0.19	-0.09	0.13	-0.37**	-0.36**
	Sestrica	<i>Q. suber</i>	0.01	0.04	-0.14	0.21	-0.02	-0.28*	-0.02	0.08	-0.06	-0.09	-0.15
		<i>Q. petraea</i>	0.09	0.12	-0.11	0.05	-0.24	-0.35**	-0.34*	0.04	0.07	-0.31*	-0.40**
	Monfragüe	<i>Q. suber</i>	-0.26	0.08	-0.14	0.06	-0.31*	-0.31*	-0.22	-0.02	0.30*	-0.30*	-0.37**
		<i>Q. faginea</i>	-0.23	0.10	-0.20	-0.01	-0.30*	-0.34*	-0.06	0.10	0.33*	-0.32*	-0.34*
Pre	Agüero	<i>Q. ilex</i>	0.50***	0.16	0.22	0.08	0.27*	0.40**	0.21	0.03	-0.21	0.42**	0.46***
		<i>Q. faginea</i>	0.37**	0.08	0.17	0.27*	0.33*	0.16	0.23	-0.23	-0.09	0.41**	0.36**
	Sestrica	<i>Q. suber</i>	0.19	0.14	0.17	0.18	0.34*	0.26	0.17	0	0.15	0.43**	0.42**
		<i>Q. petraea</i>	0.43**	0.14	0.17	0.41**	0.50***	0.44***	0.20	0.01	-0.07	0.68***	0.64***
	Monfragüe	<i>Q. suber</i>	0.39**	0.24	0.18	0.07	0.28*	0.24	0.14	0.01	-0.06	0.41**	0.33*
		<i>Q. faginea</i>	0.41**	0.13	0.21	0.15	0.26	0.33*	0.18	-0.06	-0.21	0.50***	0.35**

Significant correlations at $p < 0.05$ are in bold and asterisks give the significance level (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 4

Vaganov-Shashkin parameters estimated for each chronology and for the best-replicated common period (1962–2014).

	Agüero		Sestrica		Monfragüe	
	<i>Q. ilex</i>	<i>Q. faginea</i>	<i>Q. suber</i>	<i>Q. petraea</i>	<i>Q. suber</i>	<i>Q. faginea</i>
T_1	6.6	5.9	7.9	5.2	7.2	7.6
T_2	10.9	10.1	15.6	17.8	10.1	11.8
T_3	24.8	24.5	20.2	24.4	18.8	18.5
T_4	34.2	31.6	35.0	35.0	34.6	31.8
W_1	0.069	0.066	0.070	0.054	0.015	0.068
W_2	0.180	0.196	0.144	0.197	0.153	0.100
r	0.53	0.50	0.52	0.83	0.79	0.81

The last line shows the Pearson correlation coefficients (r) between observed and simulated chronologies which were significant ($p < 0.05$) for all chronologies (see Fig. 2). The description of each parameter is given in Table S1.

the growing season (Fig. 4). *Quercus suber* and *Q. faginea* were negatively affected by high summer temperatures, especially at the warmest site (Monfragüe). The intra-annual growth pattern simulated by the VS model was site- and species-dependent, with evergreen oaks showing a longer growing season (Figs. 3 and 4). Both evergreen and deciduous oaks showed a right-skewed unimodal growth pattern, which became more pronounced with increasing summer drought (Fig. 3) and became a bimodal growth pattern for *Q. faginea* at the Monfragüe site, with a quiescent period during the summer and growth resuming in autumn.

3.5. VS model: phenological growth events

At the three sites, the timing of growth onset ranged from late January to March (Figs. 3 and 5), with deciduous oaks starting to grow earlier than evergreen oaks. At each site, deciduous and evergreen oaks synchronized the timing of their growth peaks and showed similar intra-specific variability. In the three sites, the phenological growth event with the highest (lowest) variability was growth initiation (cessation). At the wettest site (Agüero), both oak species showed the growth peak around the summer solstice, whereas at the warmest site (Monfragüe) the growth peak occurred almost one month earlier. The timing of growth onset and cessation showed temporal differences that were species and site dependent (Fig. 5). As the simulation progressed (1962–2014),

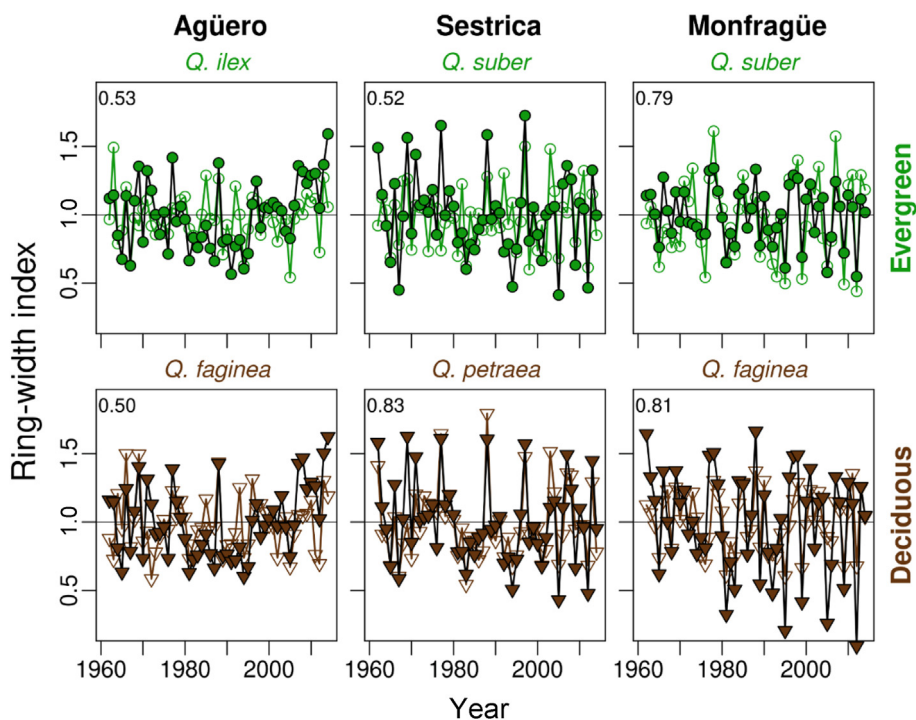


Fig. 2. Observed (color lines and open symbols) versus Vaganov-Shashkin simulated (black line and closed symbols) oak ring-width chronologies considering the best-replicated common period (1962–2014). For each site, the Pearson correlation coefficients (r) between observed and simulated chronologies are given and are significant in all cases ($p < 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

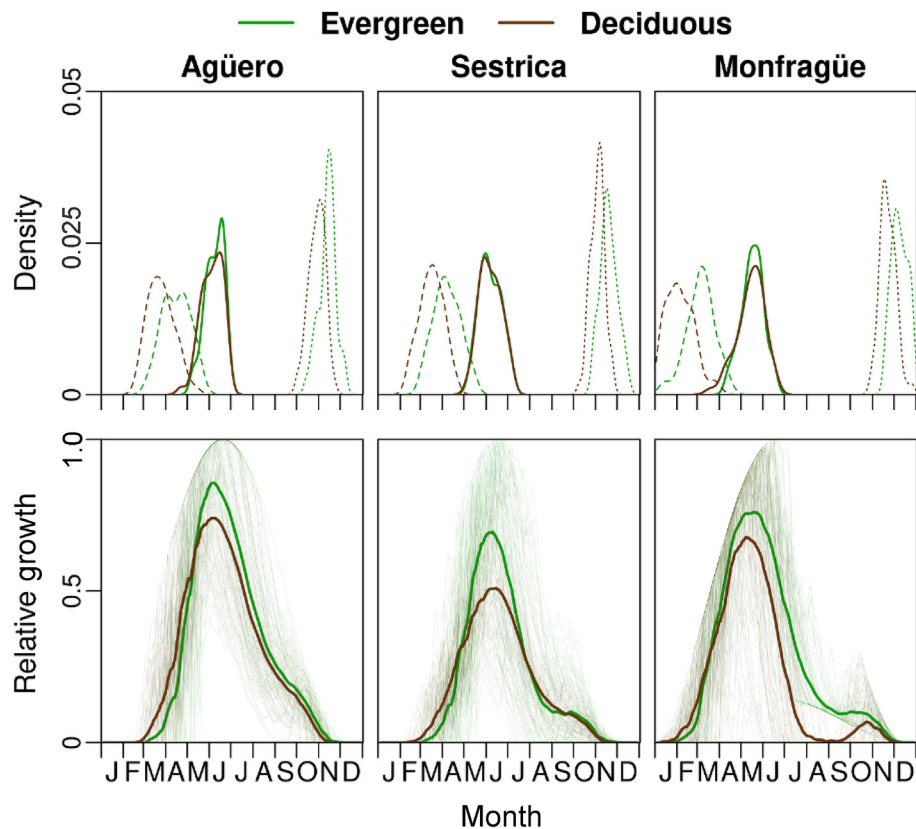


Fig. 3. Density of growth onset (dashed line), peak (solid line), and cessation (dotted line) and mean daily growth rates simulated by the VS-model for evergreen (green) and deciduous (brown) species in both study sites. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

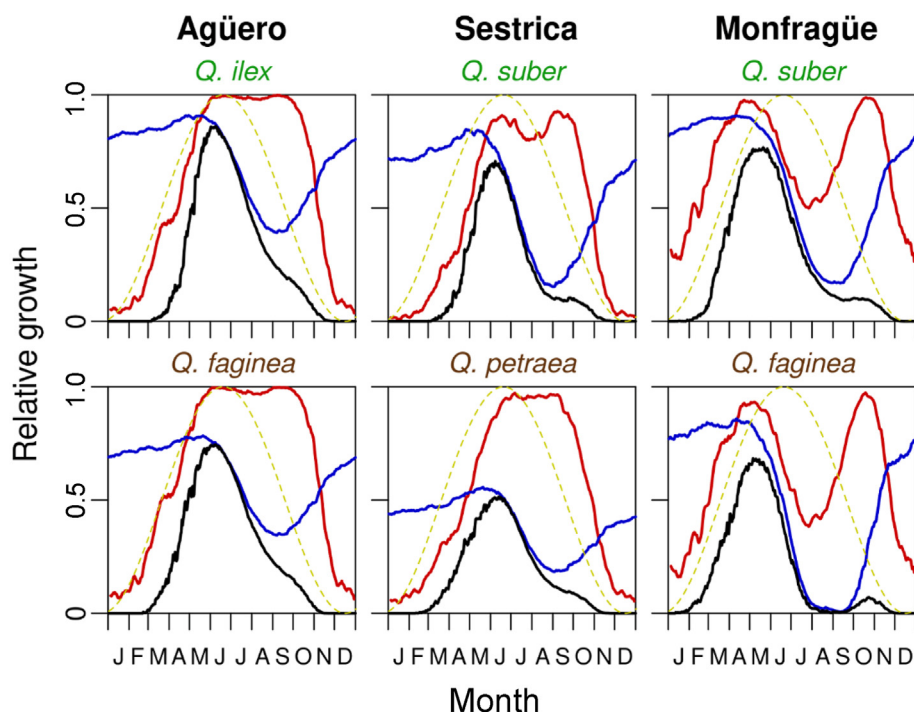


Fig. 4. Mean intra-annual patterns of daily partial growth rates related to temperature (red lines), partial growth rates due to soil moisture (gM) (blue lines) and integral growth rates (black lines) for each chronology simulated by the VS-model for the period 1962–2014. Note that mean gM values (blue lines) decrease from evergreen to deciduous species, within the same site, indicating stronger growth limitations by lower soil moisture. The dashed lines show partial growth rates explained by radiation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

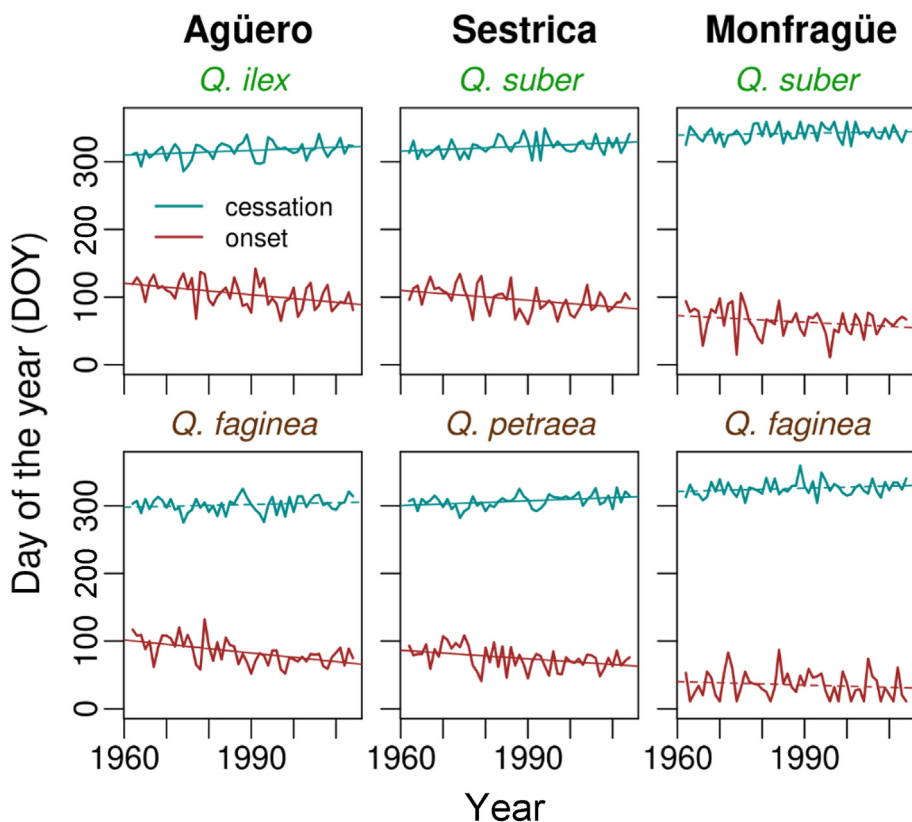


Fig. 5. Temporal variation of xylem phenological events (onset and cessation) simulated by the Vaganov-Shashkin model for evergreen (*Quercus ilex* and *Q. suber*) and deciduous (*Q. faginea* and *Q. petraea*) oak species in both study sites, for the period 1962–2014. Linear trends for both growth phenological events are added; solid lines are significant trends ($p < 0.05$), whereas dashed lines are non-significant trends.

growth onset tended to occur earlier for the four oak species, with the exception of the warmest site (Monfragüe), where no significant trend in phenology was observed.

3.6. Observed and simulated growth responses to climate

Climate-growth responses derived from the VS-model and climate-

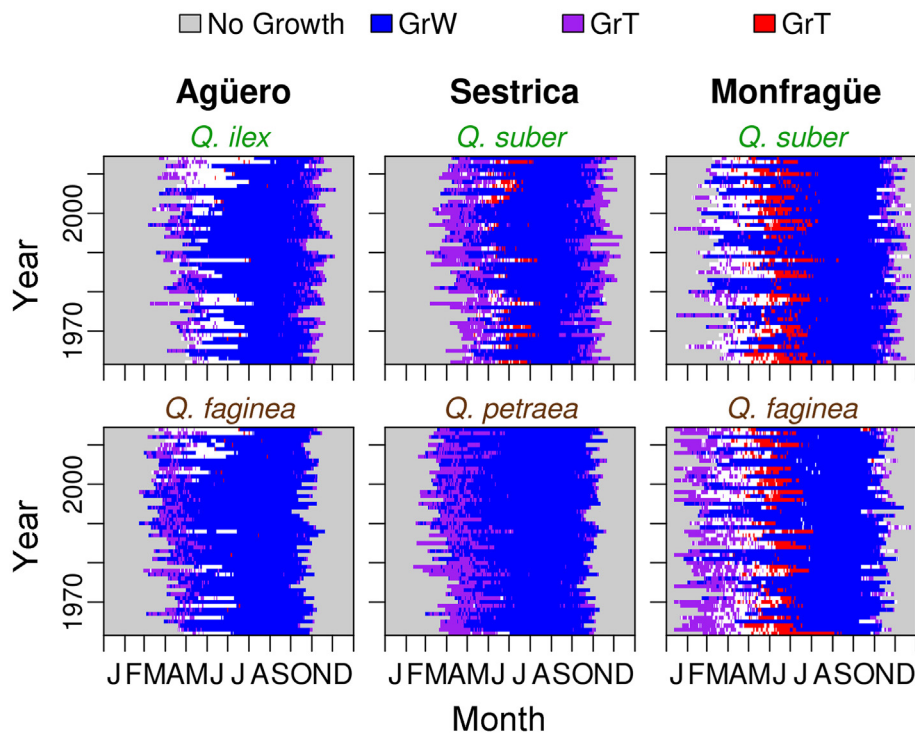


Fig. 6. Daily growth responses to climate simulated for each year. The color indicates the main climatic limiting factors: drought (GrW, blue areas), high temperature (GrT, red areas), low temperature (GrT, purple areas), optimal growing conditions (white areas), winter dormancy (grey areas). The left-axis gives the year over the best-replicated common period (1962–2014). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

growth correlations revealed a drought limitation in the three sites, especially in Sestrica (Table 3, Figs. 4 and 6). According to the daily growth responses simulated by the VS-model, growth was limited on most of the days by low soil water availability, which is consistent with the highest correlations found between tree growth and March–July precipitation (Table 3, Fig. 6). At the Monfragüe site, growth simulated by the VS-model indicated a negative effect of high summer temperatures, as detected by the significant correlations for both oak species. All oaks showed a period of favorable conditions for growth in spring, with the exception of *Q. petraea* at the Sestrica site (one of the southernmost populations of the species in Europe), which showed a sub-optimal behavior throughout the growing season. At the coldest site, *Q. faginea* and *Q. ilex* did not show a second period of optimal growth conditions after the summer. In contrast, *Q. suber* and *Q. faginea* exhibited a second period of optimal conditions at the end of the growing season at the Monfragüe site (Fig. S4).

3.7. Forecasting oak growth variations in response to predicted climate warming

Application of VS-model to future climate conditions revealed changes in potential annual growth (Fig. 7). Considering the ratio between expected growth in future and recent periods, all oak species show growth reductions due to climate change at the southern limits of their distribution ranges (Fig. 7). All oak species showed growth improvements in N-NW Iberia, where their wettest and coolest sites are currently found. However, the model simulations suggested severe growth reductions in the southernmost distribution limits, particularly in xeric sites of *Q. ilex* and *Q. faginea*.

4. Discussion

Growth-climate correlations revealed that oak growth was mainly driven by the climatic conditions (March–July precipitation and June maximum temperature) associated with water deficit around the summer solstice. Previous studies have reported that radial growth of oak species is more related to precipitation than to temperature, and that increased

precipitation in the previous winter and the current spring promotes tree growth by recharging soil moisture reserves or enhancing carbohydrate synthesis and storage (Corcuera et al., 2004a, b). Alternatively, high summer temperatures and evapotranspiration rates may lead to a decrease in growth due to reduced soil moisture levels as observed in *Q. suber*.

The highest correlation found between March–July precipitation and *Q. petraea* growth in Sestrica agrees with other studies indicating that *Q. petraea* is a mesophytic species that requires relatively high air humidity and also high soil moisture (Bertini et al., 2011), and it is more vulnerable to drought than other oak species under identical ecological conditions (Mészáros et al., 2022). This means that *Q. petraea* trees growing towards the southern edge of its range, under warmer and xeric conditions, are more sensitive to summer water shortage (Urli et al., 2014). The strong dependence of *Q. faginea* growth on spring-summer soil moisture is also confirmed by the highest correlation obtained for the VS-model, which is consistent with the increasing effect of summer water balance on *Q. petraea* growth with decreasing latitude (Bose et al., 2021).

The temperature-growth correlations indicated interspecific and inter-site differences in the temperature signal recorded by tree rings. *Quercus suber* and *Q. faginea* showed positive correlations with September temperatures in Monfragüe, suggesting the existence of a second growth peak after the summer drought. In contrast, the lack of significant correlations of growth with September temperature in Agüero may be explained by the colder conditions, which do not allow a longer growing season or growth resumption after the summer. *Quercus ilex* is known to show a facultative bimodal growth pattern in coastal sites with mild or warm winters (Campelo et al., 2007, 2018), and *Q. faginea* may also show a minor growth peak in autumn (Vieira et al., 2022). According to Camarero et al. (2021b), *Q. faginea* could show a bimodal growth pattern, but only under mesic conditions. In addition, in Agüero, significant positive correlations with minimum temperature in January and February were found for *Q. ilex* and *Q. faginea*, suggesting that warmer conditions in spring could trigger an earlier onset of tree growth.

In the Iberian Peninsula, it is expected that Mediterranean oaks such as *Q. ilex* will be more tolerant to more frequent and intense droughts

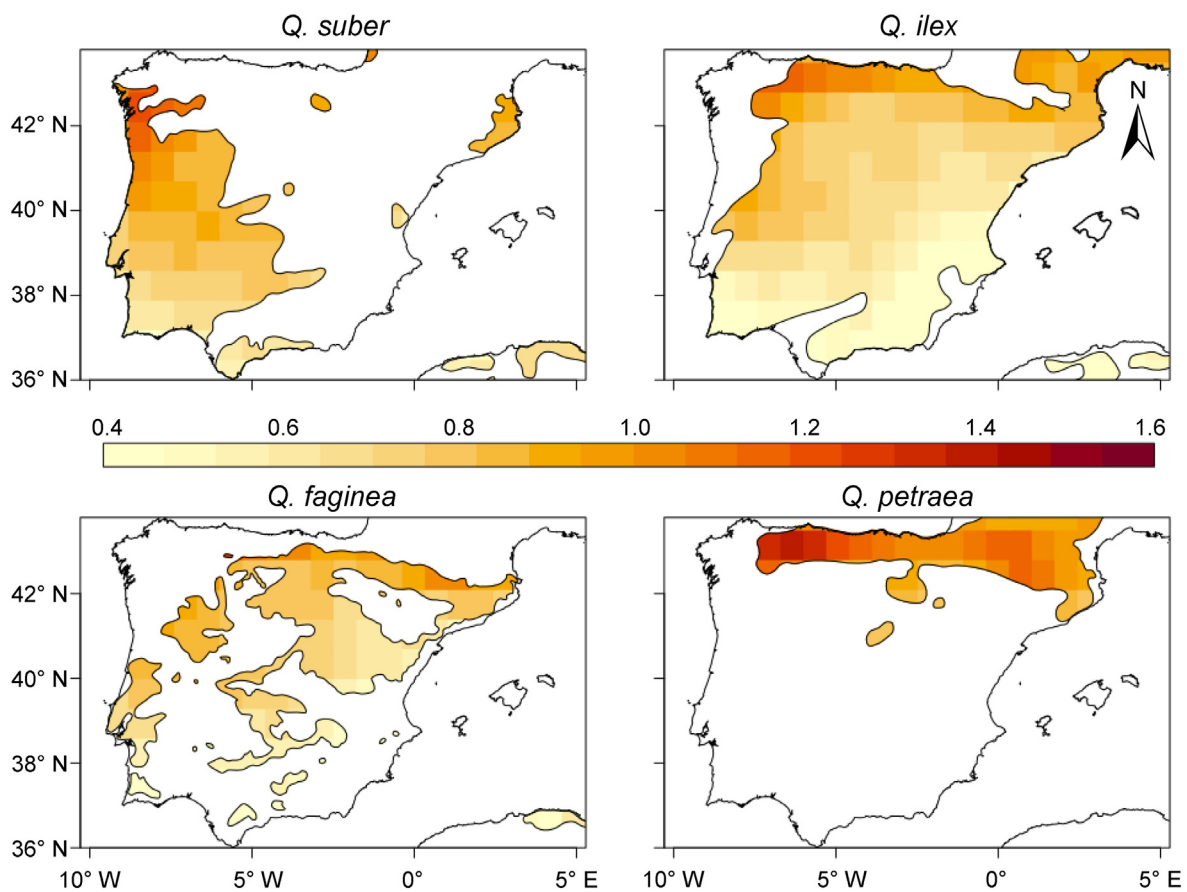


Fig. 7. Potential change in annual growth for evergreen and deciduous oaks simulated by the VS-model under RCP 8.5 emission scenario for two periods. The change of annual growth was calculated as the ration between future (2050–2099) and recent periods (1950–1999). Only grid-points within the distribution of each oak species were considered to limit extrapolation bias.

than temperate oaks such as *Q. petraea*. Our results concur with this view and suggest that more frequent spring droughts could drive the replacement of the deciduous *Q. petraea* by more drought-tolerant deciduous (*Q. faginea*) or evergreen (*Q. suber*) oaks on warmest and driest sites where they coexist. This forecast should be constrained by reverse trends due to recovery after secular land uses. For instance, in central Spain the increase in abundance of some deciduous oaks such as *Q. faginea* or *Q. pyrenaica* is explained because they were more severely logged in the past, due to their better timber of fuel wood, than more widespread species such as *Q. ilex* (Camarero and Valeriano, 2023).

Although the VS-model was able to detect an earlier onset of growth in deciduous oaks than in evergreen oaks, it failed to detect an earlier window of peak growth in deciduous, ring-porous oaks. An earlier growth peak was expected in *Q. petraea* and *Q. faginea*, given their phenology, leaf habit and xylem porosity (Montserrat-Martí et al., 2009), as earlier cambial reactivation and large earlywood vessel formation occur several weeks before bud break (Takahashi et al., 2013), although they only become functional after bud break and before the maturation of the current year leaves (Kitin and Funada, 2016). The ring-porous anatomy in deciduous oaks allows for high efficiency in water transport during favorable conditions for photosynthesis in early spring, but at the cost of a higher risk of cavitation when water becomes scarce or if spring frosts occur (Baas and Wheeler, 2011). For this reason, *Q. petraea* is highly responsive to spring water shortage, whereas *Q. ilex* and *Q. suber* are more sensitive to summer drought.

For ring-porous oaks, interannual variations in earlywood growth were buffered compared to latewood growth and mean sensitivity was extremely low for earlywood-width chronologies (Michelot et al., 2012). This could be one of the reasons why the VS-model did not detect an

earlier growth peak for ring-porous oaks. In ring-porous oaks, the large earlywood vessels develop in most years before full leaf maturity, using carbohydrate reserves from the previous growing season (Barbaroux and Bréda, 2002; Michelot et al., 2010).

In the Mediterranean Basin, an increased drought frequency and intensity are predicted by climate models negatively impacting on many agricultural and forest ecosystems (Cramer et al., 2018). This aridification trend could exacerbate the effects of different leaf habit and wood types on forest responses to drought (D'Orangeville et al., 2021). With climate change, evergreen and deciduous oaks at the southern limits of their range are likely to experience growth reductions due to sub-optimal growth conditions and a shortening of the optimal growing period, despite the growing season may be longer as suggest our simulations. At present, sub-optimal growth conditions for *Q. petraea* can already be observed in one of the southernmost populations of the Iberian Peninsula (Sestrica site; see Camarero et al., 2021a). The positive effect of future climatic conditions on the growth of *Q. petraea* in wet-cool sites of N-NW Spain should be interpreted with caution, as our approach did not take into account growth legacy effects or carbon reserves from previous years. This oak species maintains non-structural carbohydrate accumulation after growth cessation until leaf fall (Hoch et al., 2003), and dry autumn conditions could affect carbon reserves for the next growing season (Michelot et al., 2010). When carbon reserves are severely affected by intense and prolonged droughts, widespread growth reductions are expected, which could lead to dieback and even mortality of *Q. petraea* (Cailleret et al., 2017). *Quercus petraea* is characterized by low growth recovery after drought (Sanders et al., 2014). This would have long-term consequences for growth, probably due to the depletion of carbon reserves. In contrast, Mediterranean oaks are better able to

recover growth after summer drought (Gazol et al., 2020; Bose et al., 2021). Nevertheless, our simulations forecast severe growth reductions in dry areas of S and E Spain in response to warmer and drier conditions in drought-tolerant species such as *Q. faginea* and *Q. ilex*. Such predictions are supported by recent reports of drought-triggered dieback and mortality episodes in these species (Camarero et al., 2015a, 2016). In the case of *Q. suber*, mortality and dieback episodes have been also observed in SW Iberia and they have been attributed to the impacts of drought and pathogens (Gentilesca et al., 2017; Matías et al., 2019).

Along the drought gradient, the four oak species advanced their phenology (growth onset and peak) to track favorable growth periods and escape summer drought (Menzel et al., 2006). The lengthening of the period between leaf sprouting and senescence could also be accompanied by a shorter period for optimal radial growth which depends on adequate soil water availability in Mediterranean forests (Camarero et al., 2022). This phenological response to climate conditions is largely due to phenotypic plasticity (Franks et al., 2013). Therefore, understanding the ability of species to adjust phenological events through phenotypic plasticity in response to climate change is of utmost importance. Another challenge is to predict the effects of climate change on vegetative season length and thus on carbon sequestration and forest productivity. Genetic variability should be also accounted for given the common occurrence of hybridization among compatible oak species (Himrane et al., 2004).

Finally, we also identify several possible shortcomings in the VS-model that should be addressed in new versions of the model. First, the functions that determine the onset and cessation of growth only consider mean temperature over a 10-day period, without considering photoperiod or any interaction between the two sets of variables. Second, correlations between observed and simulated chronologies could be improved if the growing season only considers spring, when the main growth peak occurs. Third, future uses of the model should explicitly consider tree-to-tree competition, which we could not assess, to estimate how it impacts long-term growth trends (basal area increment) and water-use efficiency (e.g., Valeriano et al., 2023). Despite these limitations, the VS-model offers new possibilities to forecast and project growth changes as a function of different climate scenarios by focusing on year-to-year growth and climate variability. These forecasts, based on tree-ring data, could be compared with data on changes in basal area, mortality or ingrowth derived from spatially intensive national forest inventories (e.g., Gazol et al., 2022). Furthermore, it is a valuable tool to define drought-vulnerability thresholds in oak species using growth data (cf. Sánchez-Salguero et al., 2020).

Previous studies have suggested that deciduous oaks may be more vulnerable to climate change than evergreen oaks, which may reflect differences in functional traits, past management practices and current uses (Acácio et al., 2016). A decline in evergreen oaks and a replacement of deciduous oaks by more xeric species is expected under increasing human pressure and climate change (Acácio et al., 2016). Our results support growth reduction in oaks and species-specific vulnerability to extreme events, with growth reduction in evergreen oaks being driven by summer temperature extremes, whereas growth decline in deciduous oaks was better explained by low spring precipitation. Forest management practices should take into account the expected increase in the occurrence of extreme climatic events such as droughts to maintain soil water availability above critical levels. Growth forecasts from the VS-model indicate that: (i) monitoring the growth and vigour of rear-edge (southernmost) oak populations, particularly *Q. ilex* and *Q. faginea*, should be a priority for their conservation, and (ii) thinning or restoration of coppices could mitigate drought stress in the most vulnerable sites (e.g., Tonelli et al., 2023).

5. Conclusions

Our results suggest that under climate change and increased aridification, evergreen and deciduous Mediterranean oaks could experience longer growing seasons but a shorter period for optimal radial growth

and xylem development (xylogenesis) and/or lower growth rates. Evergreen oaks may be less affected by climate warming than deciduous oaks, particularly those species that are able to resume growth after summer drought. The second growth peak in autumn could be a compensatory mechanism to maintain high annual photosynthetic carbon uptake. In addition, low soil water availability caused by more intense and frequent droughts, especially in spring, is expected to have a more negative impact on the radial growth of deciduous oaks than on evergreen oaks, since deciduous oaks present stronger growth limitations by lower soil moisture. In addition, the low post-drought growth resilience of temperate deciduous oaks could result in dieback and mortality. Differences in growth responses and wood formation to drought conditions could have consequences on the distribution of both leaf habit groups, limiting the presence of deciduous oaks in the driest sites of the Iberian Peninsula and displacing them to wettest-coolest areas. Studies on high-resolution growth data of coexisting evergreen and deciduous oaks using micro-coring and automatic dendrometers, particularly in drought-sensitive oak stands close to the species rear edge (cf. Camarero et al., 2021a), and improvements of the VS model or other mechanistic growth models are needed to further understand and refine our results.

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Data availability

Data are available on reasonable request from the last author.

CRediT authorship contribution statement

J.J. Camarero, F. Campelo: Conceptualization; J.J. Camarero, M. Colangelo, C. Valeriano and Á. Rubio-Cuadrado: Data curation; J.J. Camarero, F. Campelo: Formal analysis; J.J. Camarero, F. Montes: Funding acquisition; J.J. Camarero, F. Campelo: Investigation; J.J. Camarero, F. Campelo, M. Colangelo, C. Valeriano and Á. Rubio-Cuadrado: Methodology; J.J. Camarero, F. Campelo: Writing – original draft; J.J. Camarero, F. Campelo, M. Colangelo, C. Valeriano, Á. Rubio-Cuadrado and F. Montes: Writing – review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100134>.

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