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Differences in stem radial variation between *Pinus pinaster* Ait. and *Quercus pyrenaica* Willd. may release inter-specific competition

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ABSTRACT

Species complementarity by morphological and physiological trait differences could cause distinct temporal and spatial use of resources. Accordingly, mixed stands may enhance production, biodiversity and/or provide a better adaptation to future climate conditions. We aim to identify species differences in intra-annual stem radial variation patterns, and to recognize species-specific responses to contrasting weather conditions at key intra-annual growth phases. Stem radial variation was recorded from high temporal resolution point dendrometers (2012–2014) installed on twelve dominant maritime pine and Pyrenean oak trees in two mixed stands in central Spain. Species differences in stem radial variation were analyzed by synchrony statistics, intra-annual pattern modelling, and evaluating the dependence of main intra-annual growth phases on climate conditions. Both species showed important differences on intra-annual radial increment pattern despite general stem radial variation synchrony. Radial increment onset was earlier for maritime pine during the spring and rainy autumns. Species-specific responses to weather indicate that stem radial variation increased with autumn temperature in maritime pine, but decreased in Pyrenean oak trees. However, summer vapor pressure deficit may reduce stem radial variation for maritime pine. Therefore, maritime pine would adapt more efficiently to warmer temperatures associated with climate change, although summer water stress may reduce this competitive bonus.

1. Introduction

Changes in temperature, precipitation and drought severity associated with climate change could modify the composition, structure, and biogeography of forests worldwide (Allen et al., 2010; Babst et al., 2019; Hanewinkel et al., 2012), especially in the Mediterranean region (Dankers and Hiederer, 2008; IPCC, 2014). Several recent studies have identified mixed forest stands as a possible forest management strategy to cope with climate change, since they increase resilience and resistance to biotic and abiotic stress (Forrester, 2015; Guyot et al., 2016; Pretzsch et al., 2013) and enhance temporal growth stability (del Río et al., 2017; Jucker et al., 2014). In addition, mixed-species stands could have some advantages over monospecific ones in their ecological

functions and services (Felton et al., 2016; Knoke et al., 2008; Pretzsch and Forrester, 2017). These positive mixing effects are commonly explained by the complementary effect hypothesis (Ammer, 2019), caused by reduced competition or increased facilitation (Grossiord, 2019). Ecological trait differences among tree species may increase resource use efficiency and mitigate the negative growth effects caused by a warmer climate (Forrester et al., 2013).

Understanding growth differences in co-occurring species can be used to estimate ecological consequences and production changed due to climate change. Studying intra-annual growth dynamics allows us to gain new insight into particular weather events that a classical inter-annual dendroclimatic approach may miss (Duchesne and Houle, 2011), although combining with core analysis may improve tree growth

understanding. Continuous or high-resolution dendrometer recordings provide valuable andextraordinarily precise information for studying tree stem radial variation (SRV) as a response to environmental factors (Siegmund et al., 2016). Dendrometer based studies have generally analyzed relationships between stem size variations and climate (Duchesne and Houle, 2011; Oberhuber et al., 2014; Vieira et al., 2013), as well as species-specific responses (King et al., 2013; Oberhuber et al., 2015). Intra-annual radial variation studies in Mediterranean mixed forests are still scarce. These studies often report growth and water use (Sánchez-Costa et al. 2015) or species differences in xylogenesis (Camarero et al. 2010). By analyzing band dendrometer recordings, Riofrío et al., (2017) also found that species' relative dominance was an important factor affecting intra-annual cumulative SRV patterns in mixed stand of maritime pine (*Pinus pinaster* Ait.) and Scots pine (*Pinus sylvestris* L.). Generally, synchrony analyses in forest science focus on inter-annual radial growth concurrence in the timing of ring formation over several years (Fajardo and Mcintire, 2012; Hayles et al., 2007; Shestakova et al., 2016) or flowering and fruiting phenology (Bogdziewicz et al., 2017). However, very little is known about intra-annual SRV synchrony between species. Asynchrony in intra-annual growth dynamics may be understood as a consequence of different responses to weather conditions and, hence, the existence of species niche complementarity. Accordingly, Rötzer et al., (2017) found evidence of asynchrony in coarse root growth of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) H. Karst.) in reaction to drought stress in an inter- and intra-specific tree neighborhood, though their methodology did not allow the quantification of synchrony.

Here, we assessed species differences in intra-annual cumulative SRV patterns which comprise both reversible and irreversible components (i. e. stem hydrological processes and growth) for co-occurring pine and oak trees (*Pinus pinaster* Ait. and *Quercus pyrenaica* Willd., hereafter referred as maritime pine and Pyrenean oak respectively) from electronic dendrometer measurements during a period of contrasting weather (2012–2014). A previous study by Aldea et al. (2017) in the same stands revealed greater growth for maritime pine, although it was based on data from band dendrometer measurements, which have lower temporal resolution and precision. Continuous point dendrometers from the same stands showed that daily radial increment differed between species, although both responded to the same weather variables (Aldea et al., 2018). However, different spatial resource partitioning (root and canopy packing), phenological (timing of leaf budburst) and physiological trait differences (shade and drought tolerance), could induce different species growth patterns (Fernández-De-Uña et al., 2017; Grossiord, 2019). Accordingly, niche complementarity of Mediterranean pines and Pyrenean oak species was shown to be a cause of overyielding and higher stand density in mixed vs. monospecific stands (del Río and Sterba, 2009; Nunes et al., 2013). Pine-oak mixtures increase productivity and most likely climate resistance along a wide ecological gradient (Pretzsch et al., 2019; Steckel et al., 2019). This could be important for the Mediterranean region, where pine species have generally been re-introduced into oak coppice stands as means to establish and increase stand productivity, as in these study sites. Similar

species to those studied here (i.e. Scots pine and pedunculated oak-*Quercus robur* L.) react differently to drought events (Steckel et al., 2020); while Scots pine may suffer from summer droughts, pedunculated oak would be more affected by dry springs (Merlin et al., 2015; Toïgo et al., 2015). Consequently, Zweifel et al. (2006) found that the ring-porous oak achieves about half of its annual radial growth by the end of spring, while conifer growth is concentrated in the summer and early autumn months. Therefore, an asynchronous growth pattern, as a consequence of species niche complementarity, can reasonably be expected.

The aims of the study were 1) to identify species differences in intra-annual cumulative SRV patterns, and 2) to recognize which environmental factors are driving them. We tested the hypotheses that (i) cumulative SRV patterns for both species are unsynchronized as a possible consequence of niche complementarity and hence, (ii) SRV is driven by species-specific environmental responses to temperature and summer water availability which are limiting factors in the Mediterranean region.

2. Material and methods

2.1. Study sites and climatic records

This experiment took place in two sites with contrasting drought patterns in central Spain: Lubia (Soria; 41° 39′ N, 2° 29′ W, hereafter SO) and San Pablo de los Montes (Toledo; 39° 31′ N, 4° 16.6′W, hereafter TO). The main difference between the sites is that TO has a more severe summer drought than SO. The studied forests at both sites are mixed stands composed of maritime pine and Pyrenean oak.The species are arranged in rows, due to the re-introduction of maritime pine after harvest and bulldozer ripping of a native Pyrenean oak coppice stand. Thus, maritime pine was managed as high forest and Pyrenean oak by the coppice stand system. Maritime pine and Pyrenean oak sprouts were 35–40 years old at these two sites at the time of the study. Stand basal area at SO was 38.9 m^2 ha^{-1} ($\pm$5.2 m^2 ha^{-1} standard deviation-SD) and 5.1 m^2 ha^{-1} ($\pm$1.4 m^2 ha^{-1} SD) for maritime pine and Pyrenean oak, respectively; at TO these species had basal areas of 32.2 m^2 ha^{-1} ($\pm$2.8 m^2 ha^{-1} SD) and 6.7 m^2 ha^{-1} ($\pm$1.7 m^2 ha^{-1} SD). See Aldea et al. (2017) for more details.

Weather variables were continuously monitored using a data logger (HOBO U12 4-External Channel) at SO and a weather station (HOBO) at TO. Air temperature, relative humidity, rainfall, solar radiation, wind speed and dew point were recorded at 15 min intervals. In addition, temperature, precipitation and radiation records were compiled using hourly data from the AEMET automatic network stations (Lubia-Ceder 2044B and San Pablo de los Montes 3298X) located 6 km and 5 km from SO and TO, respectively, to fill gaps in the weather information. Vapor pressure deficit (VPD) was also calculated from these weather measurements. Summer drought occurred in all sampling years (2012–2014), and was particularly extreme in 2012 at both sites (see Aldea et al. 2018 for more details). Table 1 shows the main weather variables included in the analysis for the study period.

Table 1
Weather variables considered in the analysis for the period 2012–2014.

Variable	Description	mean	min	Max
P_Ag	*Accumulated precipitation in August (mm)*	3.4	0.0	22.1
P_S	*Accumulated precipitation in September (mm)*	61.7	13.0	136.9
Tmin_MAp	*Mean daily minimum air temperature during March and April (°C)*	2.6	1.8	8.6
Tmin_S	*Mean daily minimum air temperature in September (°C)*	12.7	9.3	16.0
Tmin_O	*Mean daily minimum air temperature in October (°C)*	9.3	5.9	13.0
Tmin_ON	*Mean daily minimum air temperature during October and November (°C)*	6.1	3.9	13.0
Tmax_Jn	*Mean daily maximum air temperature in June (°C)*	25.9	21.8	29.3
Tmax_O	*Mean daily maximum air temperature in October (°C)*	18.6	17.0	21.4
VPD_Ap	*Mean daily vapor pressure deficit in April (kPa)*	0.4	0.2	0.6
VPD_Jn	*Mean daily vapor pressure deficit in June (kPa)*	1.2	0.8	1.6

2.2. Stem radial variation

Electronic point dendrometers (Vázquez-Piqué et al. 2009) were installed on three dominant trees per species and site (twelve trees in total). We installed the dendrometers on selected dominant trees for each species to increase climate sensitivity and reduce competition signal. The devices were mounted at breast height after partial bark removal (rhytidome), to avoid as much as possible the stem hydration effect. The stem radial variation was recorded at 15-minute intervals with a resolution of 1 μm using a data logger (HOBO U12 4-External Channel). Mean hourly measurements were calculated to identify and correct errors or wrong measurements for the entire 2012–2014 study period (see Aldea et al. 2018 for more details). The maritime pine trees selected averaged 26.8 cm (±1.5 cm) in diameter at breast height and 11.2 m (±0.7 m) high, while the Pyrenean oaks averaged 9.5 cm (±1.3 cm) in diameter and 7.4 m (±0.8 m) high. There were no significant differences in species height or diameter between sites.

2.3. Data analysis

2.3.1. Species differences in intra-annual cumulative SRV patterns

We explored species differences in intra-annual cumulative SRV patterns via three methodologies: *i)* synchrony evaluation, *ii)* growth function modeling and *iii)* evaluating differences at main intra-annual growth phases (timing of onset and cessation of radial increment phase, and magnitude of spring and autumn asymptotes).

2.3.1.1. Radial variation synchrony.
We identified and quantified temporal correlation of radial variability between time series for the same species and between species within each site. We analyzed synchrony at low frequency from annual SRV (Fig. 1) by fitting a cubic smoothing spline to cumulative SRV patterns to obtain the chronologies with low-frequency variability for the sampled years. A 'caterpillar' randomization procedure was employed to avoid the typical violation of the independence assumption used in classical statistics from temporal and spatial data set tests (Gouhier and Guichard, 2014). This procedure preserves the temporal within-tree autocorrelation but destroys cross-

correlation among trees, as it displaces the time series by a random amount for each randomization (Purves and Law, 2002). The level of temporal synchrony was assessed with several metrics: mean correlation coefficient, Kendall's W non-parametric statistic Legendre (2005) and the Loreau and de Mazancourt (2008) metric. All these statistical metrics were used to evaluate and quantify the temporal synchrony and its significance. Loreau and de Mazancourt (2008) show that community-wide synchrony can be quantified as the ratio between the temporal variance of the community time series and the sum of the temporal standard deviation of the time series across all trees. The last two statistics are bound between 0 and 1, so they cannot distinguish asynchrony (negatively correlated fluctuations) from lack of synchrony (independent fluctuation). All the metrics were calculated by site using the 'synchrony' R package (Gouhier and Guichard, 2014) and their statistical significance (difference from zero) was determined via 999 Monte Carlo randomizations.

2.3.1.2. Modelling intra-annual cumulative SRV patterns.
Cumulative SRV of both species showed a clearly bimodal pattern, which is typical of Mediterranean environments (Albuixech et al., 2012; Aldea et al., 2017; Pacheco et al., 2018): stem growth during the spring, contraction during the summer due to depletion of stored water (concurrent with increasing water deficit) and stem rehydration (with growth for certain species) after autumn rainfall. We considered that negative radial variation rates were a usual consequence of tree water deficit caused by the summer drought, inducing a reversible stem shrinkage for both species. Accordingly, we assumed that periods of stem shrinkage allowed relatively small growth (Zweifel et al., 2016), and thus, the SRV when the stem shrinkage occurred, indicates a growth-induced irreversible size. Consequently, non-linear equation curves were fitted separately for spring and autumn periods to find analytical solutions with biphasic curves while avoiding convergence difficulties and long calculation times. The spring period was considered to run from 1 January to the radial contraction triggered by summer drought and generalized until 1 September to ensure final and initial spring and autumn asymptotes, respectively. The autumn period is, from this point, the rest of the year.

We used a flexible Richards model for the spring and autumn periods.
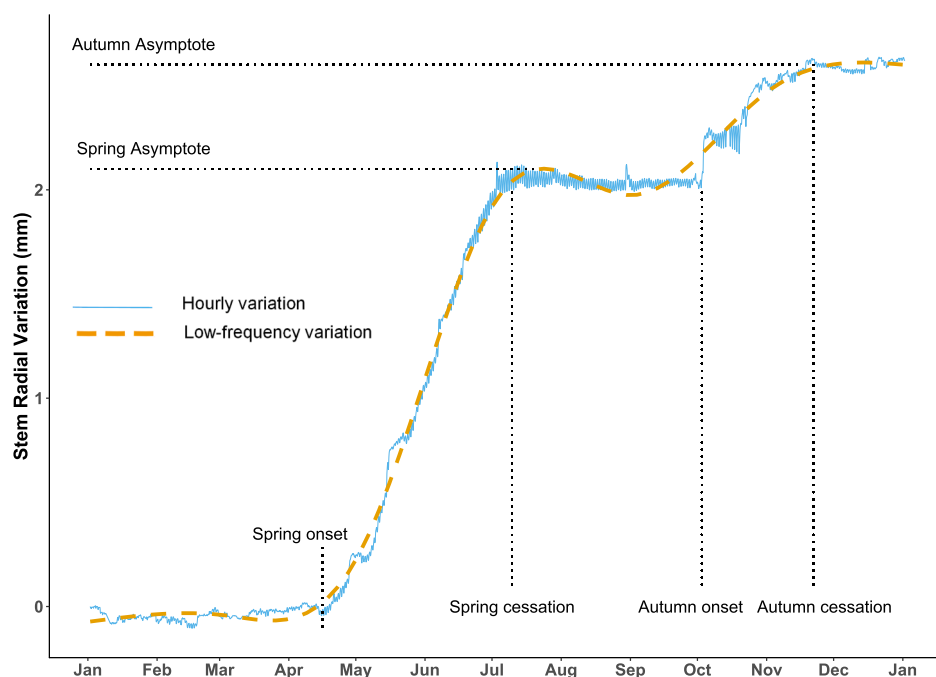

Fig. 1. Cumulative stem radial variation (SRV) at two temporal scales formed in 2013 for a maritime pine tree at the Toledo site. The light blue continuous line is hourly SRV, and the orange dashed line is low-frequency SRV from smoothed annual data. Dotted black lines show the main intra-annual growth phases analyzed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The advantage of this curve compared to the commonly-used logistic function (also known as a Gompertz function) is that it includes a fourth parameter, allowing a closer and more flexible fit to the data, avoiding convergence problems. In fact, a logistic function is a special case of a generalist Richards curve. In addition, a random effects structure was included in the Richards model to consider the spatial and temporal dependence of measurements. In this way, site and tree (nested in site) random effects were added to the model, affecting the intercept of the asymptote (A_{ij}) and the inflection point (I_{ij}). This proved to be the best random structure: a beyond-optimal model with different random structures was fitted by maximizing the restricted log-likelihood (Zuur et al., 2009) and then comparing and selecting the lowest value of the Akaike information criterion (AIC). Year and species fixed effects were also included to evaluate their effects on model parameters, which allowed us to estimate our original query: species differences in cumulative SRV patterns. The final model was as follows:

$$y_{ij} = \frac{A_{ij}}{\left[1 + m_{ij}e^{\left(-k_{ij}\left(t-I_{ij}\right)\right)}\right]^{\frac{1}{m_{ij}}}} + \varepsilon_{ij} \qquad [1]$$

$$A_{ij} = \alpha_1 + \alpha_2 year2 + \alpha_3 year3 + \alpha_4 pine + u_j + v_{ij}$$

$$I_{ij} = \beta_1 + \beta_2 year2 + \beta_3 year3 + \beta_4 pine + u_j + v_{ij}$$

$$k_{ij} = \gamma_1 + \gamma_2 year2 + \gamma_3 year3 + \gamma_4 pine$$

$$m_{ij} = \tau_1 + \tau_2 year2 + \tau_3 year3 + \tau_4 pine$$

where y_{ij} is the cumulative SRV for tree i in site j during the spring or autumn season; A_{ij}, I_{ij}, k_{ij} and m_{ij} are the asymptote, inflection point (Julian date), rate parameter and shape parameter of the Richards curve; t is time; $\alpha_i, \beta_i, \gamma_i$ and τ_i are the asymptote, inflection point, rate and shape parameter regression covariate coefficients (for a graphical demonstration of the parameters, see Supplementary Figure S1); *year2* and *year3* are year dummy variables for year 2013 and 2014 respectively (for year 2012 both are 0); *pine* is a dummy variable with a value of 0 for Pyrenean oak and 1 for maritime pine; $u_j \sim N(0, \sigma_j)$ is the site random effect; $v_{ij} \sim N(0, \sigma_{ij})$ is the tree random effect and $\varepsilon_{ij} \sim N(0, \sigma_e)$ is the error term.

Additionally, residual plots were used as a diagnostic tool for identifying heteroscedasticity and serial autocorrelation. Several variance functions (exponential, power and constant plus power of the absolute value of the variance covariate) were evaluated when necessary (Pinheiro and Bates, 2000). The 'FlexParamCurve' (Oswald, 2015) and 'nlme'(Pinheiro et al., 2015) R packages were used to fit individual Richards curves, obtain the most parsimonious curve and select appropriate parameterizations.

2.3.1.3. Timing and magnitude of main intra-annual growth phases. We used the cumulative sum chart method to automatically determine the onset and cessation dates of radial increment based on dendrometer data (see the *stem cycle approach* from Downes et al., (1999) and Deslauriers et al., (2003) for definition of radial increment phase). Results obtained by this method have a good performance in determining the onset and cessation dates of radial increase from dendrometer data (Korpela et al., 2010). This procedure detects small changes in process means using the V-Mask technique. The mask is a V-shaped overlay placed on the cumulative sum chart so that one arm of the V lines up with the slope of the data points, making it easy to see data points that lie outside the slope and to determine whether these points should be discarded as random events, or treated as a performance trend that should be addressed. For more details about V-Mask see Basu and Montgomery (1987).

We identified the onset and cessation dates of radial growth for the spring and autumn periods (Fig. 1), which are clearly differentiated by summer drought. Accordingly, the magnitude of spring and autumn asymptotes were calculated as the mean value of each respective dormant period, i.e. summer or winter dormancy, when the increment of

the daily cycles reached minimum values (Fig. 1). Onset and cessation dates were identified using the 'v-Mask' R package (Parchami, 2018). Species differences in the main intra-annual growth phases were analyzed by linear mixed models combined with the study of weather effects (see next section).

2.3.2. Species-specific weather response
The inter-year response was evaluated by the species' reactions to environmental variables driving SRV. Linear mixed models were fitted to determine the influence of meteorological variables on the timing of intra-annual growth phases (i.e., onset and cessation dates of radial increment) and magnitude of spring and autumn asymptotes. Means, sums (when necessary), maximum, and minimum values of meteorological variables were calculated monthly or for a set of several months. The structure of the linear mixed model was as follows:

$$y_{ij} = \alpha_0 + f(weather) + (\alpha_1 + f(weather))*oak + u_j + v_{ij} + \varepsilon_{ij} \qquad [2]$$

where y_{ij} is the onset or cessation date of radial increment, and asymptotic magnitude of spring and autumn seasons for tree i in site j; α_0 and α_1 are the intercept regression coefficients for maritime pine and Pyrenean oak respectively; $f(weather)$ is a linear function, i.e., a summatory, of the weather variables considered into the analysis (Table 1); *oak* is a dummy variable with values of 1 for Pyrenean oak and 0 for maritime pine; $u_j \sim N(0, \sigma_j)$ is the site random effect; $v_{ij} \sim N(0, \sigma_{ij})$ is the tree random effect and $\varepsilon_{ij} \sim N(0, \sigma_e)$ is the error term.

The best random and fixed effect structures were fitted by restricted and maximum likelihood, respectively. Explanatory variables were chosen based on stepwise backward model selection using the Akaike information criterion (AIC) to find the most parsimonious model. Multicollinearity of environmental variables was controlled by variance inflation factor value. We assumed that models with values of the variance inflation factor lower than five did not present problems of multicollinearity among climate variables (Hair et al., 2010). Heteroscedasticity was checked by visual diagnosis of residual plots (Zuur et al., 2009). The R package 'nlme' (Pinheiro et al., 2015) was used to fit the former linear mixed models to understand the different species response to weather conditions. All analyses were performed in the R statistical environment (R Development Core Team, 2020).

3. Results

3.1. Species radial variation synchrony

Maritime pine and Pyrenean oak showed high radial variation synchrony regardless of the site for all metrics calculated (Table 2), i.e., both species showed a similar seasonal radial variation at each site. Cumulative SRV was as synchronous between species as within species which suggests that the species responded at the same time to identical weather conditions.

Table 2
Synchrony of radial variation between time series. Statistical significance of mean correlation (ρ), Kendall's concordance (W), and the Loreau and de Mazancourt's metric (LdM, φ). 'P vs O' denotes comparison of maritime pine and Pyrenean oak temporal series. All p-values (difference from zero) of synchrony metrics were < 0.001.

Site	Series	Mean correlation (ρ)	Kendall's concordance (W)	LdM (φ)
SO	Pine	0.977	0.962	0.985
	Oak	0.856	0.873	0.926
	P vs O	0.998	0.823	0.842
TO	Pine	0.997	0.996	0.998
	Oak	0.984	0.987	0.993
	P vs O	0.995	0.990	0.998

Table 3
Richards model fitted for spring and autumn cumulative SRV patterns. See Eq. (1) for explanation of parameter names. n.s.: not significant.

Parameter	Spring		Autumn	
	Coefficient	p-value	Coefficient	p-value
$\alpha_1(A_{2012})$	−0.528	0.029	0.184	0.022
$\alpha_2(A_{2013})$	1.394	<0.001	n.s.	n.s.
$\alpha_3(A_{2014})$	1.858	<0.001	n.s.	n.s.
$\alpha_4(A_{pine})$	1.846	<0.001	0.389	<0.001
$\beta_1(I_{2012})$	139.657	<0.001	266.816	<0.001
$\beta_2(I_{2013})$	n.s.	n.s.	n.s.	n.s.
$\beta_3(I_{2014})$	n.s.	n.s.	n.s.	n.s.
$\beta_4(I_{pine})$	n.s.	n.s.	9.919	<0.001
$\gamma_1(k_{2012})$	0.019	<0.001	0.049	<0.001
$\gamma_2(k_{2013})$	n.s.	n.s.	n.s.	n.s.
$\gamma_3(k_{2014})$	n.s.	n.s.	n.s.	n.s.
$\gamma_4(k_{pine})$	0.021	<0.001	0.018	<0.001
$\tau_1(m_{2012})$	−0.079	<0.001	−0.328	<0.001
$\tau_2(m_{2013})$	n.s.	n.s.	n.s.	n.s.
$\tau_3(m_{2014})$	n.s.	n.s.	n.s.	n.s.
$\tau_4(m_{pine})$	0.401	<0.001	0.278	<0.001
$\sigma_j(A_{site})$	0.228		$2.6 \cdot 10^{-4}$	
$\sigma_{ij}(A_{tree})$	0.358		0.161	
$\sigma_j(I_{site})$	11.259		$1.4 \cdot 10^{-4}$	
$\sigma_{ij}(I_{tree})$	9.604		2.962	
$\sigma_e(error)$	0.154		0.061	
δ_1*	-----		0.576	

*Variance function parameter used to model variance residual structure to correct heteroscedasticity as an exponential value of the variance covariate (g_{ijk}): $Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{(2\delta_1 g_{ijk})}$

3.2. Intra-annual cumulative SRV models

SRV patterns differed between species and among years according to the models fitted (Table 3). Maritime pine always had a higher asymptote (α_4) and increment rate (γ_4) than Pyrenean oak, regardless of season (Table 3 and Fig. 2). The spring asymptotic parameter was lower in 2012 (α_1) than in 2013 and 2014 for both species, as consequence of severe summer drought. There were no significant differences in the time of

occurrence of the spring inflection point between species and years (β_2 to β_4), which was reached on 19th May. Species differences appeared in the Richards shape parameter (τ_4), which means a longer exponential period of SRV for maritime pine than Pyrenean oak (Table 3).

The best model for autumn SRV pattern did not include the year as a factor affecting any curve parameter (Table 3). However, differences between species were observed for the model parameters fitted. Asymptotic (α_4) and increment rate (γ_4) parameters were again higher for maritime pine than Pyrenean oak (Fig. 2). In addition, the autumn inflection point (β_4) occurred later for maritime pine (3rd October) than Pyrenean oak (23rd September). Although the shape parameter (τ_4) also differed between species, low values for both species reflected a sudden change in SRV that might correspond to rehydration processes.

3.3. Weather drivers for the main intra-annual growth phases

Spring radial increment onset for maritime pine (mean 31st March) was earlier than Pyrenean oak (mean 9th April). It began earlier for both species when March and April temperatures were hotter (Fig. 3), but was delayed by greater April VPD (Table 4). June maximum temperature and VPD caused radial summer increment cessation without differences between species (mean: 6th July). The spring asymptotic value was greatly reduced by June VPD for maritime pine, although not for Pyrenean oak (Fig. 4). On the other hand, late summer precipitation could increase spring growth for both species (Table 4). More detailed information is displayed in Supplementary Figures S2 and S3, which show weather variables and growth trends in the sampled years.

September precipitation was the primary driver of autumn radial increment onset for both species (mean 20th September); higher rainfall led to earlier onset. However, maritime pine showed greater sensitivity than Pyrenean oak, i.e., the radial increment onset was clearly earlier for maritime pine as precipitation increased (Fig. 3). High September minimum temperatures also led to earlier onset for both species. Similar to spring, there were no differences between species in radial increment cessation during autumn (mean 31th October, Table 4). Increased maximum and minimum temperature during October and November respectively prolonged the cessation stage for both species. The autumn asymptote was temperature dependent but with a specific species pattern (Table 4). While maritime pine growth increased with minimum
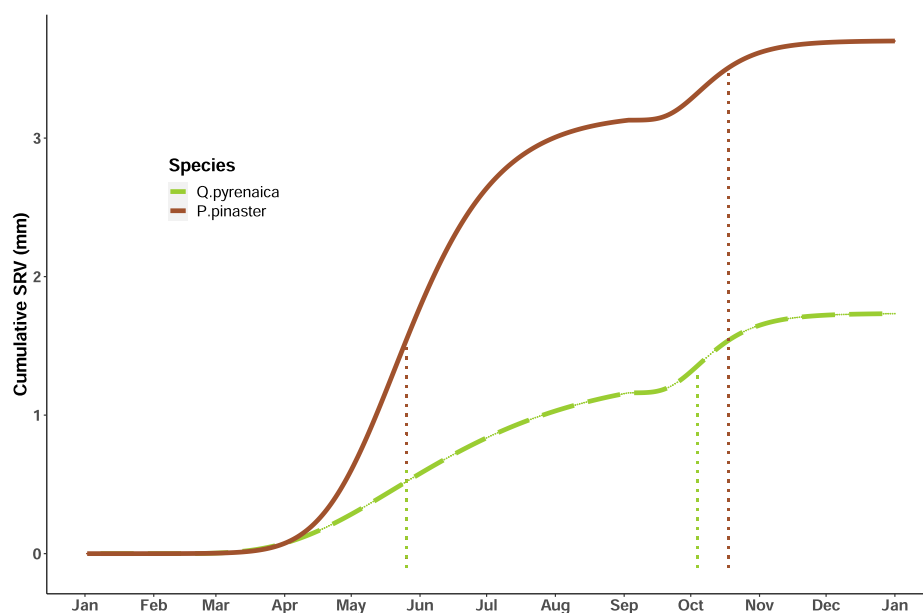
Fig. 2. Species-specific intra-annual cumulative SRV pattern simulations from the Richards curves fitted according to Eq. (1) for the entire year. Vertical dotted lines show the inflection points for both species in spring and autumn.
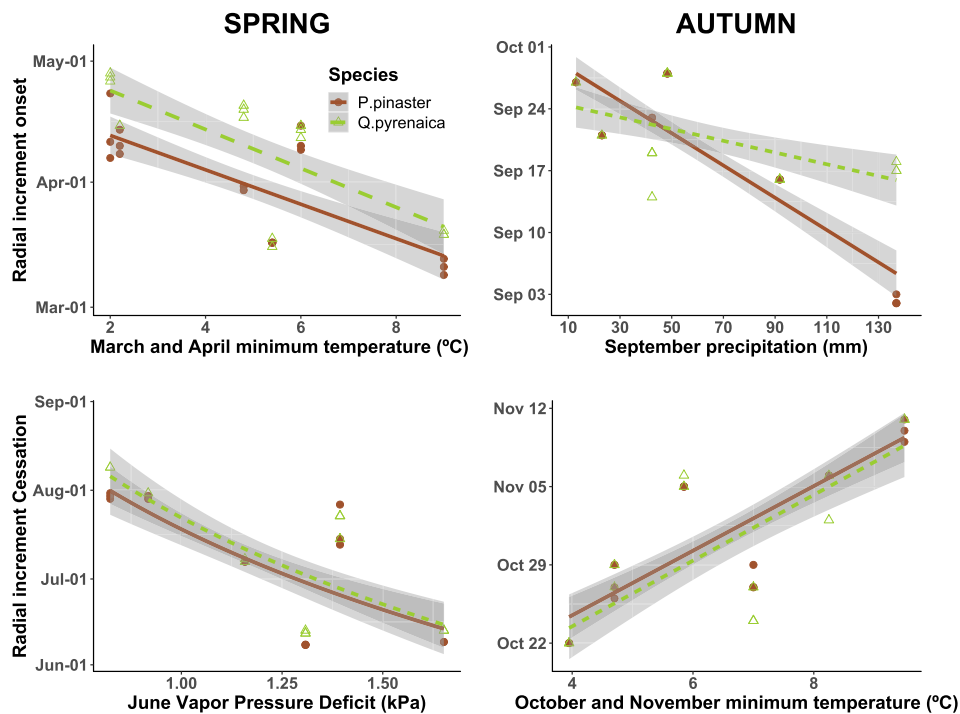
Fig. 3. Weather drivers for radial increment onset (above) and cessation (below) dates in spring (left) and autumn (right). Brown continuous lines represent maritime pine and green-dashed lines Pyrenean oak. Grey areas show the 95% confidence intervals of the estimated mean response function. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Model fitted for the weather drivers of main intra-annual growth phases (Eq. (2)). α_0 and α_1 are the intercept regression coefficients for maritime pine and Pyrenean oak respectively; σ_{ij} is the standard deviation of the tree random effect and σ_e is the standard deviation of the error term. For weather variable description, to see Table 1. The significance levels for parameters are as follows:'***' <0.001, '**' <0.01, '*' <0.05). n.s.: not significant.

| Parameter	Spring			Autumn		
	Onset	Cessation	Asymptote	Onset	Cessation	Asymptote
α_0(pine)	146.9***	382.0***	6.621***	305.1***	261.3***	−0.127
α_1(oak)	7.8*	n.s.	−5.911***	−5.6**	n.s.	0.678**
Tmin_MAp (pine)	−17.8***					
Tmin_MAp (oak)	n.s.					
VPD_Ap	21.9**					
ln(VPD_Jn)		−44.9***				
VPD_Jn (pine)			−3.864***			
VPD_Jn (oak)			3.390***			
Tmax_Jn		−7.3***				
P_Ag			0.113***			
P_S (pine)				−0.3**		
P_S (oak)				0.1***		
Tmin_S				−1.9**		
Tmin_O (pine)						0.069***
Tmin_O (oak)						−0.099***
Tmax_O					1.7***	
Tmin_ON					3.0***	
σ_j(site)	37.0	16.8	0.475	15.4	<0.1	1.476
σ_{ij}(tree)	<0.1	<0.1	0.170	<0.1	<0.1	0.001
σ_e(error)	5.5	8.8	0.232	2.5	2.4	0.721

temperature, Pyrenean oak radial increment decreased (Fig. 4), suggesting different underlying processes (growth vs. contraction by dehydration).

4. Discussion

4.1. Species complementarity

SRV synchrony suggests that both species have similar timing responses to variation in weather conditions as a consequence of seasonal rhythms. This result agrees with previous findings at short time scale (daily), where maritime pine and Pyrenean oak responded to the same weather variables during the growing season (Aldea et al., 2018), which have been also confirmed here for a larger time scale. Accordingly, competition for resources probably occurs during the main growing season (spring). However, maritime pine could be more sensitive to climate and Pyrenean oak to competition (Sánchez-Gómez et al., 2008) which could be enhanced in the study sites due to the height
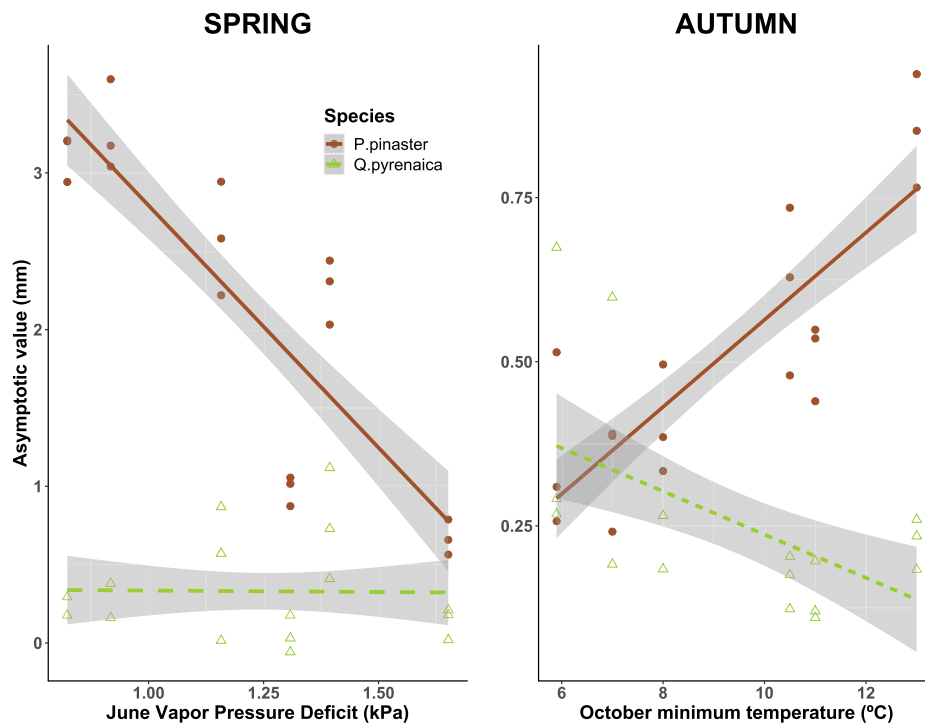
Fig. 4. Weather drivers for spring (left) and autumn (right) asymptotic value. Brown continuous lines represent maritime pine and green dashed lines Pyrenean oak. Grey areas show the 95% confidence intervals of the estimated mean response function. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

vertical stand structure. Besides, Rozas et al., (2009) found that maritime pine was affected mainly by water availability during its active period, while Pyrenean oak growth was negatively influenced by winter temperature.

The species-specific weather response at some intra-annual growth phases observed here, confirms resource competition release as a consequence of timing complementarity. Radial increment onset observations generally occurred immediately after a negative SRV period, which could be driven by the beginning of active water movement in the stem towards upper crown areas for both species (Oberhuber et al., 2014; Zweifel et al., 2000). However, species differences in spring radial increment onset showed an earlier start for maritime pine regardless of weather conditions (Fig. 3). These differences could reveal divergent endogenous control (ontogeny) involving species-specific temperature and/or photoperiod thresholds. Pine species can use preexisting needles to start photosynthesis earlier and respond faster to late-winter warm temperatures compared to deciduous oak species. Despite the temporal limitation of our study (three years), our results agree with the onset dates for tracheids (1st March – 1st April) and vessel enlargements (31st March – 4th April) reported by Vieira et al., (2015) and Fernández-De-Uña et al., (2017) respectively for the same species growing in monospecific stands in Mediterranean areas. Oberhuber and Gruber (2010) reported that the onset and maximum stem diameter increments from dendrometer recordings for Scots pine corresponded to the start and maximum number of cells observed in the enlargement phase. This corroboration increases our confidence that we indeed observed the first stage of cell enlargement, although radial increment onset can be masked by water-related swelling from stem rehydration after frost-induced shrinkage during winter (Oberhuber et al., 2015; Turcotte et al., 2011; Zweifel et al., 2000).

Both species ceased radial growth similarly in response to June VPD but with different asymptotic spring performance: while Pyrenean oak showed little variation, maritime pine's asymptote was dramatically reduced (Fig. 3). VPD is well known as the main factor controlling stomatal closure during drought episodes (McAdam and Brodribb, 2015),

so we hypothesized that this result is due to differential stomatal regulation strategies. Pine is able to maintain a relatively stable midday leaf water potential by rigid stomatal control as soil moisture conditions change (isohydric strategy), while oak tracks fluctuations in water availability, with no discernible threshold of minimum water potential (anisohydric behavior) (Grossiord, 2019). Consequently, higher transpiration rates and looser stomatal control is expected for deciduous oak trees (Fernández-De-Uña et al., 2017), so water availability may be the main limiting factor for Pyrenean oak growth.

The higher asymptote and rate parameter for maritime pine (in spring and autumn) corroborate faster growth for early successional and light-demanding species (Rozas et al., 2009; Sánchez-Costa et al., 2015; Sánchez-Gómez et al., 2008). To the contrary, later-successional species like oak are supposed to utilize resources more efficiently (Cuny et al., 2012). We think that the height species stratification in the mixed stands (Pyrenean oak trees grew under the canopy of maritime pine), and, in particular, different forest management systems (high vs. coppice), which affects species' cambial age, possibly influence these results. Over-aging could also cause a steep reduction in growth rates, evidencing a growth decline for the Pyrenean oak coppice stands (Corcuera et al., 2006). In addition, the spring inflection point was the same for both species (Table 3), which suggests that growth was similarly controlled by environmental conditions rather than endogenously in a species-specific way.

Earlier autumn radial increment onset demonstrates a faster recovery response from summer drought for maritime pine as precipitation increases (Fig. 3). Accordingly, the Richards shape parameter (τ_4, Table 3) showed a longer exponential cumulative SRV period for maritime pine at the beginning of autumn, which could also confirm a faster recovery from summer drought for maritime pine than Pyrenean oak. It may be caused by using water from different soil strata and different timing of water use. Since Pyrenean oaks coppices have shallower root systems than high forest maritime pine, Pyrenean oak trees may be less effective exploring deep soil layers than maritime pine, indicating that species rely on different water sources in the soil and show contrasting

physiological responses to drought (Grossiord, 2019). Accordingly, maritime pine's deep root system (Andivia et al., 2019; Saint Cast et al., 2019) would enable greater soil water use compared to the clonal Pyrenean oak trees, which have a shallow root system with rare vertical roots growing deeper than one meter (Salomón et al., 2016).. Therefore, root spatial stratification would give maritime pine a competitive advantage and, as consequence, accelerate post-drought growth response.

Minimum temperature during October and November was the limiting factor for autumn growth, driving cessation timing and asymptotic value for both species. However, different species' responses to temperatures could hide different autumn growth strategies (Fig. 4). Maritime pine may increase growth as temperatures increase, while Pyrenean oak would reduce cumulative SRV due to stem water loss in the absence of growth (Fernández-De-Uña et al., 2017). This could also explain species' differences in the rate and shape parameters and inflection point in the autumn Richards' model (Table 3). Mediterranean tree species generally experience seasonal stem shrinkage in response to drought (increasing water deficit) and subsequent stem rehydration after rainfall (Sánchez-Costa et al., 2015). Higher asymptote, rate parameters and also a delayed inflection point (notice that it did not happen in spring) for maritime pine could indicate not just rehydration, but also growth in autumn. In fact, Vieira et al. (2014) verified that maritime pine in Mediterranean areas can exhibit long-lasting xylem enlargement through mid-October, or even autumn cambial reactivation (Vieira et al., 2015). Other authors have even demonstrated that cambial activity can continue in other conifer species during mild winters (Cherubini et al., 2003; Liphschitz and Lev-Yadun, 1986; Pacheco et al., 2018). Accordingly, these timing dissimilarities during the autumn season (i.e., differences in onset dates, inflection point and temperature dependence for the asymptotic value) may evidence a temporal complementarity producing a clear advantage for maritime pine's growth.

These differences in growth/weather relationships between species could be mainly due to silviculture regimen dissimilarities (coppice vs. high forest) and to resource partitioning (temporal and/or spatial). Differences in water use and nutrient acquisition, canopy structure, leaf phenology (evergreen vs. deciduous), stomatal control, tree height, rooting depth or even mycorrhizal associations may drive different physiological processes during the growing season for the co-existing species studied here (Grossiord, 2019). These mechanisms related to facilitation or resource partitioning would imply a reduced competition for resources; as species use different resources in space and time, they are less likely to compete for them. Accordingly, some studies have suggested that mixed forests might be better adapted to a changing climate (Grossiord, 2019; Jactel et al., 2017; Pretzsch et al., 2019), although it may depend on species identity, forest type and local environmental conditions (Bonal et al., 2017; Grossiord et al., 2014; Merlin et al., 2015).

4.2. Ecological consequences in a climate change scenario

Warmer temperatures and more frequent and intense droughts are expected in the Mediterranean region in the next decades in the context of climate change (IPCC, 2014). It is likely to dramatically affect forests, although their response is still uncertain. In spite of water availability, usually being the limiting factor for Mediterranean species, we have shown that some intra-annual growth phases for both species studied here are also temperature dependent. Hotter spring temperatures may lead to an earlier radial onset for both species, although the lengthening of the growing season would be tempered by a probable earlier cessation due to higher summer temperatures (Table 4). Species-specific ontogenetic shifts could benefit maritime pine due to differences between species in temporal dynamics of leaf budburst. Accordingly, maritime pine may benefit from the absence of Pyrenean oak competition for water use in early spring, when Pyrenean oak is still leafless and living

off the reserves of the previous year.

Both species could prolong their growing seasons as radial increment cessation could be delayed by a rise in autumn temperatures (Fig. 3). Although a lengthening of the growing season would not assure greater stem growth (Ren et al., 2019), maritime pine could respond positively to warmer autumn temperatures (Fig. 4). In fact, abundant rainfall in September and high temperatures during October and November could allow a new growth period for maritime pine, leading to intra-annual wood density fluctuations (Vieira et al., 2015). Thereby, the capacity of maritime pine to adjust cambial activity to current environmental conditions would represent an important strategy under future climate change conditions.

On the other hand, increased summer drought intensity or frequency may drastically reduce maritime pine growth (Fig. 4). This is in agreement with other studies finding an ongoing growth decline problem in Spain for maritime pine (Prieto-Recio et al., 2015), and also for oak species (Gea-izquierdo et al., 2013). Accordingly, low spring precipitation and summer drought caused extreme spring shrinkage in 2012 for both species (Table 3); radial growth of Pyrenean oak trees was nearly suppressed, indicating higher susceptibility to water stress. Although Pyrenean oak does not suffer earlywood hydraulic diameter changes under drought, it experiences a reduction in latewood width, which could ultimately challenge its hydraulic performance (Fernández-De-Uña et al., 2017). The better pine response to drought could be related to lower transpiration rates, tighter stomatal control and higher internal stem water reserves due to their bigger size and, consequently, higher conductivity area (Fernández-De-Uña et al., 2017). However, if longer drought episodes last until late summer, maritime pine growth could be absent during the autumn. Anyway, further research is necessary to evaluate and compare the drought resilience from species studied here. Pyrenean oak could display different above/below-ground growth balance by keeping large amounts of non-structural carbohydrates in storage tissues for root-resprouting, as a strategy to ensure plant regeneration and to cope with drought stress (Salomón et al., 2013). In contrast, high energetic costs of maintaining multiple stems per tree and long-lived root systems might constrain aboveground performance and contribute to Pyrenean oak coppice stagnation (Salomón et al., 2017). To avoid that situation (coppice growth stagnation) after drought events and to ensure Pyrenean oak persistence, an adequate forest management plan would be necessary. Thinning could increase growth for both species (Aldea et al., 2017), but conversion into high forests does not always succeed or even might worsen a physiological root-to-shoot imbalance (Salomón et al., 2016).

5. Conclusion

Species weather-response differences at main intra-annual growth phases showed some degree of temporal complementarity between species, restricting the beneficial effects of mixtures to certain periods. Maritime pine presented a more effective growth strategy by earlier onset during spring and a high likelihood of additional growth in autumn, which may suppose an adaptive advantage into a future warmer climate scenario compared to Pyrenean oak. In contrast, longer summer droughts due to climate change could counteract the maritime pine benefits due to increased temperature. Although maritime pine showed a higher cumulative stem radial variation and likely more efficient response to climate change, mixing stands with Pyrenean oak should be preserved as they would contribute to improving other ecosystem services such as biodiversity, recreational values, long-term productivity and increase resilience to biotic and abiotic hazards.

CRediT authorship contribution statement

Jorge Aldea: Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Writing - original draft. **Felipe Bravo:** Supervision, Funding acquisition, Resources, Writing - review & editing.

Javier Vázquez-Piqué: Investigation, Writing - review & editing.
Ricardo Ruíz-Peinado: Investigation, Writing - review & editing.
Miren Del Río: Conceptualization, Methodology, Project administration, Supervision, Funding acquisition, 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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118779.

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