



Radial increment dynamics of Maritime pine (*Pinus pinaster* Ait.) in pure and mixed stands with Scots pine (*Pinus sylvestris* L.) under changing environmental conditions

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Received: 21 July 2023 / Revised: 31 October 2023 / Accepted: 12 December 2023
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Abstract

Forest dynamics are undergoing profound alteration due to the fact that climate change is increasing the frequency and severity of abiotic and biotic forest disturbances. Because of the unpredictable nature of the drought periods and the variation in their severity, Mediterranean forests are typically more vulnerable. Mediterranean *Pinus pinaster* forests are showing decay symptoms linked to climate change. There is clear evidence that promoting mixtures can serve as an effective forest adaptation strategy. In this regard, we sought to better understand the responses of *P. pinaster* radial growth dynamics to various factors, in both mixed and pure forest stands, and provide valuable insights into *P. pinaster* dynamics when mixed with *P. sylvestris*. In this study, we examined the variation of intra-annual cumulative radial increment patterns in response to the climate of *P. pinaster* between pure and mixed stands with *P. sylvestris*. Using data from band dendrometers collected over five consecutive climatically distinct years (2016–2020), a nonlinear mixed-effect model approach was used to analyze the differences in intra-annual cumulative radial increment patterns for *P. pinaster* between years in mixed and pure stands. The intra-annual radial increment pattern of *P. pinaster* showed significant year-to-year variation and varied with tree size, with greater increment in larger trees. Trees in mixed stands had a higher mean radial increment compared to corresponding ones in pure stands. Increased summer maximum temperatures negatively affected tree cumulative annual increment regardless of composition, but with a lower impact on trees in pure stands. Spring precipitation increased the length of the growing season, while higher spring maximum temperatures triggered an earlier inflection point. Our results highlight the high plasticity of *P. pinaster* in adapting to varying intra- and inter-annual environmental conditions and competition with other species and suggest that promoting mixtures with *P. sylvestris* may be an interesting management strategy for adaptation to climate change.

Keywords Dendrometer band · Climate change · Intra-annual radial increment · Logistic model · *Pinus sylvestris* L · *Pinus pinaster* Aiton

Introduction

In the throes of climate change, forest dynamics are profoundly altered by increasing temperature, CO₂, vapor pressure deficit, and the frequency and severity of abiotic and biotic forest disturbances (McDowell et al. 2020). More precisely, the combination of climate change-related factors is unfavorably modifying forest dynamics and growth, raising forest decline, trees death, and causing higher susceptibility to pests, diseases, and wildfires (Prieto-Recio et al. 2015; Senf et al. 2020; Hartmann et al. 2022; María et al. 2022).

The Mediterranean forests tend to be more vulnerable because of unforeseen and more severe drought episodes in light of current climate change (Cramer et al. 2018; Tuel and Eltahir 2020). Although the knowledge of the impacts of climate change on Mediterranean forests dynamics significantly increased during the last decades (e.g., Martín-Benito et al. 2008; Herguido et al. 2016; Rodríguez de Prado et al. 2020; Vergarechea et al. 2021; Olivar et al. 2022), a great interest persists on how to anticipate and mitigate climate change effects on such valuable ecosystems (Vilà-Cabrera et al. 2018; Peñuelas and Sardans 2021).

Tree radial growth is one of the main sources of information for forest management to derive adapting plans to the expected climate change scenarios. It can be considered as the proxy of tree growth performance (Cailleret et al. 2017).

Communicated by Tianjian Cao.

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Accordingly, interpreting tree radial growth responses to weather factors is crucial to decipher the mechanisms underlying forest carbon storage (Nabeshima et al. 2010) and to evaluate different factors affecting tree growth response to climate change (e.g., Linares et al. 2010; Calama et al. 2019; Aldea et al. 2022). The timing of the radial increment and growth rates could also provide insights into the species-specific functional traits drawing life strategies for tree species (Cuny et al. 2012). Moreover, tree growth patterns could explain niche differentiation, contributing to a better understanding of some of the factors ruling coexistence processes among tree species (Martínez-Sancho et al. 2021). All the above can help us to develop sustainable and adaptive management programs.

Tree growth response to different climatic factors has been well studied using mainly two kinds of tree growth data sources, measurements from dendrometers (Deslauriers et al. 2007; Nabeshima et al. 2010; Aldea et al. 2017; Vourlitis et al. 2022) and tree-ring series from increment cores (Speer 2010, Cook and Kairiukstis 2013). Both data sources give distinctive insights into tree growth dynamics. Dendrometer data proved its reliability in studying the cambial phenology phases and the intra-annual increment of trees (Deslauriers et al. 2003; Campelo et al. 2018). The analyses of intra-annual data give more details on growth responses and variability to specific weather incidents during the year for better projection of growth responses to stressful and limiting climate conditions (Duchesne and Houle 2011; Martínez-Sancho et al. 2021), including changes in growth phenology triggered by climate change (Peñuelas and Filella 2001). On the other hand, tree-ring data analysis has been commonly used to study inter-annual growth responses and stability to weather conditions (King et al. 2013). However, some information on intra-annual growth can be also obtained from tree cores by analyzing early- and late-wood widths (Pichler and Oberhuber 2007; Martín-Benito et al. 2008) or xylem anatomy in tree rings (Ziaco 2020), although they provide less information than dendrometers as the exact timing of tree growth is not known. Both approaches have recently been applied together to evaluate the different adaptation strategies to drought, to assess the coexistence between distinct species (Martínez-Sancho et al. 2021).

In the Mediterranean region, some tree species tend to exhibit growth plasticity by having different intra-annual growth patterns, i.e., unimodal and bimodal patterns, depending on the annual weather conditions variability and site conditions (Camarero et al. 2010; Gutiérrez et al. 2011; Aldea et al. 2017, 2018; Campelo et al. 2018; Tumajer et al. 2021). Such tree species can change from a unimodal to a bimodal intra-annual growth pattern if the soil moisture levels are suitable following a dry summer (Touchan et al. 2012). This means that the species is well adapted to the stressful conditions during the dry summers, but can

maximize its productivity (Maseyk et al. 2019). Different species have distinct coping strategies to face dry summer, being bimodal vs unimodal pattern character mandatory or facultative depending on species and sites (Campelo et al. 2021).

Intra- and inter-annual growth patterns have been recently studied in different mixtures, evidencing the potential of species mixing to cope with climate change (Michelot et al. 2012; Aldea et al. 2021; Martínez-Sancho et al. 2021). A number of studies have shown that mixed stands' productivity is higher and more stable over time than that of corresponding pure stands (Jucker et al. 2014; del Río et al. 2017), and that species mixing can mitigate the effects of extreme droughts (e.g., Pretzsch et al. 2013; Pardos et al. 2021). Facilitation and niche complementarity have the potential to produce a higher supply, capture, or use efficiency of resources across more diverse communities (Loreau and Hector 2001; Naeem 2002, Forrester and Bauhaus 2016). Temporal complementarity, which can be analyzed by between species growth asynchrony in mixed forests (del Río et al. 2021), may allow the release of stress under extreme droughts and sustain more constant productivity in mixed stands in comparison to monocultures (del Río et al. 2017; Morin et al. 2014; Pretzsch and Forrester 2017). Therefore, species interactions can modify species-specific growth patterns, as reported in studies comparing tree growth patterns in mixed vs. pure stands (Pretzsch et al. 2021; Strieder and Vospersnik 2021).

P. pinaster (maritime pine) is a forest tree species native to the western Mediterranean basin, mostly found in the Iberian Peninsula, France, and Italy (Alía et al. 1995). It occupies roughly 1.06 million hectares in monospecific stands and another 0.62 million hectares in mixtures with other species, being the second most important tree species in Spain in terms of distribution area (DGCONA, 2000). Some recent studies report the decline of *P. pinaster* forests in several regions of its distribution in Spain, due to precipitation decrease during the growing season and more frequent and severe drought periods, combined in some cases with biotic factors which synergistically increase tree stress (Prieto-Recio et al. 2015; Gea-Izquierdo et al. 2019). Mixed stands of *P. pinaster* and *P. sylvestris* were found to be a good alternative where these two species share a distribution area and promoting these mixed stands is considered a measure of adaptation to climate change (del Río et al. 2022; Ruano et al. 2022). *P. pinaster*-*P. sylvestris* mixed forests are frequent in North-Central Spain, with about 120,000 hectares mostly in the Iberian and Central Mountain Range (Riofrío et al. 2018).

Despite the two species are light demanding, higher productivity in mixed stands compared to pure stands was found by Riofrío et al (2017a, 2017b), owing to complementarity and its consequent inter-specific competition reduction,

which emerge from crown complementarity environment and the efficient canopy vertical stratification (Riofrío et al. 2017b; Cattaneo et al. 2020). Further evidence of complementarity between both species in mixed stands was reported by López-Marcos et al. (2021), stating that over-yielding does not solely dependent on above-ground interspecific complementarity, but also on belowground niche complementarity, that is to say, a better partitioning and efficient exploitation of soil resources (water and nutrient elements). However, at tree level, the effects of species interactions on *P. pinaster* growth vary depending on the study area (Riofrío et al. 2017a, 2019; Rodríguez de Prado et al. 2022). Thus, to what extent the admixture of *P. sylvestris* can modify *P. pinaster* tree growth and its response to climate is still unclear.

In this study, we focus on *Pinus pinaster* intra- and inter-annual growth pattern in pure and mixed stands with *P. sylvestris* with the aim of determining its vulnerability to climate change and the use of species admixture as an adaptation strategy. Here, a nonlinear mixed-effect model approach was used to analyze the differences in intra-annual cumulative radial increment patterns of *Pinus pinaster* in mixed and pure stands and to identify whether mixing these two species (*Pinus pinaster*-*Pinus sylvestris*) modifies *P. pinaster* intra-annual radial growth response to climate. We used data from band dendrometers recorded during five

consecutive years to insight i) the intra-annual radial increment pattern of *P. pinaster* and the potential influence by the admixture of *P. sylvestris*, ii) to find out if the admixture effect depends on tree size and year weather conditions, and iii) to identify the weather variables that explain the intra-annual variability in radial increment patterns.

Materials and methods

Study area and design

The current study was carried out in the Sierra de la Demanda (41° 47.713' N, 2° 56.328' W) (Fig. 1), at an elevation of 1145 m above sea level, in pure and mixed pine forests of *P. pinaster* and *P. sylvestris*, where the species cover around 50,000 ha. The targeted admixture appears in the ecotone between the distribution areas of both species. The study area is characterized by a subhumid Mediterranean continental climate. Soils are acidic (pH 3.9–5.4) with sandy loam to sandy texture, low cation exchange capacity (2.4–18.1 cmol_c kg⁻¹), and medium to low water-retention capacity (1.5–18 g cm⁻²) (Marcos et al. 2018). These forests are managed with timber production as the main objective,

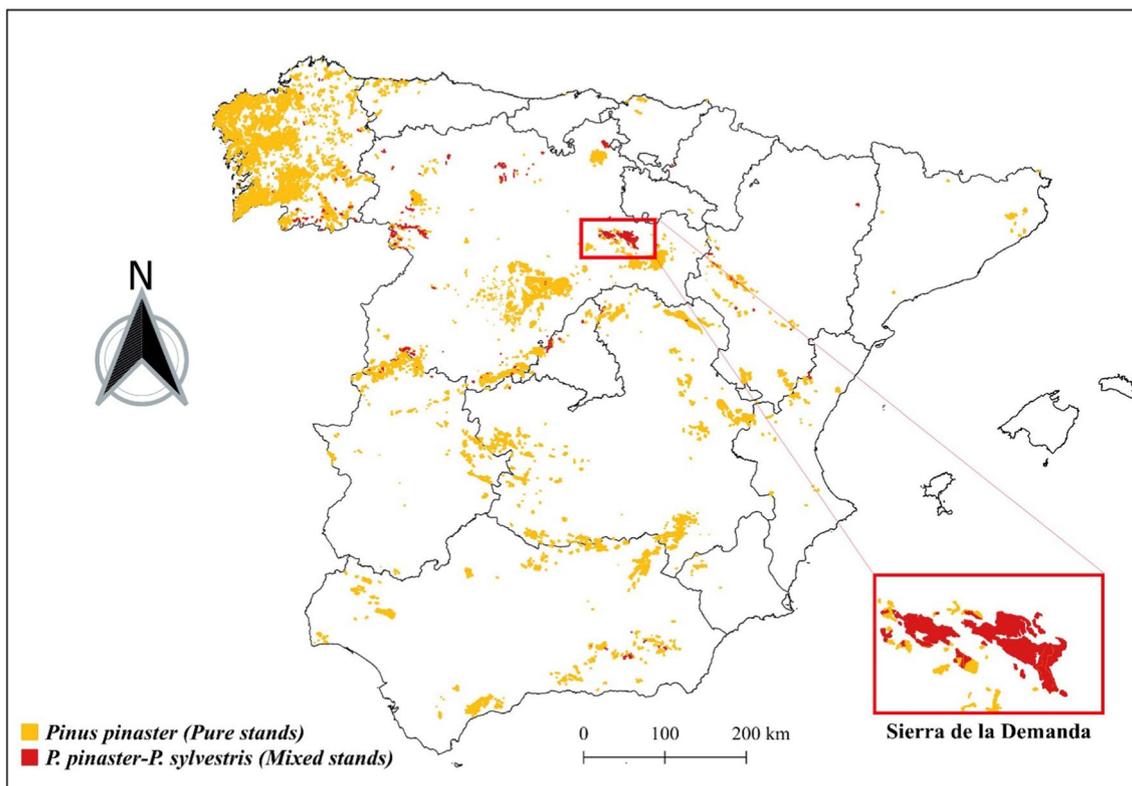


Fig. 1 Study area (Sierra de la Demanda). (Color figure online)

although there is a growing interest in managing for different provisioning services (Aldea et al. 2014).

A set of 6 circular plots with a radius of 15 m grouped into 3 pairs was used (Table 1), each pair including one pure plot of *P. pinaster* and one mixed plot with *P. sylvestris*. The plots belong to a network of triplets, which includes also pure plots of *P. sylvestris*, established in 2014–2015 in the study area (Riofrío et al. 2017b; Cattaneo et al. 2020). Pairs are located less than 1 km from each other, in a way that each pair of plots has similar conditions of site, age, density, and management. The stands were approximately fully stocked, and none of the plots had been thinned for at least 15 years. In mixed plots, the species proportion ranged from 61 to 33% of the total basal area.

Dentrometer and climatic data

A total of 49 trees (8–9 trees per plot) from the three pairs were selected, taking into consideration diameter classes

distribution (Table 2). Dendrometer bands (DB 20, EMS Brno) were installed at breast height (1.30 m) three months before the first circumference reading to ensure the stability of the bands. The outermost dead bark was removed and smoothed prior to installing the bands to avoid any incorrect readings resulting from stem deformities and possible bark shrinking and swelling due to changes in air humidity. Girth measurements were taken every other week throughout the year from February 2 of 2016 until December 2 of 2020 (bands resolution of 0.1 mm). The final girth increment data were translated into radial increments data. It is worth noting that there are different valid approaches to modeling the secondary growth of trees: stem cross-sectional area (basal area increment (BAI)), radial growth or diameter growth, and girth growth. All of the approaches are methodologically sound because our study targets examining the intra- and inter-annual variations in tree growth in both pure and mixed stands. Radial or diameter increment measurements have been previously employed as alternatives to stem

Table 1 Plots' main characteristics

Pair	Plot	Density (trees/ha)	G (m ² /ha)	dq (cm)	Ho (m)	Proportion <i>P. pinaster</i> (%)
1	<i>P. pinaster</i> mixed	679 (total)	33.26	24.97	16.1	61
		283 (<i>P. pinaster</i>)	20.23	30.17	16.1	
1	<i>P. pinaster</i> pure	594 (total)	37.53	28.36	16.9	100
		594 (<i>P. pinaster</i>)	37.53	28.36	16.9	
2	<i>P. pinaster</i> mixed	552 (total)	68.22	39.68	24.3	33
		198 (<i>P. pinaster</i>)	22.35	37.9	25.8	
2	<i>P. pinaster</i> pure	722 (total)	70.31	35.22	21.4	100
		722 (<i>P. pinaster</i>)	70.31	35.22	21.4	
3	<i>P. pinaster</i> mixed	1103 (total)	54.86	25.16	19.3	58
		538 (<i>P. pinaster</i>)	31.87	27.47	18.8	
3	<i>P. pinaster</i> pure	1259 (total)	69.06	26.43	15.6	96
		1146 (<i>P. pinaster</i>)	66.04	27.09	15.6	

G stand basal area (m²/ha); dq quadratic mean diameter (cm); Ho dominant height (m); Proportion *P. pinaster* in terms of basal area

Table 2 Trees characteristics per plot

Pair	Plot	N	DBH (cm)				Mean radial increment (mm)				
			Mean	Max	Min	Std. Dev	2016 Feb–Dec	2017 Feb–Nov	2018 March–Dec	2019 March–Nov	2020 Feb–Dec
1	<i>P. pinaster</i> mixed	8	28.8	35.4	22.1	4.1	1.84	1.83	1.68	1.79	1.84
1	<i>P. pinaster</i> pure	8	30.5	40.8	21.7	6.2	2.14	2.11	0.8	0.93	2.3
2	<i>P. pinaster</i> mixed	8	37.8	40.9	28.1	3.9	0.82	0.69	0.83	1.05	0.79
2	<i>P. pinaster</i> pure	8	34.3	41.0	27.7	5.1	0.79	0.61	0.66	0.6	0.29
3	<i>P. pinaster</i> mixed	8	28.3	44.2	18.7	8.0	0.98	1.07	1.19	1.11	1.23
3	<i>P. pinaster</i> pure	9	27.5	48.0	15.9	10.4	1.03	1.06	1.31	1.24	1.2

N number of sampled trees per plot; DBH diameter at breast height (cm)

cross-sectional area (Deslauriers et al. 2007; Strieder and Vospernik 2021; Donfack et al. 2023).

Meteorological data were provided by the State Meteorological Agency—AEMET. Climatic data contained daily data of temperature, and precipitation during the period September 2015 and December 2020 of the station Hontoria del Pinar "2079" in Burgos (about 25km from the study area). The daily data were used to obtain monthly, seasonal, and annual averages (hydrological year, starting the 1 October) of temperature and precipitation. We used the function "diagwl" from the R Package 'climatol' (Guijarro 2019) to build Walter and Lieth climate diagrams for each of the studied years (Fig. 2). Throughout the study period, the mean annual temperature fluctuated from 9.9 °C (in 2018) to 11.3 °C (in 2017), while annual precipitation ranged from 589 mm (in 2017) to 939.5 mm (in 2016). Year 2017 distinctly differed from the rest of the years, characterized by its elevated mean annual temperature and reduced annual precipitation.

***Pinus pinaster* Intra-annual cumulative radial increment patterns**

P. pinaster frequently shows a bimodal intra-annual growth pattern (Aldea et al. 2018; Garcia-Forner et al. 2019). The observed annual tree growth series constantly showed a unimodal growth pattern (Figure 6 in supplementary material). In this way, we compare the Richard function with three and four parameters. The logistic growth model with three parameters (Eq. (1)) showed the best results and was used to analyze cumulative radial increment data (2016 to 2020) based on a mixed-effects approach that considers the hierarchical structure of the sampling design (tree and plot). Processing such type of data using a mixed-effects model entails accounting for the spatial and temporal dependence of data by adding a random effect structure into the model. Thereby models with different random structures were compared (i.e., plot and/or tree affecting the three parameters of the model) and fit through restricted maximum likelihood estimation (REML). All models were evaluated and compared by likelihood ratio test, and model selection was based on the Akaike information criterion (AIC). The model with the lowest AIC value was selected as the best-fitting model. Specifically, model with plot and tree level affecting the asymptote ($Asym_{ij}$) proved to be the optimal random structure.

In order to investigate if cumulative growth pattern was influenced by admixture, tree size, and year, fixed effects of the following variables were included in the three parameters of the logistic function: stand composition (Co) as a dummy variable (Pure = 0 and mixed = 1), initial tree diameter (DBH)

and year. Interaction among covariables was also included in the model. In this regard, all possible models with different combinations of the variables and their interactions were fit with maximum likelihood estimation (ML) and all resulting models were compared (Table 6 in supplementary material) selecting the final model according to the lowest (AIC). This process started with the following generic model:

$$CRI_{ij} = \frac{Asym_{ij}}{1 + e^{-K_{ij}(t - Infl_{ij})}} + \varepsilon_{ij} \quad (1)$$

$$Asym_{ij} = Year + DBH + Co + Year * DBH + Year * Co + Co * DBH + \rho_j + \tau_{ij}$$

$$K_{ij} = Year + DBH + Co + Year * DBH + Year * Co + Co * DBH$$

$$Infl_{ij} = Year + DBH + Co + Year * DBH + Year * Co + Co * DBH$$

where CRI_{ij} is the cumulative radial increment for tree i in plot j (mm); $Asym_{ij}$, K_{ij} , and $Infl_{ij}$ are the asymptote, inflection point, and growth parameter rate respectively; t is the day of year variable; Year is the year factor variable, a variable of five levels (2016 as the base year, 2017, 2018, 2019 and 2020); Co is the abovementioned plot composition dummy variable; DBH is the tree diameter at breast height (mm); $\rho_j \sim N(0, \sigma_j)$ and $\tau_{ij} \sim N(0, \sigma_{ij})$ are the plot and tree random effect; $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon)$ is the error term.

Once we have defined the final model from the previous step, we analyzed the effect of weather on the cumulative radial increment substituting the year factor variable with meteorological variables. Based on a biological meaning, meteorological variables (Table 3) highly correlated to radial increment were included in the fixed structure to evaluate their effects on model parameters. Similar to the previous model, we tested different fixed structures with meteorological variables (Table 7 in supplementary material), compared the fit models in terms of AIC, and select the most parsimonious one using maximum likelihood estimation (ML). The model fitting procedure was performed using R-package "nlme" (Pinheiro et al. 2023).

To assess the final models' performance and goodness of fit, we calculated various regression evaluation metrics. Mean bias, representing the mean difference between the predicted values and the observations, and the root mean square error (RMSE), which measures the square root of the mean of the squared differences between the predicted values and the observations. Furthermore, we calculated both marginal R-squared and conditional R-squared using the function "R2M" from the R-package 'nlraa' (Miguez 2023).

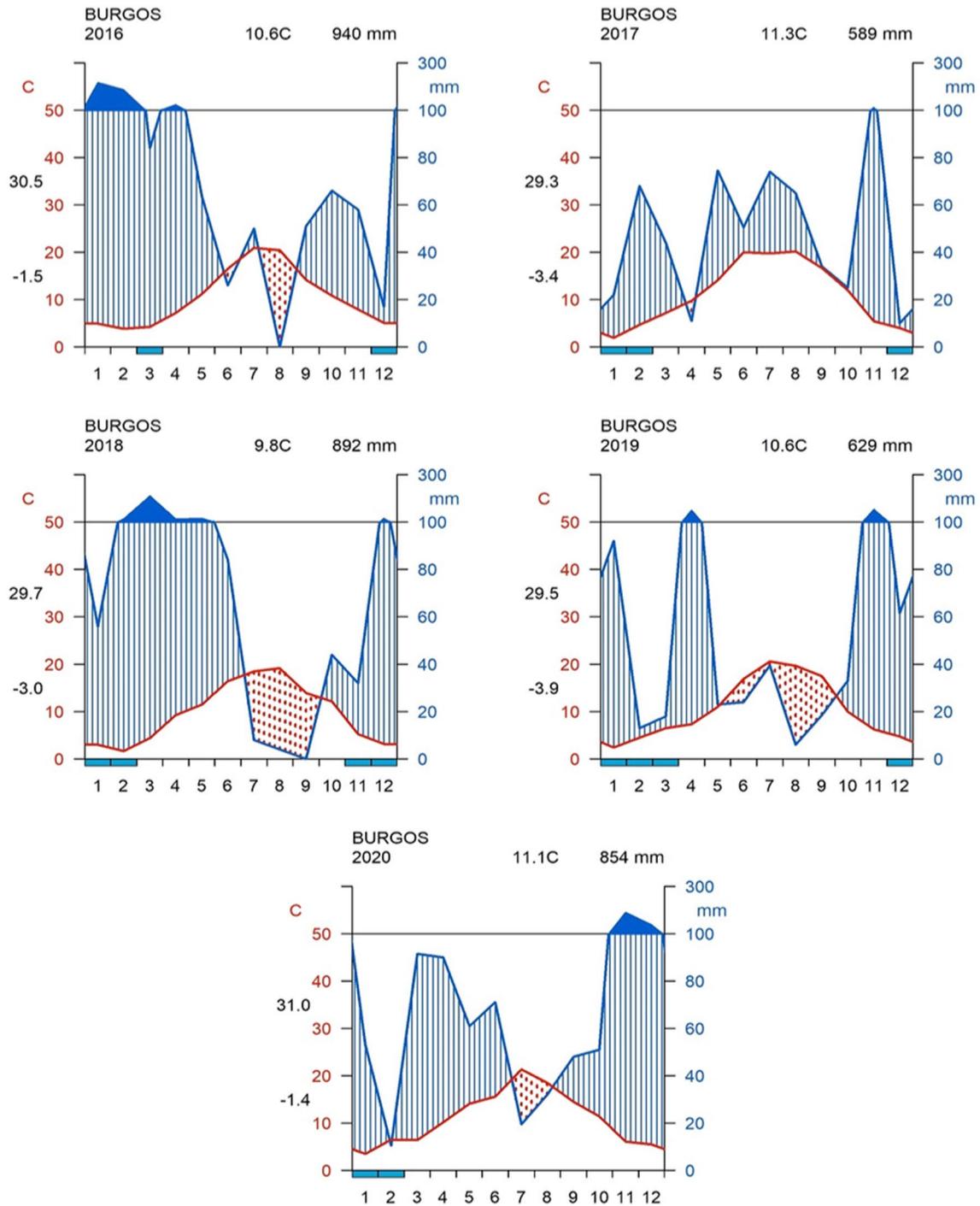


Fig. 2 Walter and Lieth climate diagrams for studied years 2016–2020. Blue lines represent precipitation (mm) while red lines represent temperature (°C). Blue and red areas represent the wet and dry seasons, respectively. The horizontal line at 100 mm precipitation

and 50 °C marks the origin of the logarithmic scale. Dark blue areas above the horizontal line indicate seasons of sure frost and light blue rectangles indicate months of probable frost. (Color figure online)

Table 3 Weather variables considered in the model fitting for the hydrological period 2016–2020

Variable*	Description	Mean	Min	Max	Std. Dev
Autumn_P	Autumn precipitation (mm)	182.7	76	289	76.4
Winter_P	Winter precipitation (mm)	233.8	100	419	122.7
Spring_P	Spring precipitation (mm)	253.5	129.5	436.5	115.5
Summer_P	Summer precipitation (mm)	110.7	69.5	189.5	48.6
Autumn_Tmax	Autumn maximum temperature (°C)	17.9	16.7	18.8	0.9
Autumn_Tmin	Autumn minimum temperature (°C)	4.0	2.0	4.7	1.1
Autumn_Tmed	Autumn average temperature (°C)	11.0	10.4	11.4	0.4
Winter_Tmax	Winter maximum temperature (°C)	9.2	7.1	10.5	1.4
Winter_Tmed	Winter average temperature (°C)	3.9	2.6	5.1	1.0
Spring_Tmax	Spring maximum temperature (°C)	15.4	12.9	17.7	2.0
Spring_Tmin	Spring minimum temperature (°C)	2.5	0.5	3.9	1.3
Spring_Tmed	Spring average temperature (°C)	8.9	7.5	10.3	1.2
Summer_Tmax	Summer maximum temperature (°C)	27.9	26.8	28.7	0.8
Summer_Tmin	Summer minimum temperature (°C)	10.0	9.2	11.2	0.7
Summer_Tmed	Summer average temperature (°C)	18.9	18.0	19.9	0.7

*Autumn: from September to November of the previous year, Winter; from December of the previous year to February of the current year; Spring from March to May of the current year; and Summer: from June to August of the current year

Results

Effect of stand composition, year, and tree size on intra-annual radial increment

The summary and the coefficients for the final nonlinear mixed model (Eq. (2)) examining the effects of stand composition, DBH, and year on the radial increment are shown in Table 4. All factors and covariables in the resulting model were significant at 95% significance level. The plotted residuals against the predicted cumulative radial increment, suggest compliance with the homoscedasticity assumption (Figure 7 in supplementary material).

$$CRI_{ij} = \frac{Asym_{ij}}{1 + e^{-K_{ij}(t - Infl_{ij})}} + \epsilon_{ij} \quad (2)$$

$$Asym_{ij} = \alpha_0 + \alpha_1 2017 + \alpha_2 2018 + \alpha_3 2019 + \alpha_4 2020 + (\alpha_5 + \alpha_6 2017 + \alpha_7 2018 + \alpha_8 2019 + \alpha_9 2020) \times Co + \alpha_{10} DBH + \rho_j + \tau_{ij}$$

$$K_{ij} = \beta_0 + \beta_1 2017 + \beta_2 2018 + \beta_3 2019 + \beta_4 2020$$

$$Infl_{ij} = \gamma_0 + \gamma_1 2017 + \gamma_2 2018 + \gamma_3 2019 + \gamma_4 2020 + \gamma_5 Co + \gamma_6 DBH$$

where α_0 – α_{10} , β_0 – β_4 and γ_0 – γ_6 are the asymptote, growth rate parameter, and inflection point regression coefficients related to covariables and interactions; ρ_j and τ_{ij} are the plot and tree random effect; $\epsilon_{ij} \sim N(0, \sigma_e)$ is the error term.

The stand composition dummy variable (Co) increased the asymptotic parameter (α_5), with a different magnitude of the effect between years (α_6 – α_{10}), and negatively affecting the inflection point (γ_5) (Table 4). Figure 3 shows the higher mean intra-annual radial increment for trees in mixed stands compared to the corresponding ones in monospecific stands (0.5 mm higher on average α_5). The inflection point occurred later in pure stands (γ_5), which means a shift in the growing season for trees in mixtures in comparison to pure stands, although the effect is small (2.5 days).

The year factor clearly had different effects on the three parameters (Fig. 3 and Table 4). During the years 2018, 2019, and 2020 the asymptote increased compared with 2016 (α_0), while year 2017 the asymptote was lower than 2016. The growth rate was highest in 2018 (β_2) and the lowest in 2016 (β_0). Likewise, the inflection point also varied

depending on the year ($\gamma_1, \gamma_2, \gamma_3, \gamma_4$), with a later inflection point observed during the year 2018 contrary to years 2017, 2019, and 2020, in comparison with the reference year 2016. The strongest variation was in 2017 (γ_2), when the inflection point occurred 20 days earlier than in 2016 (in 15 May instead of 4 June). Moreover, the year factor affecting the asymptote differed between mixed and pure plots, implying that the year weather conditions modify the mixing effect.

Table 4 Nonlinear mixed effect model fit to analyze the effect of year, composition, and tree size on intra-annual radial increment. α_0 – α_{10} , β_0 – β_4 and γ_0 – γ_6 are the asymptote, growth rate parameter, and inflection point regression coefficients, respectively

Parameter	Coefficient	Std. Error	<i>p</i> value
α_0 (Intercept)	−0.20886	0.5589409	0.7087
α_1 (2017)	0.09000	0.0185922	0.0000
α_2 (2018)	0.18682	0.0208380	0.0000
α_3 (2019)	0.12501	0.0216744	0.0000
α_4 (2020)	0.25108	0.0226749	0.0000
α_5 (Co)	0.53514	0.5590900	0.3386
α_6 (2017 × Co)	−0.20015	0.0228179	0.0000
α_7 (2018 × Co)	−0.06712	0.0265002	0.0114
α_8 (2019 × Co)	−0.07652	0.0281297	0.0066
α_9 (2020 × Co)	−0.01749	0.0286568	0.5417
α_{10} (DBH)	0.00414	0.0012652	0.0011
β_0 (Intercept)	0.03224	0.0009974	0.0000
β_1 (2017)	0.00015	0.0013496	0.9120
β_2 (2018)	0.01013	0.0019863	0.0000
β_3 (2019)	0.00361	0.0019489	0.0644
β_4 (2020)	0.00080	0.0010785	0.4592
γ_0 (Intercept)	155.20534	2.0464412	0.0000
γ_1 (2017)	−20.25772	0.9740724	0.0000
γ_2 (2018)	3.62928	1.2377579	0.0034
γ_3 (2019)	−5.13528	1.3543402	0.0002
γ_4 (2020)	−9.51314	1.3772840	0.0000
γ_5 (Co)	−2.44934	0.8681401	0.0048
γ_6 (DBH)	0.01357	0.0053120	0.0107
σ_j (plot)	0.6520202		
σ_{ij} (tree)	0.5881373		
σ_e (error)	0.1651428		
AIC	−1734.639		
Mean Bias	0.003658897		
RMSE	0.1690618		
Marginal R^2	0.4793649		
Conditional R^2	0.9671425		

Tree size influenced the asymptote (α_{10}) and the inflection point (γ_6) of the cumulative radial increment curve in a similar way in both mixed and pure stands (Fig. 4 and Table 4). Both the asymptote and inflection point increased with tree size, which means that larger trees showed a higher intra-annual increment and a delay in their inflection point.

Weather effects on intra-annual radial increment

Equation (3) shows the structure of the final nonlinear mixed effect model fitted for the analysis of weather influence on the intra-annual cumulative radial increment pattern. The coefficients of all the variables in the resulting model were significant at 95% significance level (Table 5), evidencing

the crucial role of spring and summer weather conditions. The observed homogeneous variation of the residuals across all predicted values (Figure 8 in supplementary material) implies compliance with the homoscedasticity assumption.

Increased summer maximum temperature negatively affected the asymptote parameter with a lower impact for pure (α_1) compared to mixed stands (α_4). In addition, higher spring precipitation was linked to a higher growth rate (β_1), whereas higher spring maximum temperature caused an earlier inflection point (γ_1) of the growth curve (Fig. 5). In accordance with the model based on the year factor (Eq. (2)), tree radial increment asymptote is still greater and the inflection point is earlier in mixed stands than in pure stands for given tree size, spring precipitation and spring and summer maximum temperatures (Fig. 5 and Table 5).

$$CRI_{ij} = \frac{Asym_{ij}}{1 + e^{-K_{ij}(t - Infl_{ij})}} + \epsilon_{ij} \quad (3)$$

$$Asym_{ij} = \alpha_0 + \alpha_1 \text{Summer_Tmax} + \alpha_2 \text{DBH} + (\alpha_3 + \alpha_4 \text{Summer_Tmax}) * \text{Co} + \rho_j + \tau_{ij}$$

$$K_{ij} = \beta_0 + \beta_1 \text{Spring_P}$$

$$Infl_{ij} = \gamma_0 + \gamma_1 \text{Spring_Tmax} + \gamma_2 \text{DBH} + \gamma_3 \text{Co}$$

where Summer_Tmax: is summer maximum temperature; Spring_P: is spring precipitation; Spring_Tmax: is spring maximum temperature affecting asymptote, growth rate, and inflection point parameter, respectively. other covariables and error terms as defined before.

Discussion

The distinct intra-annual radial increment patterns that we identified for *Pinus pinaster* growing in pure and mixed stands, and the dependency of radial increment pattern on tree size and annual weather conditions confirm the high plasticity of the species in terms of growth response. This would enable *P. pinaster* to adapt its growth not only to the high intra- and inter-annual environmental variability, typical of Mediterranean climates, but also to different intra- and inter-specific competition conditions.

P. pinaster is a typical Mediterranean evergreen species classified as a drought-avoiding species (Picon et al. 1996), and that exhibits high plasticity, making it able to adapt its growth to various growing conditions (Alía et al. 1995; Picon et al. 1996; Corcuera et al. 2010; Vizcaíno-Palomar et al. 2017; Feinard-Duranceau et al. 2018; Sánchez-Salguero et al. 2018). As a consequence, *P.*

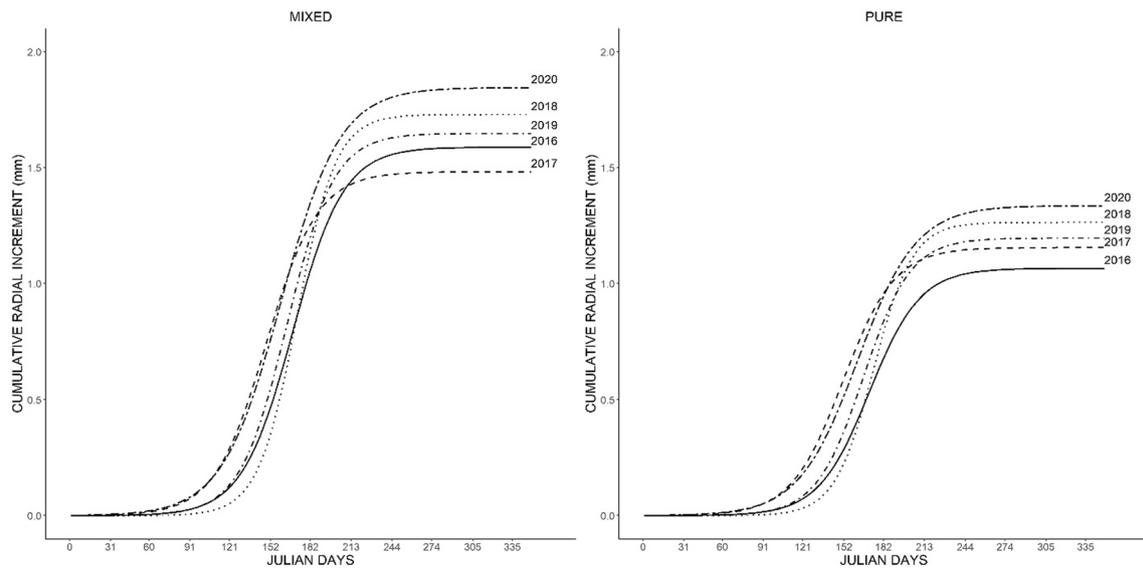


Fig. 3 Year effect on the cumulative radial increment in mixed plots and pure plots. Cumulative curves show tree with DBH=31.5 cm (mean tree diameter) in mixed (left) and pure (right) plots over the years (2016, 2017, 2018, 2019, and 2020)

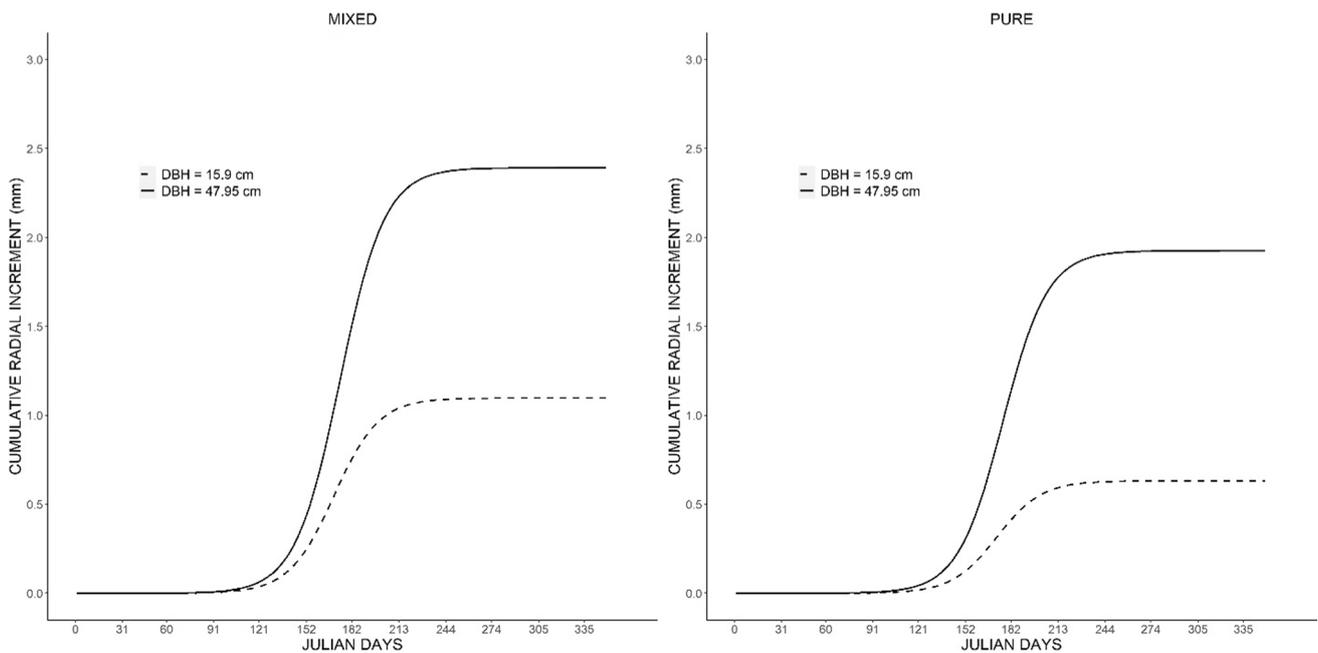


Fig. 4 Tree size effect on the cumulative radial increment in mixed and pure plots. Cumulative curves show the pattern for two trees for the year 2018. The solid line represents a tree with DBH=47.95 cm,

while the dashed line represents a tree with DBH=15.9 cm (maximum and minimum tree diameter, respectively)

pinaster tends frequently to profit from the favorable conditions that happen after summer stress to recommence its radial growth in autumn, resulting in an evident bimodal growth pattern (Vieira et al. 2015; Garcia-Forner et al. 2019) as a strategy to adapt to limited water availability during dry summer. Although our study site presents a

Mediterranean climate with a drought period during summer and mild and wet early autumn, which could allow a second growth period, we did not find a bimodal growth pattern. Campelo et al. (2018b) stated that the bimodality growth behavior in some species might be facultative according to the sites and the variability in climate factors.

Table 5 Nonlinear mixed effect model fit for weather variables, composition, and tree size effect on intra-annual radial increment. α_0 – α_4 , β_0 – β_1 and γ_0 – γ_3 are the asymptote, growth rate parameter, and inflection point regression coefficients, respectively

Parameter	Coefficient	Std. error	p value
α_0 (Intercept)	2.25714	0.611996	0.0002
α_1 (Summer_Tmax)	–0.08353	0.009148	0.0000
α_2 (DBH)	0.00410	0.001263	0.0012
α_3 (Co)	1.81586	0.651640	0.0054
α_4 (Summer_Tmax *Co)	–0.04877	0.012206	0.0001
β_0 (Intercept)	0.03077	0.001291	0.0000
β_1 (Spring_P)	0.00001	0.000005	0.0114
γ_0 (Intercept)	216.99938	3.326281	0.0000
γ_1 (Spring_Tmax)	–4.54892	0.178525	0.0000
γ_2 (DBH)	0.01267	0.005270	0.0163
γ_3 (Co)	–1.97379	0.877845	0.0246
σ_j (plot)	0.6467932		
σ_{ij} (tree)	0.587174		
σ_e (error)	0.1715051		
AIC	–1581.838		
Mean Bias	0.004568245		
RMSE	0.1759765		
Marginal R^2	0.4757348		
Conditional R^2	0.9476151		

Thus, we expect that the unimodal pattern we found in our study could be caused by several reasonable factors: First, the relatively cold study site compared with other studies that showed a bimodal pattern for this species (Aldea et al. 2017, 2018, 2021; Rubio-Cuadrado et al. 2018). This is in line with other studies that found unimodal pattern at cold sites and bimodal at warmer and drier sites for other Mediterranean species (Tumajer et al. 2021, 2022). Accordingly, Valeriano et al (2023) report through

growth simulations a clear bimodality in *P. pinaster* at mild coastal sites, but less evident in a continental site close to our study area. Second, the interaction between precipitation, temperature, and evapotranspiration restricts atmospheric moisture, which, in turn, affects tree development in *P. pinaster* forests (Bogino and Bravo 2008). In other words, this interaction could have resulted in an inadequately dry microclimate at our study site that could not trigger a second growth period. As a third point of emphasis, it is important to highlight that soil characteristics could play a pivotal role in the observed unimodal growth pattern. Our study in sandy loam soils revealed a different growth pattern than the bimodal growth pattern found in a close area with sandy soils (Aldea et al. 2017). In this way, a greater water holding capacity in our soil may allow trees to grow during the summer, resulting in a unimodal growth pattern. Finally, the uncertainty in our intra-annual radial increment monitoring, as the period of two weeks' measurements might prevent us to identify the second peak. Autumn growth resumption in *P. pinaster* after growth cessation during dry summer has been less pronounced than spring growth (Vieira et al. 2015), so it can be difficult to identify. However, we assume that this cause is less probable, as Aldea et al. (2017) detected a second increment period in autumn in *P. pinaster* using a similar methodology (band dendrometers read every two weeks), which was later confirmed by more detailed data from continuous dendrometers (Aldea et al. 2021).

The unimodal intra-annual radial increment pattern showed high variability between years, depending on weather conditions. The intra-annual radial increment pattern showed differences between years in the three parameters of the growth function that resulted in different maximum cumulative radial increments. For example, in mixed stands, the highest cumulative increment was

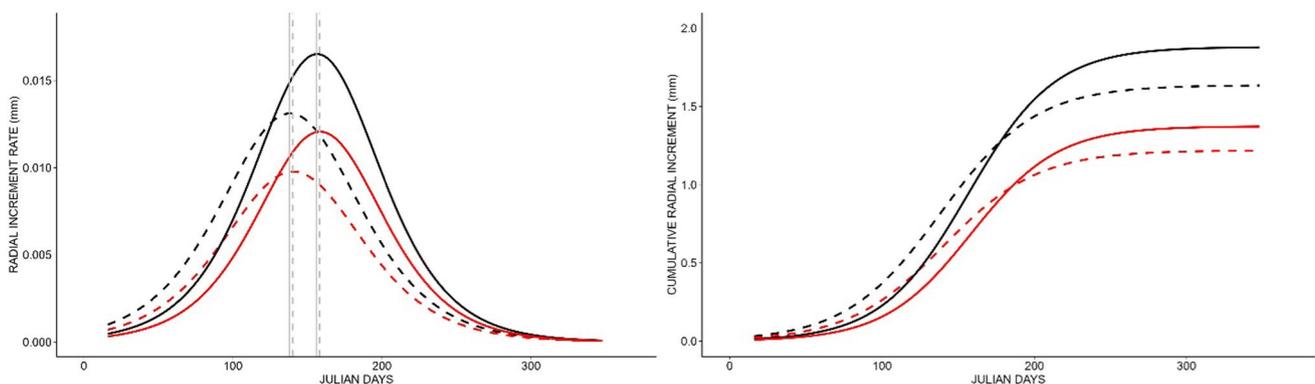


Fig. 5 Weather effect on (left) radial increment rate; (right) the cumulative radial increment, in mixed (black line) and in pure plots (red line) influenced by the best year weather conditions “2018” (summer maximum temperature = 26.8°C, spring precipitation = 436.5 mm and

spring maximum temperature = 13.7°C) solid line, and the driest year “2017” (summer maximum temperature = 28.7°C, spring precipitation = 129.5 mm and spring maximum temperature = 17.7°C) dashed line. (Color figure online)

found in 2020, whereas the lowest occurred in 2017, with a decrease of almost 20% compared to 2020. In pure stands, a similar trend was observed, with the highest cumulative increment occurring in 2020 and the lowest in 2016, corresponding to about a 20% decrease compared to 2020. Other studies in *P. pinaster* also report important variations between years in maximum cumulative radial increment (Vieira et al. 2014; Aldea et al. 2021), but not in other parameters of the growth function as found for other species (Rossi et al. 2006; Strieder and Vospernik 2021). However, we found a significant year effect on the inflection point and growth rate parameters, indicating phenological shifts and differences in growing period duration between years (Strieder and Vospernik 2021). The differences in the inflection point between years can be even longer than 20 days (in year 2017) (Table 4), which reflects that *P. pinaster* is able to adapt its growth to contrasting annual weather conditions.

Intra-annual radial increment also varied significantly within each year depending on stand composition, changing both the annual asymptote and the inflection point between pure and mixed stands (Fig. 3). Comparisons between intra-annual growth patterns in pure and mixed stands for different mixtures also indicated changes in both the cumulative annual increment and the timing of growth patterns (Strieder and Vospernik 2021). The conducted regression analysis plainly shows higher *P. pinaster* cumulative growth when growing mixed with *P. sylvestris* (Fig. 5), which agrees with the findings in the study area based on periodic tree diameter increment data (Riofrío et al. 2019). The increased cumulative annual radial increment implicitly imposes the presence of positive interaction between *P. pinaster* and *P. sylvestris* owing to niche complementarity processes between both species (Riofrío et al. 2017a). Previous studies on tree allometry and canopy structure in this mixture point to niche complementarity between the two pines in canopy space use (Riofrío et al. 2017b; Cattaneo et al. 2020; Condés et al. 2020). Also our results show a shift in radial growth pattern with a later inflection point in pure stands than in mixed stands, i.e., trees in pure stands tend to grow at the highest growth rate for a longer period of time, implying inter-specific competition for light and water resources. These light asynchronies in growth patterns between trees in mixed and pure stands suggest the presence of species interactions that modify tree growth pattern in mixtures, which may be linked to temporal and/or niche complementarity between species (del Río et al. 2017, 2021; Riofrío et al. 2017b). Vergarechea et al., (2021) also observed changes in the magnitude of *P. pinaster* growth response to climate between trees in pure stands and mixtures with *P. pinea*, corroborating that the species adapts its growth to different species admixtures.

Species mixing modified the year effect on the asymptote parameter. This means that species admixture modulates

the tree growth response to annual weather conditions, as found for other species (Strieder and Vospernik 2021). These results corroborate the presence of inter-annual variability in species interactions, which can shift from positive to negative linked to variation in environmental conditions (del Río et al. 2014; Condés and del Río, 2015; Zalloni et al. 2019). In our study, the net effect of the mixture was always positive in all the years. Mixed stands show greater maximum cumulative radial increment compared to pure stands. However, the lowest admixture effect was found in 2017 (the driest year), suggesting that resistance to drought is lower in mixed than in pure stands. This is in line with recent findings that indicate that although on average there is a positive effect of species mixing on tree growth resilience to drought, the effects depend on species mixtures, site conditions, and timing and strength of the drought events (Grossiord 2020; Bottero et al. 2021; Pardos et al. 2021; Aldea et al. 2022).

Tree size also influenced the intra-annual radial increment pattern, modifying the asymptote and inflection point. However, we did not find any interaction between tree size and species mixing. This contradicts the findings stated by Strieder and Vospernik (2021) that the composition of tree species had an impact on tree social class effect, where this effect was considerably greater in the pure *Picea abies* stands, compared to the mixed stands with *Larix decidua*. It is well known that tree growth is related to tree size (Pretzsch 2009), a relationship that generally depends on tree age (lower growth in mature trees) and tree competition status (greater growth in dominant trees). We found a positive relationship between tree size and the annual maximum cumulative increment, which may be reflecting the effect of tree competitive status, i.e., larger growth of dominant trees. This positive effect of tree size can be explained by the fact that in light-demanding species, like *P. pinaster*, competition for light is driving tree growth (Gómez-Aparicio et al. 2011), resulting in higher increments of dominant trees. The size-related asynchrony in growth pattern, where smaller trees showed an earlier inflection point compared to trees with a larger diameter, is likely to be attributable to temporal niche complementarity among different-sized trees, agreeing with the often different responses to the climate of dominant and large trees (Pretzsch et al. 2022), which can make more size-heterogeneous stands more resilient to drought.

Our model with climate variables as predictors (Eq. (3)) reveals that the most influential variables were maximum temperatures in spring and summer and spring precipitation. The maximum summer temperature during the growing year has a detrimental impact on cumulative stem growth, as has been previously reported in several studies (Bogino and Bravo 2008; Rozas et al. 2011; Mazza et al. 2015; Versace et al. 2022). This inverse relationship is presumably attributed to the atmospheric water deficiency as a result of the interactions between precipitation, temperature, and

evapotranspiration mentioned above (Bogino and Bravo 2008). Spring weather conditions modulate the length and timing of the growth period, with a positive effect of the amount of spring precipitation on the growing period duration and an earlier inflection point with a higher spring maximum temperature. These inferences tie well with previous studies on *P. pinaster*, wherein it was stated that the girth increment period of the *P. pinaster* stem is regulated by spring temperature and the summer's limited short-term water supply, leading to growth onset and cessation, respectively (Vieira et al. 2014, 2015; Camarero et al. 2015; Aldea et al. 2021). We speculate that longer growth length caused by spring precipitation is due to its effect on soil water availability in early summer, allowing a later cessation of tree growth.

We found that the maximum summer temperature reduced tree radial increment more in mixed than in pure stands. Our results agree with (Pardos et al. 2021), who found that *P. pinaster* showed greater or similar relative resilience and recovery to drought in pure stands as compared to *P. pinaster* growing with broadleaf and conifer species, respectively. On the contrary, *P. pinaster* showed less sensitivity to climate in *Pinus pinaster*-*Pinus pinea* mixed stands than in pure conditions, although tree growth response to drought was similar in pure and mixed stands (Vergarechea et al. 2021). These contrasting findings indicate that this species has fluctuating sensitivity to drought in mixed stands, depending on the species' admixtures. Nevertheless, it is noteworthy that the cumulative increment of *P. pinaster* was higher in mixed stands in all the years. This suggests that irrespective of relative changes between years, mixtures with *P. sylvestris* may provide greater *P. pinaster* yield, so the promotion of these mixtures in ecotone areas, especially in the upper border, appears as a good management alternative in the face of climate change (del Río et al. 2022). Nevertheless, tree growth responses to climate conditions could vary in other populations within the species distribution area (Sánchez-Salguero et al. 2018; Zas et al. 2020).

The findings of this study have to be seen in the light of some limitations, as inferring intra-annual growth patterns from band dendrometer data measured every two weeks does not allow a high precision due to the low monitoring frequency and the possible stem changes by rehydration or thermal shrinkage (Mäkinen et al. 2008). The limited data by year could explain why the best results were obtained with the three-parameter function. Such a function is less flexible and informative in comparison to other functions (Bewley and Fiebig 1988; Pödör et al. 2014; Cao et al. 2019), especially for a plastic species like *P. pinaster*. Our statistical analysis incorporates the use of R-package "nlme" (Pinheiro et al. 2023) to model the cumulative radial increment. It is worth mentioning that this package is widely

employed in mixed-effects models, yet it faces a limitation in handling crossed random effects well (e.g., "Year" crossed with "Plot"). In the methodology, we addressed the effect of weather on the cumulative radial increment by substituting the year factor variable with meteorological variables. However, the possibility of the weather variables not fully explaining temporal variability is worth considering, as it could lead to the problem of the lack of independence of the residuals at the year level. Accordingly, it is necessary to approach the interpretation of the model's results with caution. Nevertheless, our study revealed a favorable growth pattern for *P. pinaster* in mixed forests during all years. On this basis, future research should explore the pattern of *P. sylvestris* and investigate the potential presence of temporal complementarity among the two species.

Conclusion

Our study highlights the high plasticity of *P. pinaster* in growth response to varying intra- and inter-annual environmental conditions and competition with other species, which may provide some advantages for adapting to new growing conditions. However, at our study sites *P. pinaster* does not show the characteristic bimodal pattern reported at other sites as an adaptation to Mediterranean climates. The intra-annual radial increment pattern was modulated by weather conditions, being spring precipitation and spring maximum temperatures the most influential variables in our growth model.

The higher cumulative annual radial increment for *P. pinaster* in mixed than in pure stands suggests the presence of niche complementarity between *P. pinaster* and *P. sylvestris*. However, the lowest admixture effect was found in the driest year, suggesting lower resilience to drought in mixed stands. Additionally, the distinct intra-annual radial increment pattern with tree size indicates some asynchrony between large and small trees, suggesting a more effective use of resources in stands with more complex structures.

Overall, the study emphasizes that promoting species mixtures in regions where they have a shared distribution can be an effective strategy for addressing the impacts of climate change. Further thorough research on the factors shaping intra-annual growth patterns in Mediterranean tree species is needed to better inform forest management and conservation strategies, particularly considering climate change effects.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10342-023-01650-0>.

Acknowledgements Thanks for the support by the Spanish Ministerio de Ciencia e Innovación for funding the Project PID2021-126275OB-C21/C22—GESTIÓN FORESTAL INTEGRADA EN GRADIENTES

DE COMPLEJIDAD. Thanks go furthermore to the Junta de Castilla y León, Spain, and the European Union for funding the Projects VA183P20 (SMART—Bosques mixtos: Selvicultura, Mitigación, Adaptación, Resiliencia y Trade-offs) and CLU-2019-01—iuFOR Institute Unit of Excellence of the University of Valladolid through the ERDF "Europe drives our growth." Ali Askarieh also receives funds through a pre-doctoral contract co-financed by the European Social Fund and the Junta de Castilla y León through the Consejería de Educación 2019 call.

Author contributions Conceptualization, A.A., M.dR. and F.B.; methodology, A.A., M.dR, F.B., J.A. and J.R.; validation and formal analysis, A.A., M.dR. and F.B.; data curation, A.A.; writing—original draft preparation, A.A.; writing—review and editing, M. dR, F.B., J.A. and J.R.; supervision F.B. and M.dR; project administration, F.B. All authors have read and agreed to the published version of the manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Data availability Data are available from the corresponding author on reasonable request.

Declarations

Conflict of interests The authors declare no conflict of interest.

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