Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands

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ABSTRACT

Radial increment analyses allow us to determine tree responses to weather and tree competition, thus enabling the development of management strategies for adapting forest stands to forecasted climate change scenarios. In this study, the responses of pine-oak mixed stands (*Pinus pinaster* Ait. and *Quercus pyrenaica* Willd.) to thinning treatments were assessed at two sites in central Spain with contrasting drought conditions. Inter- and intra-annual radial increments were recorded every two weeks from dendrometer band measurements, using a Latin square design. Each site consisted of a control (unthinned) and two thinning intensities: moderate (25% of pine basal area removed) and heavy (40% of pine basal area removed). Thinning effects were monitored over three years of different weather conditions (2010–2012), with an extreme drought event in 2012. Linear mixed models were fitted to analyze weather and thinning effects on the inter- and intra-annual radial increment rates. Additionally, the sum of two logistic functions was used to estimate cumulative radial increment patterns. Heavy thinning resulted in the greatest annual radial increment for pine, regardless of site and year, even during the 2012 drought, when compared to densely stocked forest stands. The model results indicated that heavy thinning positively affected the intra-annual pattern, increasing inflection point and spring and autumn asymptotes. Thinning also had a slight positive effect on inter- and intra-annual radial increment in oak, although this was not clear during extreme drought in 2012. The radial increment rate was related to weather variables, which reflected light (positive for solar radiation) and water availability dependence (increased with precipitation, but decreased with vapor pressure deficit) for both species. Besides water status, air humidity (positive relation with air temperature and relative humidity) also affected oak. Reducing competition by thinning stimulated radial increment in oak-pine mixed stands, which may provide an adaptive forest management tool for reducing tree vulnerability to extreme droughts, which are linked to climate change.

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1. Introduction

Climate change is likely to modify growth patterns and species distribution in forest stands, but response to global warming is species-specific (Camarero et al., 2010; Sánchez-Costa et al., 2015; Zweifel et al., 2006). Hence, biodiversity and ecosystem functioning could be affected by climate change (Carnicer et al., 2011), resulting in phenological alterations (Büntgen et al., 2015), species-specific

range shifts (Peñuelas et al., 2007), changes in forest production (Lara et al., 2013; Linares and Camarero, 2012; Pretzsch et al., 2014) and subsequent changes in carbon storage (Vayreda et al., 2012).

The frequency and the intensity of extreme droughts will probably increase in central and southern Europe (Dankers and Hiederer, 2008), resulting in soil water deficits that could alter tree growth according to species sensitivity (Lara et al., 2013; Michelot et al., 2012). Climate change forecasts are particularly severe for the western Mediterranean Basin (Luterbacher et al., 2012), where rising temperatures and decreased precipitation will increase the likelihood of drought events (Hoerling et al., 2012). Early signs of the consequences of climate change are already evident in the Iberian Peninsula, where a long-term drying trend in recent decades has

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led to declining growth for some tree species (Bogino and Bravo, 2009; Büntgen et al., 2013; Camarero et al., 2013; Prieto-Recio et al., 2015).

Climate change could entail severe loss in the economic value of forest land in southern Europe. This in turn may lead to changes in traditional timber harvesting or diversification in the use of non-woody forest products and other forest resources (Bravo et al., 2008; Hanewinkel et al., 2012). Thus, forest management plans must take into account future drought risk and water resource management strategies as adaptation measures for climate change (Botterill and Hayes, 2012).

Along these lines, several studies have highlighted the advantages of mixed forest stands over monospecific stands, such as increased resistance and resilience to biotic and abiotic factors (like drought stress) through differentiated and complementary use of resources as a result of species niche partitioning (Condés and del Río, 2015; Knoke et al., 2008; Pretzsch et al., 2013). This may be ecologically and economically significant, in light of future climate change scenarios. Mixed forest stands might also increase productivity, diversify production and reduce the risk of damage from pests or diseases (e.g. Condés et al., 2013; Griess and Knoke, 2011; Kelty, 2006; Pretzsch et al., 2015; Pretzsch and Schütze, 2009). Therefore, understanding growth dynamics in mixed forest stands under different drought conditions and competition levels may serve to establish strategies for adapting forest stands to climate change.

Accordingly, thinning has been widely recommended to mitigate climate change impacts on growth by increasing water availability and water use efficiency (D'Amato et al., 2013; Magruder et al., 2013). Trees growing in conditions of low competition prevent stand growth stagnation and are less vulnerable to the drought events predicted by climate change scenarios (Fernández-de-Uña et al., 2015; Martín-Benito et al., 2010; Martínez-Vilalta et al., 2012). Thus, controlling competition through thinning may provide a drought adaptation tool that would minimize potentially adverse ecological and socio-economic impacts of climate change (Sohn et al., 2016a,b, 2013).

Stem growth analyses can provide valuable information about how Mediterranean ecosystems will respond to forecasted climate change (Martín et al., 2014). In this study, we analyzed radial increment response to thinning of Mediterranean mixed stands of *Pinus pinaster* Ait. and *Quercus pyrenaica* Willd. in two localities with different temperature and precipitation regimes in central Spain. Both species are widely distributed throughout the Western Mediterranean Basin and occupy 105,325 ha of mixed forest stands in Spain (Ministerio de Agricultura y Pesca, 2006; Fig. S1).

We assessed the inter- and intra-annual radial increment patterns of a mixed stand of *P.pinaster* and *Q.pyrenaica* using dendrometer band measurements every two weeks. The main objective in this study was to determine how thinning affects the species-specific response to climate in terms of the radial increment dynamic in mixed oak-pine stands. Our specific aims were i) to evaluate the effects of thinning and climate on seasonal and inter-annual radial increment, and ii) to describe the effects of thinning and weather conditions on intra-annual radial increment patterns for both species.

2. Materials and methods

2.1. Sampling sites and experimental design

The study was located at two sites with different drought conditions in central Spain: Lubia (Soria; 41° 39′N, 2° 29′W) and San Pablo de los Montes (Toledo; 39° 31′N, 4° 16.6′W). The Lubia experimental site was located in the Duero Basin at an altitude of 1,134 m.a.s.l. on a continental plateau. This site is characterized by a sub-humid continental Mediterranean climate with an annual rainfall of 512 ± 133 mm, of which 100 ± 49 mm falls during the summer drought period, between June and August (AEMET, 2016; Spanish State Meteorological Agency). July is the driest month, with 30 ± 25 mm rainfall, and May is the wettest month, with 67 ± 33 mm rainfall. Annual mean temperature is $10.0 \pm 1.6\,°C$, with frost occurring from September to May. The hottest month is July, with an average temperature of $18.9 \pm 2.9\,°C$, and the coldest is January, with a mean temperature of $2.3 \pm 1.9\,°C$. The soils are regosols and arenosols, characterized by a slightly acidic pH (5–6), sandy texture and low fertility, composed of predominately tertiary and quaternary materials (IGN, 1991).

The other study site was established in the Montes de Toledo mountain range, which separates the drainage basins of the Tagus and Guadiana rivers at 1,102 m.a.s.l. This site has a continental Mediterranean climate, with an average rainfall of 469 ± 122 mm and a marked summer drought between June and August, with 49 ± 51 mm recorded rainfall (AEMET, 2016). The driest month is July, with 8 ± 11 mm, while the month with the highest rainfall is May, with 55 ± 32 mm. Annual mean temperature is $12.9 \pm 0.6\,°C$ and the hottest month is July, with an average temperature of $23.9 \pm 1.1\,°C$. January is the coldest month of the year, with an average temperature of $4.1 \pm 1.3\,°C$. The geological composition of the soil is mainly sandstones and quartzites from the mesozoic period that have given rise to slightly acidic arenosol soils (pH 5–6) (IGN, 1991).

BIOdry software (Lara et al., 2013) was used to calculate the Walter-Lieth annual aridity index (WAI) for both sites (Fig. S2). This index is defined as the quotient between the dry and wet season areas, based on historical climate records. The clear drought difference between sites is reflected in a WAI of 0.22 for Lubia and 0.65 for San Pablo de los Montes. Hereafter, we will refer to these sites as WAI-0.22 and WAI-0.65, respectively.

The forest stands at both sites were generated by afforestation over a *Q. pyrenaica* coppice stand in the 1970s. The ground was prepared by bulldozer screefing, followed by strip sowing with *P. pinaster*. Today, these stands are a mixed even-aged forest composed of the two species mentioned, with a horizontal strip structure where oak occupies ridge space (area between screefed lines). Initial stand density was higher at WAI-0.22 than at WAI-0.65, regardless of species (Table 1).

Nine rectangular plots ($600–800$ m^2) were established at each site, using a Latin square design. The experimental design consisted of an unthinned control (treatment A) and two treatments with three replicates each: moderately-thinned plots with 25% of basal area removed (treatment D) and heavily-thinned plots with 40% of basal area removed (treatment E). Only maritime pine (*P.pinaster*) was removed, applying thinning from below, which involved logging the suppressed or intermediate trees (Table 1). Felled logs and branches were removed from plots. Thinning was carried out at the end of 2009, applying a buffer zone of 10 m around each plot. With the R package 'nparcomp' function (Konietschke et al., 2015), we implemented a studentized permutation test for small sample sizes, which enabled us to explore possible stand differences between treatments before and after thinning. There were no statistical differences between treatments for each species and site before thinning. However, statistical differences were evident after thinning for pine density and basal area, though mean height and diameter at breast height from each site were not statistically different for moderate and heavy thinning (Table 1). Additionally, there was no visual evidence of new shrub vegetation or oak sprout after thinning.

Table 1

Main stand characteristics before and after thinning for the two study sites. Data shown are mean and standard deviation values by treatment and site.

Site	Treat.	Plot Area (m²)	H₀ (m)	Quercus pyrenaica Hm (m)	Density (n ha⁻¹)	DBH (mm)	BA (m² ha⁻¹)	Pinus pinaster Before thinning Hm (m)	Density (n ha⁻¹)	DBH (mm)	BA (m² ha⁻¹)	After thinning Hm (m)	Density (n ha⁻¹)	DBH (mm)	BA (m² ha⁻¹)
WAI-0.22 Age: 40	A	801±21	11.0±0.7	4.8±1.2	2203±399	45.4±17.9	5.1±1.4	9.4±1.7	1388±225	182.8±55.6	38.9±5.2	9.4±1.7	1388±225	182.8±55.6	38.9±5.2
	D	804±10	11.0±1.1	5.7±1.8	2284±401	55.1±22.9	6.7±1.8	9.9±1.7	1257±69	185.2±58.7	39.5±6.0	10.5±1.2*	681±77	221.3±39.9*	29.5±4.3
	E	805±44	11.3±1.0	5.1±1.6	2406±484	46.5±19.6	6.7±2.8	9.8±1.7	1228±235	187.7±57.7	39.3±4.9	10.6±1.2*	482±112	225.5±40.5*	23.4±2.9
WAI-0.65 Age: 35	A	650±87	10.9±1.5	5.8±1.6	2013±458	65.5±18.6	6.7±1.7	10.8±1.4	591±46	258.8±49.4	32.2±2.8	10.8±1.4*	591±46	258.8±49.4	32.2±2.8
	D	625±80	11.1±0.8	5.4±1.5	1725±366	58.7±17.6	5.5±0.4	10.4±1.2	574±98	252.1±54.0	30.2±1.6	10.6±1.2*	394±63	272.6±46.0*	23.5±1.1
	E	631±81	11.1±1.2	5.3±1.5	1633±313	60.6±17.4	5.5±2.1	10.8±1.2	606±45	263.8±51.3	34.2±3.1	11.0±1.1*	301±21	289.2±37.9*	20.1±0.7

Treat.: thinning treatment intensity; H₀: dominant height; Hm: mean height; DBH: diameter at breast height; BA: basal area. *No statistical differences after thinning by site.

2.2. Stem girth and climatic measurements

After thinning, and three months before sampling (in order to ensure tool stabilization), dendrometer bands (DB 20, EMS Brno) were placed on ten trees per species and plot. A total of 360 dendrometer bands were fitted at breast height (1.30 m) after smoothing and removal of the outermost dead bark to avoid stem deformities. Trees were selected within the plot using a stratified sampling approach that took diameter distribution into account. Dendrometer bands were read every two weeks throughout the year to the nearest 0.1 mm from April 2010 to December 2012. All measurements were taken in the morning to reduce diurnal bias, which is caused by stem shrinkage from transpiration. The measurements were corrected for temperature effects and dendrometer thermal expansion (11.2×10^{-6} mm °C^{-1}). Girth increment data were transformed to radial increments based on a cylindrical tree shape.

A meteorological station was installed at each site to record rainfall, relative humidity, air temperature, solar radiation and wind speed. Mean vapor pressure deficit (VPD) was also estimated from former weather measurements. Due to the lack of data on several dates, gaps in the climate information were completed using data from the automatic stations of the Spanish Meteorological Agency, located 6 km and 5 km from the Lubia and San Pablo sites, respectively. CLIMATOL software (Guijarro, 2016) was used for climatological series homogenization and to obtain Walter & Lieth climograms (Fig. 1). Drought was limited during the summer of 2010 (dotted red area in Fig. 1), but the long period of summer aridity in 2011 was exacerbated at both sites by low autumn rainfall. In 2012, spring rainfall was low, especially at the WAI-0.65 site, though the autumn was wet. The WAIs for the 2010–2012 period show that low precipitation in autumn 2011 and spring 2012 provoked an extreme drought in 2012 at both locations, but especially at the WAI-0.65 site (Table S1).

2.3. Data analysis

The following statistical analyses were carried out using the R package 'nlme' function (RStudio 1.0.44) for fitting linear and non-linear mixed-effect models (Pinheiro et al., 2015).

2.3.1. Effects of thinning on seasonal and inter-annual radial increment

According to the increment patterns from the dendrometer bands, both species showed a bimodal pattern of radial increment with two maxima, one in spring and one in autumn (Fig. 2). Therefore, we analyzed the seasonal (spring and autumn) and the annual radial increment in order to study inter-annual variation in the effect of thinning on radial increment. The spring increment period was reckoned from the beginning of the year to the decrease triggered by the summer drought (generalized as Aug. 1), while the autumn period referred to the rest of the year.

Linear mixed models were used to avoid time-space dependence from the experimental design. Models were fitted for each species and site, as follows:

$$ri_{ijsk} = \alpha_k + \beta_s + \gamma_{sk} + \delta_i dbh_{ij} + u_j + v_{ij} + \varepsilon_{ijsk} \tag{1}$$

$$\alpha_k = \alpha_1 2010 + \alpha_2 2011 + \alpha_3 2012$$

$$\beta_s = \beta_1 TrtD + \beta_2 TrtE$$

$$\gamma_{sk} = \gamma_{11} TrtD \cdot 2011 + \gamma_{12} TrtD \cdot 2012 + \gamma_{21} TrtE \cdot 2011 + \gamma_{22} TrtE \cdot 2012$$

where ri_{ijsk} is the spring, autumn or annual radial increment for tree i in plot j subjected to thinning treatment s and year k (mm);
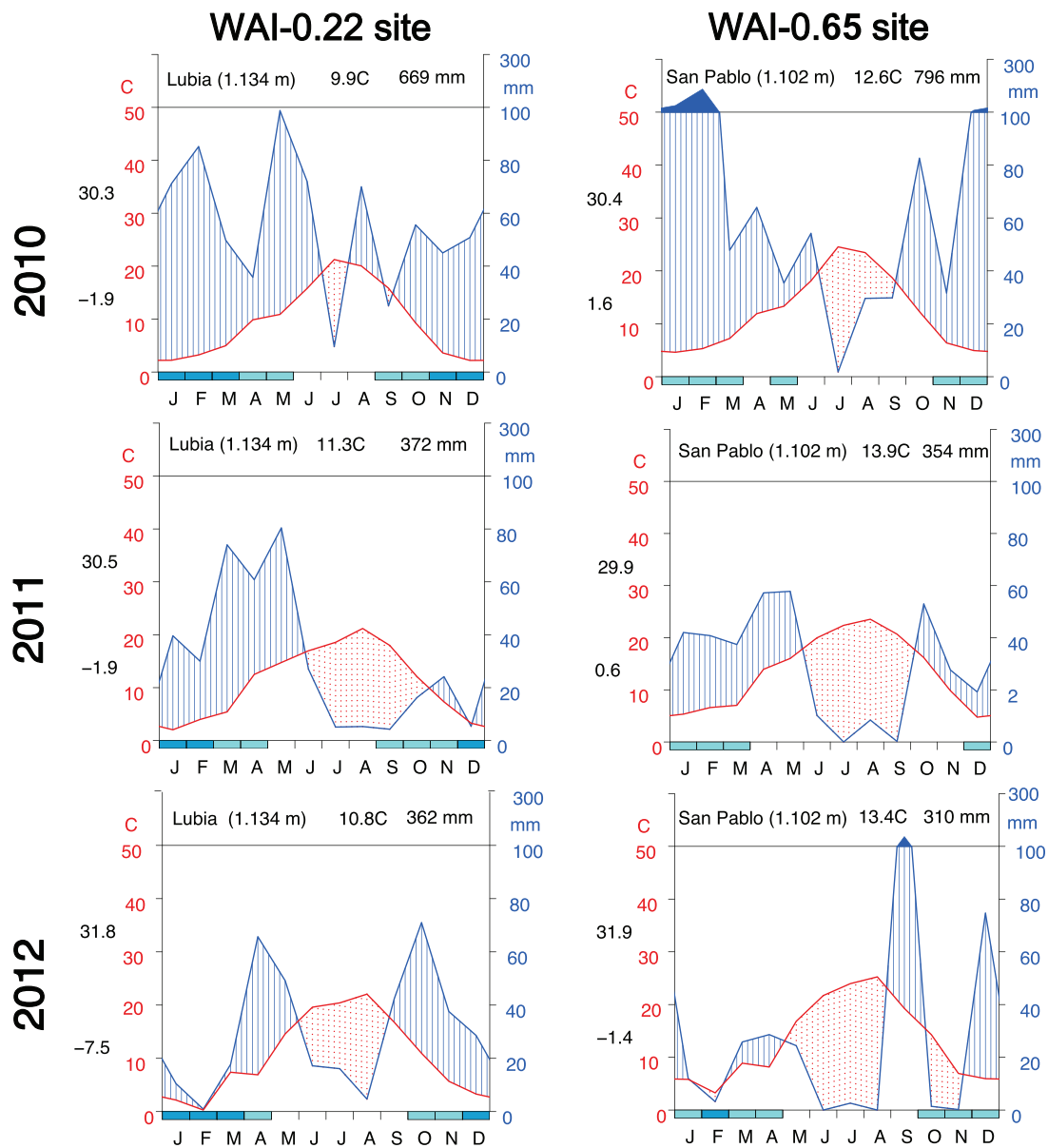
Fig. 1. Climograms during sampling of both sites. Blue and red lines are precipitation (mm) and temperature(°C), respectively. Vertical blue lines and red dotted areas represent the wet and dry seasons, respectively, defined as the difference between precipitation and temperature. The horizontal line at 100 mm precipitation marks the origin of the logarithmic scale. Dark blue rectangles below the time axis indicate months of sure frost and light blue rectangles indicate months of probable frost. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

α_k is the year effect vector, with α_1, α_2, α_3 regression coefficients for the 2010, 2011 and 2012 dummy variables, respectively; β_s is the treatment effect vector, β_1, β_2 are the regression coefficients for *TrtD* and *TrtE* thinning treatment dummy variables; γ_{sk} is the treatment-year interaction vector, with γ_{11}, γ_{12}, γ_{21}, γ_{22} regression coefficients; dbh_{ij} is the diameter at breast height (mm), with δ_i as the regression coefficient; $u_j \sim N (0,\sigma_j)$ is the plot random effect; $v_{ij} \sim N (0,\sigma_{ij})$ is the tree random effect and $\varepsilon_{ijsk} \sim N (0,\sigma_{ijsk})$ is the error term. Additionally, we did a *post-hoc* analysis based on simultaneous tests for general linear hypothesis through multiple comparisons of means, using Tukey contrasts when necessary to identify differences between thinning intensities.

2.3.2. Thinning effect on the intra-annual radial increment pattern

Mathematical functions were fitted separately by thinning treatments, species and sites to describe the cumulative radial increment and analyze differences between these factors. As

mentioned previously, an initial visual analysis of scatter plots confirmed a bimodal pattern of radial increment for both species (Fig. 2), as a consequence of the typical summer drought in Mediterranean environments (Albuixech et al., 2012; Camarero et al., 2010). Therefore, the function fitted for cumulative radial increment was the result of the sum of two logistic functions (Eq. (2)). The first part of the sigmoid function represented the cumulative radial increment for spring time and the second part represented the autumnal increment.

$$cri_{ijk}(t) = \left\{ \beta_1 + \frac{\beta_2 - \beta_1}{\left(1 + e^{(t-\beta_3)/\beta_4}\right)} \right\}$$
$$+ \left\{ (\beta_5 - \beta_1) + \frac{\beta_1 - \beta_5}{\left(1 + e^{(t-\beta_6)/\beta_7}\right)} \right\} + \varepsilon_{ijk} \qquad (2)$$
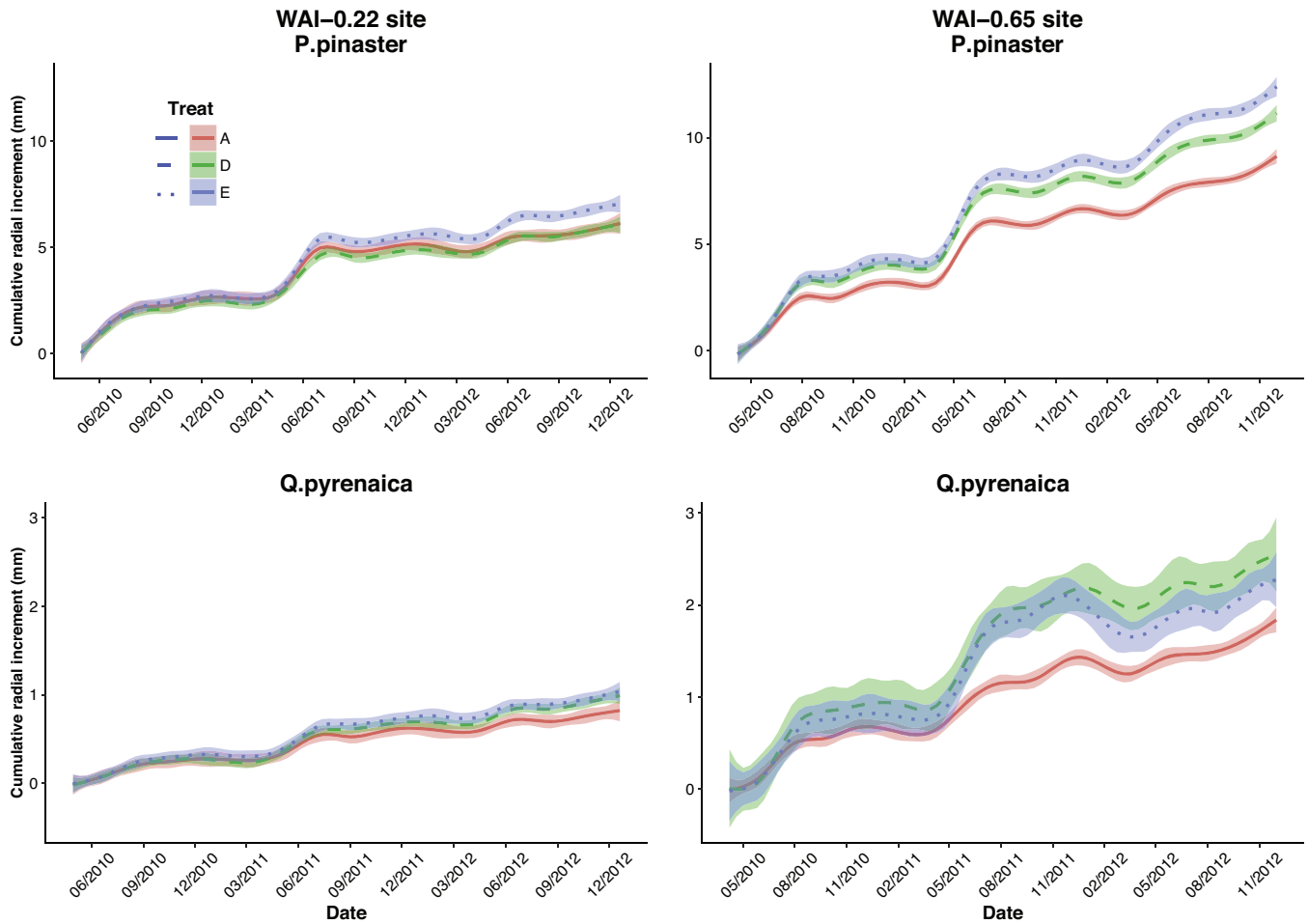
Fig. 2. Mean observed cumulative radial increment values for each species and thinning treatment by site during the three sampling years. Confidence intervals (filled area) show significant differences between thinning treatments.

where cri_{ijk} is the cumulative radial increment for tree i in plot j and year k (mm); β_i are the regression coefficients: $\boldsymbol{\beta}_1$ is the spring radial increment asymptote, $\boldsymbol{\beta}_2$ is the initial asymptote (null), $\boldsymbol{\beta}_3$ is Julian days occurred since 1 January at the spring inflection point, $\boldsymbol{\beta}_4$ is a spring scale parameter on the time-axis which represents the time when three-quarters of the distance from $\boldsymbol{\beta}_1$ occurs (the smaller it is, the greater the radial increment rate), $\boldsymbol{\beta}_5$ is the autumnal radial increment asymptote or radial increment reach at the end of autumn, $\boldsymbol{\beta}_6$ is the Julian days at the autumn inflection point and $\boldsymbol{\beta}_7$ is an autumnal scale parameter on the time axis that represents the time when three-quarters of the distance from $\boldsymbol{\beta}_1$ to $\boldsymbol{\beta}_5$ occurs, t is the Julian day transpired since 1 January and $\boldsymbol{\varepsilon}_{ijk} \sim N(0, \sigma_e)$ is the error term (for clarification of parameters, see Fig. S3).

Due to the spatial and temporal dependence of measurements, the model was extended with a random structure that only affects (to avoid over-parameterization) the $\boldsymbol{\beta}_1$ parameter. This which resulted in the lowest value of the Akaike information criterion (AIC) with respect to other parameters tested (Eq. (3)).

$$cri_{ijk}(t) = \left\{ \left(\beta_1 + \omega_k + u_{jk} + v_{ijk} \right) + \frac{\beta_2 - \left(\beta_1 + \omega_k + u_{jk} + v_{ijk} \right)}{\left(1 + e^{(t - \beta_3)/\beta_4} \right)} \right\}$$
$$+ \left\{ \left(\beta_5 - \left(\beta_1 + \omega_k + u_{jk} + v_{ijk} \right) \right) + \frac{\left(\beta_1 + \omega_k + u_{jk} + v_{ijk} \right) - \beta_5}{\left(1 + e^{(t - \beta_6)/\beta_7} \right)} \right\} + \boldsymbol{\varepsilon}_{ijk} \quad (3)$$

where $\omega_k \sim N(0, \sigma_k)$ is the year random effect; $u_{jk} \sim N(0, \sigma_{jk})$ is the plot random effect; $v_{ijk} \sim N(0, \sigma_{ijk})$ is the tree random effect. The other parameters are the same as in Eq. (2).

Different-patterned variance-covariance matrices were evaluated for random effects, such as the multiple of an identity, diagonal, and general positive-definite matrices. Additionally, residual and autocorrelation function plots were used as diagnostic tools for identifying heteroscedasticity and residual autocorrelation. A constant plus power of covariate variance function was selected for modeling heteroscedasticity when necessary (Pinheiro and Bates, 2000).

2.3.3. Effects of weather and thinning on radial increment rate

Linear mixed models were fitted per species and site to estimate the intra-annual increment rate based on meteorological variables and thinning treatment. Meteorological variables were calculated for different ranges of days before the sampling measurement: cumulative or mean weather variables over five, ten, fifteen, and twenty days before each measurement was taken. Multicollinearity was controlled by variance inflation factor values, autocorrelation was assessed by autocorrelation function plot and AIC was employed to find the most parsimonious model. The final structure of the linear mixed model was as follows:

$$rir_{ijk} = \beta_0 + \beta_1 TrtD + \beta_2 TrtE + \beta_3 dbh_{ij}$$
$$+ f(weather) + \omega_k + u_{jk} + v_{ijk} + \varepsilon_{ijk} \quad (4)$$

Table 2
Model-fitted coefficients for spring, autumn and annual radial increment (Eq. (1)) for species and site. Significant parameters are in bold with significance level as follows: '***' <0.001, '**' <0.01, '*' <0.05,' .' <0.1).

Species	Parameter	WAI-0.22			WAI-0.65		
		Spring	Autumn	Annual	Spring	Autumn	Annual
P. pinaster	$\delta_i(\boldsymbol{dbh_{ij}})$	**0.007*****	**0.001*****	**0.008*****	0.002	**0.001***	**0.003**·
	α_1 (2010)	0.364	0.019	0.570	**1.545****	**0.321****	**2.020****
	α_2 (2011)	**0.611**·	−0.079	0.577	**2.062*****	**0.375*****	**2.320*****
	α_3 (2012)	**−0.805***	**0.111***	**−0.854***	0.571	**0.866*****	**1.247***
	$\boldsymbol{\beta_1}$ (**TrtD**)	−0.187	0.001	−0.158	**0.691***	0.042	**0.815***
	$\boldsymbol{\beta_2}$ (**TrtE**)	−0.053	−0.005	−0.003	**0.782***	0.080	**1.056****
	γ_{11} (**TrtD**2011)	0.102	−0.005	0.087	0.017	−0.051	−0.085
	γ_{12} (**TrtD**2012)	**0.280***	0.001	−0.218	**−0.278***	0.011	**−0.315***
	γ_{21} (**TrtE**2011)	**0.454*****	−0.019	**0.372***	**0.336****	**−0.099****	0.046
	γ_{22} (**TrtE**2012)	**0.358****	0.010	**0.289***	−0.027	0.020	−0.126
	σ_j (plot)	0.132	$9.49 \cdot 10^{-6}$	0.122	0.200	0.018	0.204
	σ_{ij} (tree)	0.439	0.071	0.489	0.522	0.102	0.649
	σ_{ijsk} (error)	0.350	0.076	0.404	0.338	0.090	0.344
Q. pyrenaica	$\delta_i(\boldsymbol{dbh_{ij}})$	**0.002***	**0.001*****	**0.002***	**0.012*****	**0.003*****	**0.012****
	α_1 (2010)	−0.061	−0.036	−0.002	**−0.771***	**−0.220*****	−0.532
	α_2 (2011)	0.047	−0.006	0.095	**−0.732***	**−0.123***	−0.480
	α_3 (2012)	−0.086	0.023	−0.027	**−1.017****	−0.025	**−0.774***
	$\boldsymbol{\beta_1}$ (**TrtD**)	−0.014	−0.003	−0.028	**0.308**·	0.008	**0.344**·
	$\boldsymbol{\beta_2}$ (**TrtE**)	0.010	0.006	0.041	0.241	−0.003	0.231
	γ_{11} (**TrtD**2011)	**0.086***	−0.028	**0.095***	0.242	0.020	0.215
	γ_{12} (**TrtD**2012)	0.043	−0.014	0.050	−0.169	0.014	−0.189
	γ_{21} (**TrtE**2011)	**0.067**·	**−0.036**·	0.034	**0.270**·	**0.035***	**0.294**·
	γ_{22} (**TrtE**2012)	−0.001	−0.025	−0.024	−0.042	**0.044****	0.037
	σ_j (plot)	0.058	$1.26 \cdot 10^{-6}$	0.052	0.115	0.013	0.097
	σ_{ij} (tree)	0.110	0.027	0.138	0.256	0.049	0.325
	σ_{ijsk} (error)	0.092	0.046	0.111	0.379	0.040	0.431

where rir_{ijk} is the radial increment rate for tree i in plot j and year k (mm); β_i are the regression coefficients ; $TrtD$ and $TrtE$ are dummy treatment variables; dbh_{ij} is the diameter at breast height (mm); $f(weather)$ is a linear function of weather variables; $\omega_k \sim N(0,\sigma_k)$ is the year random effect; $u_{jk} \sim N(0,\sigma_{jk})$ is the plot random effect; $v_{ijk} \sim N(0,\sigma_{ijk})$ is the tree random effect and $\varepsilon_{ijk} \sim N(0,\sigma_e)$ is the error term for each individual i in each plot j for year k. Finally, we did a *post-hoc* analysis based on multiple comparisons of means, using Tukey contrasts to identify differences between thinning intensities when necessary.

3. Results

3.1. Effects of thinning on seasonal and inter-annual radial increment

Results for the treatment-year interaction from the fitted model for spring, autumn and annual radial increment (Eq. (1)) are compiled in Table 2.

In 2010 there were no thinning effects on radial increment, regardless of species, at the WAI-0.22 site (β_1 and β_2). However, the effect of thinning was greater in all years for pine at the WAI-0.65 site. Radial increment of oak for moderate thinning was also higher at the WAI-0.65 site (β_1).

A large spring radial increment occurred for both species in 2011 (Fig. 3)coinciding with a period of high spring rainfall (see Fig. 1). During this period, the effect of heavy thinning on pine increased (γ_{21}) at both sites (Table 2 and Fig. 3). There was also a positive thinning effect for oak compared to the control (γ_{11}, γ_{21}, β_1), but there were no differences between thinning intensities at either site (Fig. 3).

In 2012, spring radial increment was lower at both sites regardless of species (α_3), coinciding with a period of low rainfall (Fig. 1). Heavy thinning had a positive effect, similar to the previous year, for pine during the drought event and the effect increased for moderate thinning at the WAI-0.22 site (γ_{22} and γ_{12}). Thinning effect was also maintained in 2012 but was reduced for moderate thinning at the WAI-0.65 site (γ_{12}). No differences between thinning treatments were identified for oak in 2012 (γ_{12}, γ_{22} and Fig. 3), although moderate thinning effects were similar over time at the WAI-0.65 site (β_1).

There were no significant differences in autumn radial increment between thinning treatments each year for either species (β_1 and β_2) during the study period, though their effects varied over time according to the amount of autumn rainfall (α_1, α_2, α_3, Fig. 3 and Fig. 1). Heavy thinning had a positive effect on annual radial increment for pine species, regardless of site and year, though the difference was not significant in 2010 at the WAI-0.22 site (Fig. 3). This effect remained almost constant over time at both sites (γ_{21}, γ_{22} for WAI-0.22 and β_2 for WAI-0.65 site).The annual radial increment for oak differed between sites: moderate thinning had a positive effect during the entire study period at the WAI-0.65 site (β_1), but only in 2011 at the WAI-0.22 site (γ_{11}). The effect of heavy thinning was only significant in 2011 at WAI-0.65 site (γ_{21}).

3.2. Effects of thinning on the intra-annual radial increment pattern

The block diagonal variance-covariance matrix was chosen to fit the most parsimonious convergent model, based on AIC values. This assumes that random effects are independent of each other and have the same variance at each random level. The results from the mathematical functions fitted for intra-annual cumulative radial increment (Eq. (3)) can be seen in Table S2. Figs. 4 and 5 highlight the differences, according fitted models, in the mean behavior of the cumulative and radial increment rate over the sampling years between species, treatments and sites.

Table 3 and Figs. S4 and S5 show significant differences between the fitted model set parameters for each species, treatment and site. The spring and autumn radial increments (β_1 and β_5) were higher at WAI-0.65 than at WAI-0.22 for the two species (p-value lower than 0.05 in all cases except for β_1 oak control, with a *p*-value of 0.911; results not shown). In general, the spring radial increment (β_1) exceeded the autumnal increment ($\beta_5 - \beta_1$) regardless of site and species (radial increment rate from Figs. 4 and 5).
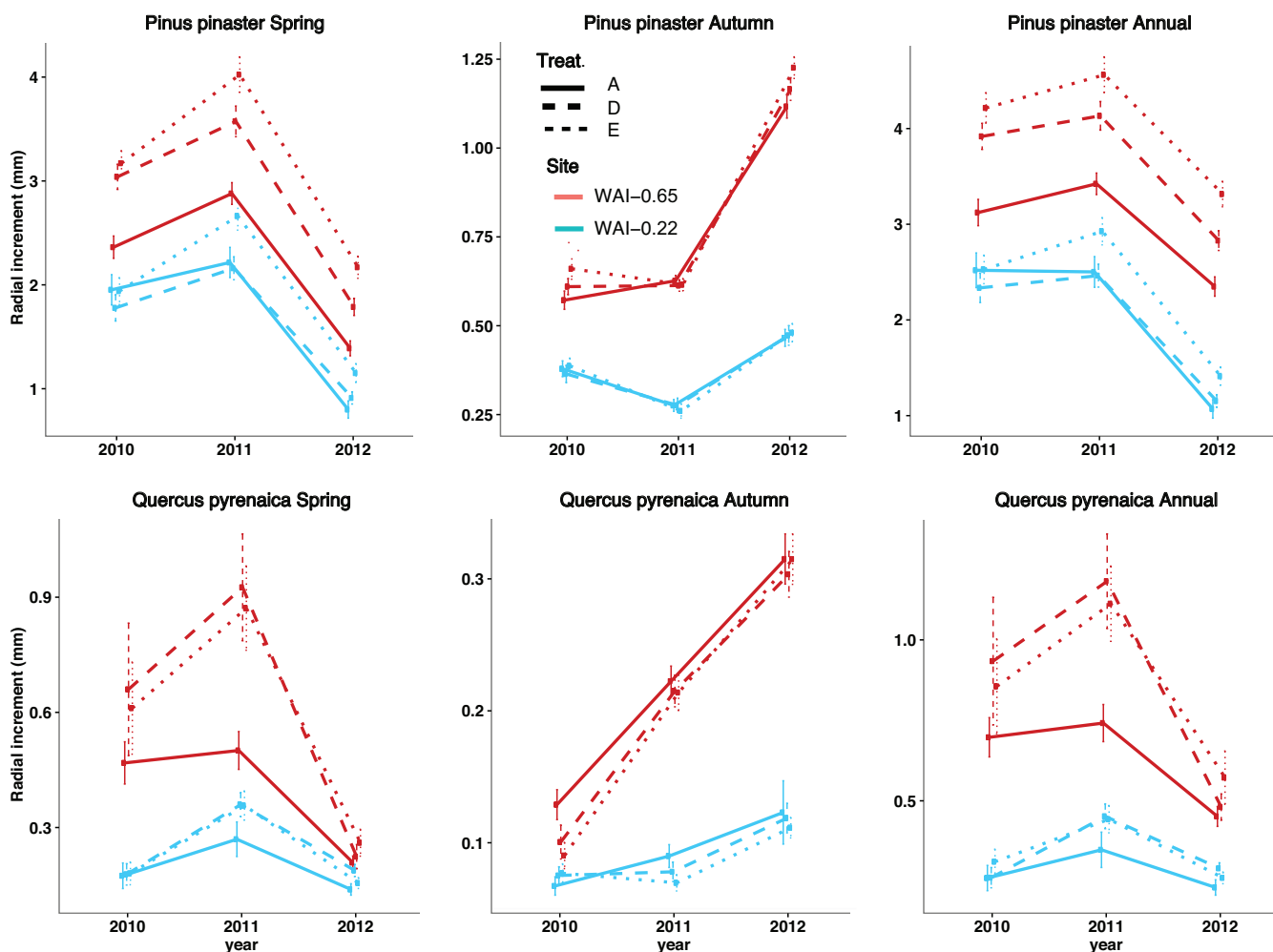
Fig. 3. Spring, autumnal and annual radial increment differences for treatments, years, species and sites. Note the different scales on the ordinate axis.

Table 3
Cumulative radial increment model parameter set differences between treatment and species for each site separately. Different letters denote significant differences at the 0.05 significance level.

| Parameter	Species	WAI-0.22			WAI-0.65		
		Treat.A	Treat.D	Treat.E	Treat.A	Treat.D	Treat.E
β_1	*P.pinaster*	1.581 **b**	1.581 **b**	2.098 **c**	2.308 **c**	2.867 **d**	3.184 **d**
	Q.pyrenaica	0.362 **a**	0.351 **a**	0.372 **a**	0.353 **a**	0.456 **ab**	0.479 **b**
β_2	*P.pinaster*	- 0.032**ab**	-0.052 **a**	-0.025 **b**	0.063 **d**	0.060 **d**	0.045 **d**
	Q.pyrenaica	-0.001 **d**	-0.012 **bc**	-0.010 **c**	-0.068 **b**	-0.035 **c**	-0.137 **a**
β_3	*P.pinaster*	142.333 **a**	143.618 **ab**	144.157 **b**	140.528 **b**	142.172 **bc**	142.928 **c**
	Q.pyrenaica	158.050 **cd**	154.981 **c**	158.660 **d**	153.803 **d**	134.597 **a**	157.655 **e**
β_4	*P.pinaster*	16.271 **b**	13.973 **a**	13.842 **a**	19.204 **d**	17.349 **c**	15.080 **b**
	Q.pyrenaica	19.229 **c**	23.762 **d**	23.595 **d**	20.077 **de**	12.400 **a**	21.839 **e**
β_5	*P.pinaster*	2.069 **c**	2.073 **c**	2.703 **d**	2.868 **c**	3.594 **d**	3.976 **e**
	Q.pyrenaica	0.384 **a**	0.448 **b**	0.475 **b**	0.783 **a**	1.150 **b**	1.392 **b**
β_6	*P.pinaster*	269.335 **a**	284.969 **bc**	285.014 **b**	271.508 **a**	272.277 **a**	273.701 **a**
	Q.pyrenaica	293.703 **c**	325.002 **d**	317.600 **d**	326.000 **b**	292.690 **ab**	283.090 **a**
β_7	*P.pinaster*	27.918 **b**	17.528 **a**	15.943 **a**	16.905 **ab**	21.643 **b**	14.755 **a**
	Q.pyrenaica	15.499 **a**	40.631 **c**	21.098 **a**	44.121 **c**	49.637 **c**	59.093 **c**
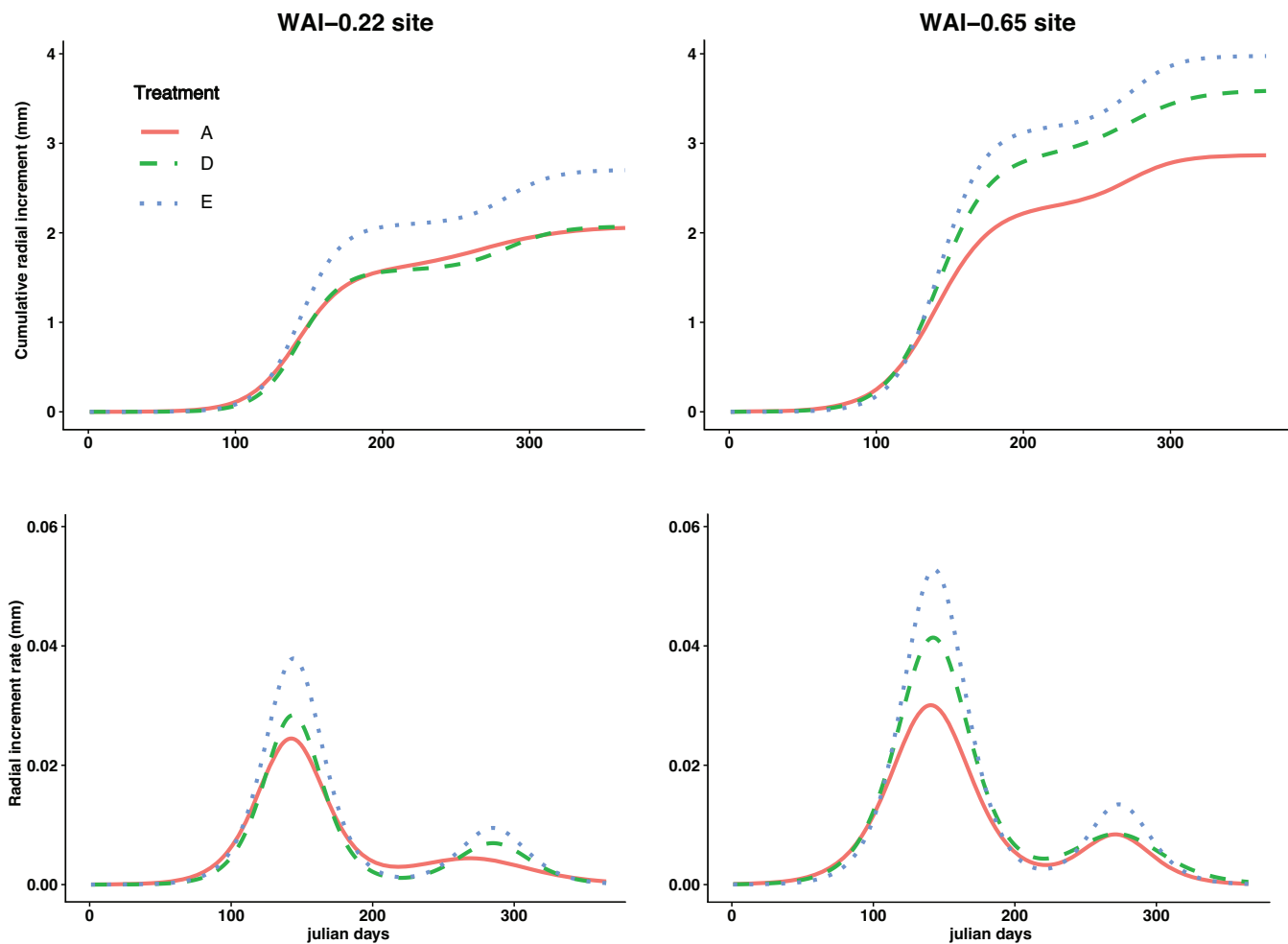
Fig. 4. Cumulative radial increment and radial increment rates by treatment and site for P.pinaster.

Concerning differences between species, higher spring and autumnal accumulated radial increment (asymptotes β_1 and β_5) and generally lower scale parameter (β_4 and β_7) for pine confirm a more pronounced radial increment for this species than for oak. Conversely, the spring and autumn inflection point (β_3 and β_6) was generally lower for pine (Figs. S4 and S5).

Heavy thinning increased radial increment in spring and autumn (β_1 and β_5) and prolonged the increment period (β_3 and β_6 at the WAI-0.22 site, β_3 at the WAI-0.65 site) for pine, though the increment period was lower than the sampling frequency (every two weeks). Additionally, the scale parameter (β_4 and β_7) was lower for heavy thinning, again reflecting a higher radial increment rate. Moderate thinning also had a positive effect, enhancing radial increment (β_1, β_4 and β_5) for pine at the WAI-0.65 site, but had no effect on the spring and autumn asymptotes (β_1 and β_5) at the WAI-0.22 site.

Heavy thinning also increased radial increment in spring (β_1) and prolonged the increment period (β_3) at the WAI-0.65 site for oak species. The autumn radial increment for oak (β_5) was also higher for thinning treatments, regardless of site, and increased with thinning intensity, but with no statistically significant differences between moderate and heavy thinning.

3.3. Effects of weather and thinning on radial increment rate

The results from fitted models for radial increment rate (Eq. (4)) are shown in Table 4. The autocorrelation function plot showed that it was not necessary to correct the correlation. Weather variables for the five days prior to measuring were exclusively included in the models, based on the lowest AIC index analysis. Statistically significant weather variables that were included in the final fitted model were cumulative rainfall (P; mm), solar radiation (SR; 10KJ/m^2) and mean vapor pressure deficit (VPD; kPa). Two additional variables, minimum air temperature (Tmin; °C) and minimum relative air humidity (RHmin; %), were incorporated into the oak model.

All weather variables from fitted models were positively correlated with increment rate except for vapor pressure deficit, which was especially acute in the summer (Fig. S6 and S7). Solar radiation, as well as the amount and frequency of rainfall, caused higher increment rates in spring than in autumn. The increment rate in autumn was also negatively influenced by high vapor pressure deficit values, as previously mentioned. Additionally, the minimum temperature variable penalized low temperatures, and relative air humidity improved the radial increment rate for the oak species (Fig. S6 and S7).

Tree size (diameter at breast height) was also a significant explanatory variable in the model for all species and sites. Positive thinning treatment effects were found for the pine species at both sites, especially for heavy thinning (Table 4 and Figs. S6 and S7). However, there were no differences in the radial increment rate between the moderate thinning treatment and the control at the WAI-0.22 site. The results for oak also pointed to a positive effect from thinning treatments at the WAI-0.65 site, although there were no differences between thinning intensities (0.917 *p*-value
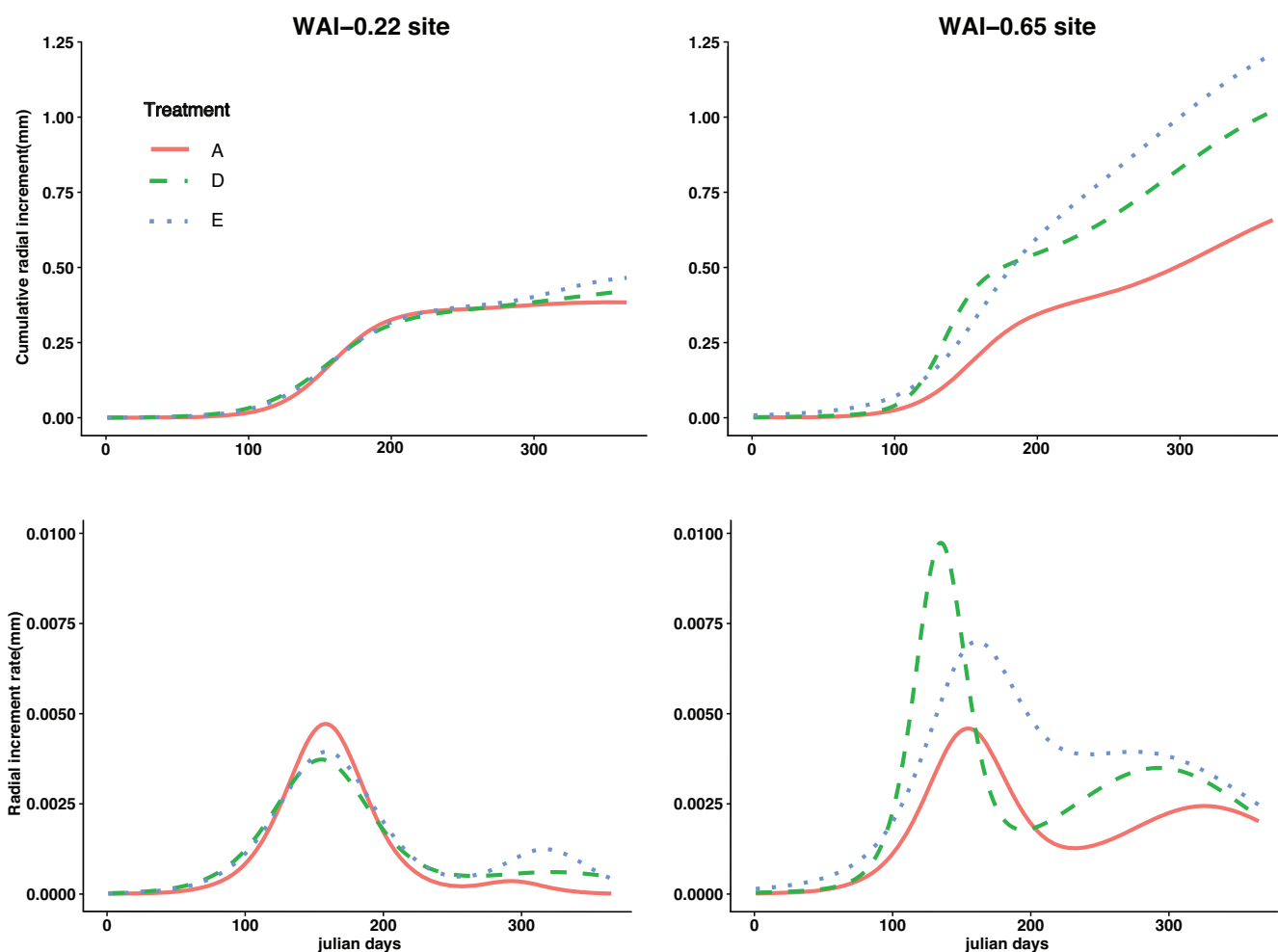
Fig. 5. Cumulative radial increment and radial increment rates by treatment and site for Q.pyrenaica.

Table 4
Model fitted for radial increment rate (Eq. (4)) for species and site. Significant parameters are in bold (0.05 significance level).

Species	Parameter	WAI-0.22		WAI-0.65	
		Coefficient	p-value	Coefficient	p-value
P. pinaster	$\beta_0(TrtA)$	**$-1.52 \cdot 10^{-2}$**	**<0.001**	**$-5.71 \cdot 10^{-3}$**	**0.003**
	$\beta_1(TrtD)$	$-1.78 \cdot 10^{-4}$	0.649	**$2.52 \cdot 10^{-3}$**	**0.002**
	$\beta_2(TrtE)$	**$8.15 \cdot 10^{-4}$**	**0.046**	**$3.49 \cdot 10^{-3}$**	**<0.001**
	$\beta_3(dbh_{ij})$	**$3.17 \cdot 10^{-5}$**	**<0.001**	**$1.78 \cdot 10^{-5}$**	**0.006**
	$\beta_4(P)$	**$3.49 \cdot 10^{-4}$**	**<0.001**	**$2.55 \cdot 10^{-4}$**	**<0.001**
	$\beta_5(SR)$	**$4.39 \cdot 10^{-5}$**	**<0.001**	**$5.47 \cdot 10^{-5}$**	**<0.001**
	$\beta_6(VPD)$	**$-1.83 \cdot 10^{-2}$**	**<0.001**	**$-2.14 \cdot 10^{-2}$**	**<0.001**
	σ_k (year)	$1.44 \cdot 10^{-3}$		$8.80 \cdot 10^{-4}$	
	σ_{jk}(plot)	$2.83 \cdot 10^{-4}$		$1.07 \cdot 10^{-3}$	
	σ_{ijk}(tree)	$3.02 \cdot 10^{-7}$		$2.03 \cdot 10^{-7}$	
	σ_e(error)	$1.06 \cdot 10^{-2}$		$1.52 \cdot 10^{-2}$	
Q. pyrenaica	$\beta_0(TrtA)$	**$-8.00 \cdot 10^{-3}$**	**<0.001**	**$-1.06 \cdot 10^{-2}$**	**<0.001**
	$\beta_1(TrtD)$	**$1.07 \cdot 10^{-3}$**	**0.001**	**$1.26 \cdot 10^{-3}$**	**0.004***
	$\beta_2(TrtE)$	$-1.84 \cdot 10^{-4}$	0.518	**$1.11 \cdot 10^{-3}$**	**0.013***
	$\beta_3(dbh_{ij})$	**$3.52 \cdot 10^{-5}$**	**<0.001**	**$5.37 \cdot 10^{-5}$**	**<0.001**
	$\beta_4(P)$	**$6.11 \cdot 10^{-5}$**	**<0.001**	**$7.02 \cdot 10^{-5}$**	**<0.001**
	$\beta_5(SR)$	**$6.24 \cdot 10^{-6}$**	**<0.001**	**$6.17 \cdot 10^{-6}$**	**<0.001**
	$\beta_6(VPD)$	**$-2.24 \cdot 10^{-3}$**	**<0.001**	**$-3.18 \cdot 10^{-3}$**	**<0.001**
	$\beta_7(T_{min})$	**$2.77 \cdot 10^{-4}$**	**<0.001**	**$4.25 \cdot 10^{-4}$**	**<0.001**
	$\beta_8(RH_{min})$	**$5.13 \cdot 10^{-5}$**	**<0.001**	**$5.79 \cdot 10^{-5}$**	**<0.001**
	σ_k (year)	$1.73 \cdot 10^{-7}$		$1.71 \cdot 10^{-4}$	
	σ_{jk}(plot)	$3.97 \cdot 10^{-8}$		$4.91 \cdot 10^{-4}$	
	σ_{ijk}(tree)	$1.46 \cdot 10^{-3}$		$1.52 \cdot 10^{-3}$	
	σ_e(error)	$4.49 \cdot 10^{-3}$		$5.09 \cdot 10^{-3}$	

*No statistical differences according post-hoc Tukey analysis.

according to the Tukey test). However, exclusively moderate thinning had a significant effect on the radial increment rate of oak at the WAI-0.22 site, compared to the control treatment (Table 4).

4. Discussion

4.1. Effect of thinning on radial increment response to inter-annual climatic conditions

The results support the initial hypotheses that radial increment is sensitive to climatic variation and that response differs depending on thinning treatment and species. Despite worse drought conditions (Table S1), higher annual radial increment for both species was observed at the WAI-0.65 site than at the WAI-0.22 site, probably due to differences in tree size and tree competition (Table 1). Heavy thinning led to the greatest annual radial increment for pine, regardless of site and year, albeit with clear inter-annual variation. In 2010, there was higher precipitation but a lower response to thinning at the WAI-0.22 site. This might be due to the aforementioned higher initial tree competition level, which was probably reflected in greater decompensation between subterranean and aerial parts of trees in the first year after thinning, pointing to a lag in root growth response (Vincent et al., 2009). Our results also revealed that heavy thinning had a positive effect for pine − similar to that of the previous year − during the drought event, regardless of site (Table 2). These results agree with those of many other studies in confirming that increasing the availability of growing space through thinning can enhance tree resistance and resilience in terms of height, diameter, and volume growth (D'Amato et al., 2013; Rais et al., 2014). Differences in drought resistance may be related to water availability or adjustments in water use efficiency, so an unthinned stand is more likely to be more vulnerable to drought due to higher competition (Bogino and Bravo, 2014; Sohn et al., 2016a,b, 2013). Sohn et al. (2016b, 2013) found that thinning treatments also improve growth recovery following drought events, so greater drought resilience might also be expected in maritime pine subjected to heavy thinning (Magruder et al., 2013). A longer study period would be required to determine stand resilience to the extreme drought of 2012. In contrast, effects of moderate intensity thinning during the drought event were reduced at the WAI-0.65 site (Table 2), which may be due to the combination of lower initial tree competition and/or a more intense drought event at this site. A similar result was reported for Norway spruce stands in southern Germany, where a relative decline in basal area increment during drought was identified, along with more variable gas exchange, in thinned vs. unthinned stands (Sohn et al., 2013). The overall positive effect of heavy thinning identified at both sites suggests that it could provide a useful drought adaptation strategy for densely stocked forest stands. However, dominated oak trees did not respond so clearly to increased availability of light and water, as thinning did not affect intraspecific competition. Thus, thinning did not appear to affect drought response in oak, but thinning was found to have a positive effect on radial increment, especially two years after thinning (Fig. 3). The effect of moderate thinning was greater in 2011 at the WAI-0.22 site and was more prolonged at the WAI-0.65 site (Table 2), which is most likely linked to increased soil water availability (Sohn et al., 2016b). Heavy thinning effects could be masked in oak by other factors (confounding factors) such as cloning or different intraspecific competition.

4.2. Spring and autumnal radial increment

Higher radial increment occurred in spring, but was very sensitive to each year's climatic conditions and varied between the two species. These results agree with those of Michelot et al. (2012), who found that abundant precipitation during the month prior to the start of the growing period increased available soil water and promoted earlywood formation during spring. Some studies have reported that total ring growth for oak and pine is also sensitive to the climate of the previous year (Bogino and Bravo, 2008; Camarero et al., 2013; Michelot et al., 2012). This suggests that the production of new earlywood, promoted by spring recovery of hydraulic conductivity, also depends to a large degree on the use of carbon reserves. Carbohydrate storage may be greater in pines as photosynthesis can occur in conifers during mild winters (Lebourgeois et al., 2010). Consequently, dry conditions in the previous autumn may impact carbon reserves and even affect the spring radial increment. This might have occurred in 2012 at our study sites. In contrast, no clear differences between thinning treatments were identified for the autumn radial increment, regardless of species and site (Table 2 and Fig. 3). One hypothesis for explaining this, as we will discuss below, is that autumn radial increment may mainly be associated with rehydration, since the radial increment pattern coincides with the amount of autumn rainfall (Fig. 1).

4.3. Species-specific response to thinning

The different social classes occupied by the two species (Table 1) could explain the differences observed between them in radial increment response to thinning. Since pine is an early successional and shade intolerant species, a relatively high radial increment is expected compared to oak (Baraza et al., 2004; Sánchez-Costa et al., 2015). The main reason for the lower response of oak to thinning may reside in the fact that only pine trees were removed in the thinning treatments applied. Therefore, thinning led to a decrease in intraspecific competition for maritime pine, whereas interspecific competition was reduced for the oak species. Given the horizontal and vertical tree distribution pattern of the stand (strip species distribution and dominant height of pine, respectively, see Table 1), intra-specific competition was expected to be greater than interspecific competition for both species. Previous studies focusing on growth in pine-oak forests in the Iberian Peninsula pointed to the presence of complementarity between the two species (Río del and Sterba, 2009), which implies lower inter- than intra-specific competition, probably because of the different above- and belowground traits of the two species. Thus, a thinning treatment that also focused on oak could enhance the growth of the remaining trees (Cañellas et al., 2004; Corcuera et al., 2006; Cotillas et al., 2009). However, selective thinning is not always successfully accomplished in oak coppice stands (Amorini et al., 1996) and is further complicated by intense root sprouting. The unknown clone factor could also mask the results of thinning on oak radial increment. Accordingly, Salomón et al. (2013) proposed thinning or clonal silvicultural treatments in managed Q.pyrenaica coppice stands, to control root aging and increase stem growth.

4.4. Intra-annual radial response to thinning

Our results show a positive effect of thinning on cumulative intra-annual radial increment patterns for both species, affecting both the amount and the duration of radial increment (Table 3, Figs. S4 and S5). However, the prolongation of radial increment due to heavy thinning that we observed for pine especially was lower than the sampling frequency (every two weeks), so it could not be verified by real measurements or real growth. Heavy thinning increased the cumulative radial increment in pine and enhanced the increment rate in spring and in autumn, regardless of site (Table 3). This result is consistent with prior thinning studies on stands of other species. Linares et al. (2009) and van der Maaten (2013), for example, reported that thinning provides a useful management tool

for reducing stand transpiration and interception, increasing water availability and temporarily accelerating spring radial increment. In the present study, thinning also increased radial increment in oak at both sites, which might point to the significant influence of water variability, rather than temperature, on spring radial increment during the growing season. This has been reported also for other species in Mediterranean areas (Linares and Camarero, 2012). The small differences we observed in autumn radial increment parameters between thinning treatments (Table 2 and Fig. 3) suggest that the diameter shrinkage which occurs during a relatively long summer drought is recovered in autumn and is probably water-related. As mentioned earlier, and according to xylem anatomy studies for maritime pine in the Iberian Peninsula (Vieira et al., 2014, 2013), rehydration may involve mere cell enlargement rather than the differentiation of new xylem cells by the cambium. Similarly, summer droughts induce premature leaf withering in oak species as a mechanism to avoid earlywood vessel cavitation, but it also causes a decline in latewood production (Peguero-Pina et al., 2015). Moreover, overaged coppice oak stands may offset the effects of thinning by avoiding latewood formation (Corcuera et al., 2006). Thus, premature leaf withering and competition among stools (caused by previous coppice) could lead to growth oak stagnation (reduced latewood production). Consequently, intra-annual increment patterns for oak may be better adjusted to a shape typical of a unimodal logistic function. Future research could include cellular analysis to clarify the existence of real growth and rule out radial increment due to rehydration or thermal shrinkage (Mäkinen et al., 2008).

4.5. Intra-annual radial increment response to weather conditions

The radial increment rate varied with the degree of competition, but also with weather conditions. Our results for the effect of the previous five days' weather on the radial increment rate corroborate those of similar studies for Mediterranean species, such as Camarero et al. (2010). Weather variables that influenced the radial increment rate for both species were light (SR) and overall water availability (P and VPD) dependence. Solar radiation promotes photosynthesis and carbon fixation (Zweifel et al., 2005), while rainfall affects soil water availability, which is a major limiting factor for tree growth in Mediterranean areas. The VPD index reflects the physiological response of trees to the atmospheric environment. Water stress led to the cessation of radial increment in summer time and is associated with high VPD values and low precipitation, producing a marked bimodal pattern typical of Mediterranean species (Fig. 2). Differences in increment rates between seasons might be explained by the fact that precipitation and solar radiation were usually higher in spring than autumn (Figs. S6 and S7). Nevertheless, the high VPD index values and low precipitation would be responsible for lower radial increment at both sites in spring 2012.

The radial increment rate for oak is related to humidity and air temperature, based on a generally greater dependence of water status on air humidity in deciduous trees than in conifers (Zweifel et al., 2005). Low temperatures negatively affect the increment rate, which could be related to reduced photosynthesis or radial contraction. Additionally, cambial activity in oak appears to be controlled by temperature, which influences the onset of cambial reactivation (González-González et al., 2013). Relative air humidity reduces the negative effect of vapor pressure deficit when the temperature is very high (Fig. S6 and S7). Pines often display more conservative use of water compared to co-occurring deciduous oaks (Sánchez-Costa et al., 2015; Zweifel et al., 2006). In agreement with Sánchez-Costa et al. (2015), we suggest that both species achieved the highest possible radial increment through contrasting functional strategies. Higher values of β_1 and β_5, and lower β_3 for pine (Table 3) could be interpreted as differences between evergreen (pine) vs. winter-deciduous (oak) photosynthetic activity. Moreover, the trend of lower β_4 values for pine (Table 3) could be understood as the difference between strict (pine) vs. moderate (oak) physiological control of transpiration in response to drought.

5. Conclusions

The combined effect of mixed stands and thinning treatments is proposed as an effective strategy in response to forecasted warmer climate conditions involving more frequent and severe drought. The findings of this study may provide guidance to forest owners and managers seeking a satisfactory management tool for pine-oak mixed stands. Reducing competition by thinning of pines stimulated radial increment in both species. The effect of heavy thinning was maintained during the 2012 drought, compared to densely stocked forest stands, and thus may be considered as an effective strategy for adapting to foreseeable climate change. However, the variable response of the oak species highlights the need for further research to determine the effects of intra-specific competition. An increase in drought frequency and intensity, as predicted by the (IPCC Intergovernmental Panel for Climate Change, 2014), could affect the two species differently. Therefore, it is important to understand the influence of forest management practices, such as the thinning treatments implemented in our study, for optimal adaptation of pure and mixed stands to predicted climate change.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.02.009.

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