Short-term effect of thinning on inter- and intra-annual radial increment in Mediterranean Scots pine-oak mixed forests

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ABSTRACT

Thinning treatments along with the establishment of mixed forest stands have been put forward as possible adaptation strategies to cope with climate change, although the effectiveness of combining these two measures has scarcely been studied and may vary depending on stand conditions and the thinning regime employed. The aim of this study was to better understand the effect of commercial thinning and of the different growth behavior of two coexisting species on their inter- and intra-annual cumulative radial increment patterns. For this purpose, we studied radial increment in a Scots pine-Pyrenean oak (Pinus sylvestris L.-Quercus pyrenaica Willd.) Mediterranean mixed forest in north-west Spain over two climatically contrasting years (2016–2017). The data came from a thinning trial consisting of a randomized latin square design with a control and two commercial thinning treatments from below; one moderate and the other heavy, removing 25% and 50 % of initial basal area, respectively, of both species. The radial increment was analyzed based on bi-weekly readings from band dendrometers installed on 90 oak and pine trees. A non-linear mixed model based on double-Richards curve was fitted to explore the differences between thinning treatments and species response in the intra-annual cumulative radial increment patterns. Inter-annual basal area increments for each species at stand level were quantified by aggregating the tree estimates obtained from the model fitted in the first step. Tree and stand level growth were greater in Scots pine, which also showed a greater growth response to early spring droughts than the Pyrenean oak. Heavy thinning increased radial increment in trees of both species at the expense of decreased total stand basal area. At species level, basal area growth in Scots pine decreased through thinning, whereas for Pyrenean oak, the heavy thinning intensity resulted in the same basal area growth as the control. Thus, heavy thinning induced a trade-off between total stand growth and tree-level response to climatic conditions for Scots pine but with no loss in productivity in the case of the Pyrenean oak. Hence, heavy thinning may be an appropriate measure to attain productive stability of the oak coppice in the studied mixed forest as well as to adapt tree growth to future droughts associated with climate change.

1. Introduction

Climate change is one of the greatest threats to forest vitality and therefore the challenge for managers is to develop adaptive strategies that minimize ecosystem vulnerability (Allen et al., 2010). Several studies have already evidenced decreases in forest productivity and increased tree mortality or dieback in different regions of the world, especially in southern Europe (Calama et al., 2023; Hammond et al., 2022; Hartmann et al., 2022; Martínez-Vilalta et al., 2012). Some strategies such as changes in forest structure and/or species composition have been proposed to reduce the impacts of climate change (D'Amato et al., 2013).

Competition affects the way tree growth responds to climate (Castagneri et al., 2022; Fernández-de-Uña et al., 2015; Sánchez-Salguero et al., 2015). Thus, forest management techniques such as commercial thinning have been proposed in order to promote climatic resilience in

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forest stands by reducing tree competition and changing stand structure (Moreau et al., 2022; Olivar et al., 2014; Sohn et al., 2016a, 2016b). After thinning, the remaining trees increase access to environmental resources (i.e., soil moisture, light), thus enhancing their vigor and decreasing stress from climatic conditions (Magruder et al., 2013). On the other hand, density reduction may increase soil water evaporation and worsen nutrient cycling and tree growth on dry sites (Calama et al., 2019). Tree response to thinning treatments depends on the thinning regime (age at first thinning, intensity, type, and frequency). Heavy thinning is a suitable approach to improve the growth response of remaining trees to drought in both conifers and broadleaves (Sohn et al., 2016b). However, positive effect of the thinning treatment may decrease over time and could even become negative when compared to unthinned stands of Scots pine (Sohn et al., 2016a, 2013). Reduced competition through thinning was also found to increase growth and prolong the duration of the growing season for other species, regardless of weather conditions (van der Maaten, 2013). The reduction of stand density increases drought resistance and resilience in xeric Scots pine forests, thus, may decrease stand vulnerability to drought (Giuggiola et al., 2013). Similarly, thinning treatments have been shown to increase growth, reduce long-term stress caused by competition for water, and reduce the vulnerability of trees to drought in Mediterranean environment (del Río et al., 2017b; Navarro-Cerrillo et al., 2019).

Together with thinning, another forest management technique suggested as a possible adaptation strategy to mitigate the effects of climate change is to promote mixed forest stands, as they have been shown to increase resilience to biotic and abiotic factors (Grossiord, 2019; Guyot et al., 2016; Jactel et al., 2017; Pardos et al., 2021; Steckel et al., 2020) and enhance both the level and temporal stability of productivity (Bauhus et al., 2017a; del Río et al., 2017b, 2022). They can also present certain advantages compared to monospecific stands with regard to ecological functions and services (Felton et al., 2016; Huuskonen et al., 2021). Hence, under the current climate change scenario, a possible adaptation strategy would be to implement thinning regimes in mixed forest, which could also contribute towards promoting social, economic and environmental functions as part of this adaptive forest management (Ammer, 2016). However, scarce information currently exists with regard to the effects of commercial thinning on the resilience of mixed forest stands (Navarro-Cerrillo et al., 2016; Vernon et al., 2018).

Radial increment analysis is commonly used to quantify tree growth as well as to evaluate the ecological consequences and changes in production associated with climate change or management interventions (Siegmund et al., 2016). Understanding the differences in inter-annual tree growth of co-existing species allows us not only to assess stand stability with regard to aboveground wood production but also to predict changes in species composition (Jucker et al., 2014). Intra-annual radial increment analysis allows us to identify differences in growth among trees of different species in response to specific climatic events that may not be captured using a standard inter-annual dendroclimatic approach (Duchesne and Houle, 2011). However, intra-annual radial variation studies focusing on mixed forests in the Mediterranean region are still scarce (Aldea et al., 2018; de-Dios-García et al., 2018).

In this study, we evaluated differences in intra- and inter-annual radial increment patterns of the species *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. (hereinafter Scots pine and oak, respectively) in thinned and unthinned mixed stands under a Mediterranean climate. These stands are the result of forest management strategies over the second half of the twentieth century which included the re-introduction of pine species in oak coppice stands as a method to increase soil protection and stand productivity. The abandonment of these stands has allowed the oak to resprout under the Scots pine canopy resulting in spontaneous mixed pine-oak stands. Scots pine is a typical light-demanding pioneer species with a high radial growth rate (Sánchez-Costa et al., 2015). Deciduous oak trees, however, utilize resources more efficiently, so predominate in the late-successional stage (Cuny et al., 2012; Rodríguez-Calcerrada et al., 2010). These differences in functional traits and

growth strategies could mean reduced competition between species and increased supply, capture or use efficiency of site resources (Condés et al., 2023; Forrester, 2017, 2014; Grossiord, 2019). Therefore, Scots pine-oak mixed stands can tolerate greater volume increment per occupied area than pure stands (del Río and Sterba, 2009; Steckel et al., 2019). This spatial and temporal complementarity could also imply reduced climate sensitivity (Merlin et al., 2015; Steckel et al., 2020; Toïgo et al., 2015) and more stable productivity (del Río et al., 2022).

Although a large number of thinning experiments have been established for Scots pine in the last century across Europe (Castro-Segtowich et al., 2023; del Río et al., 2017a; Linkevičius et al., 2023; Saarinen et al., 2020), thinning experiments in mixed stands are currently scarce (Bauhus et al., 2017c; Primicia et al., 2016). Heavy thinning is commonly associated with yield loss at stand level in the case of pure Scots pine stands (del Río et al., 2017a). In contrast, thinning may increase growth at both tree and stand levels for oak coppice stands (Cañellas et al., 2004; Corcuera et al., 2006). The effect of the thinning may be sustained even during the most unfavorable climatic years. Cotillas et al., (2009) also found that selective thinning (removing 20–30 % of total basal area) improved tree growth for oak mixed-coppice stands under normal and reduced rainfall conditions. Aldea et al., (2017), in a study of intra- and inter-annual radial increment, found a positive effect of thinning on growth (regardless of drought conditions) in mixed stands of maritime pine and oak. However, the growth response to thinning in Scots pine-oak mixed forests in the Mediterranean area has not been studied to date. Despite its ecological and socio-economic importance and the fact that forests of this mixture are widespread, there is no specific silviculture for mixed stands of these species.

We used band dendrometer measurements, over two climatically contrasting years (2016 and 2017), from a thinning trial in order to identify differences between the species and short-term effects of commercial thinning (1–2 years after treatment application) on inter- and intra-annual cumulative radial increment patterns. The aims of the study were: 1) to decipher the differences in species growth; and 2) to quantify the short-term effect of commercial thinning at different spatio-temporal scales (tree vs. species and stand levels, and intra- vs. inter-annual levels).

2. Materials and methods

2.1. Study site

The experiment was located in Palacio de Valdellorma (León, 42°45′42.4′′N, 05°12′39.6′′W) in north-western Spain. The thinning trial was located at 990 m.a.s.l. under a continental Mediterranean climate, where the average annual rainfall is 515 mm with a marked summer drought period between July and August, when recorded precipitation averages 42 mm (AEMET, 2018, Spanish State Meteorological Agency. 2661 weather station code, based on 1981–2010 historical records). The annual mean temperature is 11.1 °C and the hottest month is July, with an average temperature of 27.4 °C. The period in which frosts may occur (temperature below 0 °C) is from December to February. Topography is moderate with a slope of 16 % and soils are acid conglomerates based on Miocene clay sediments (IGN, 1991).

Initially, an original oak coppice stand was harvested during the 1970′s and reforestation was carried out with Scots pine planted in rows. The oak coppice grew back via asexual reproduction in the form of sprouts between the rows of pine, so that by the start date of the experiment the stand resembled a 40-year old even-aged pine-oak mixed stand, although the real cambial age of each species differed. The stand basal area was dominated by pine, with a mean species proportion in basal area of 70 %.

Nine rectangular plots (50 × 40 m) were established following a complete randomized latin square design, with a buffer zone of 20 m between plots (Figure S1). The experimental design consisted of two

commercial thinning treatments with different intensities and an unthinned control (C) with three replicates each. The thinning treatment consisted of moderate (MT) and heavy thinning (HT), removing 25 % and 50 % of the initial basal area, respectively (Table 1). Trees of both species were removed by thinning from below, which involved logging the suppressed and intermediate trees and those with forked stems or low-quality timber specimens. The species proportion per plot was approximately maintained, so that there was 60–70 % Scots pine and 30–40 % oak in the remaining basal area. The commercial thinning was carried out during winter 2015 and the felled logs and branches were removed from the plots. In each plot, the diameter at breast height of all trees was measured while tree height was only measured in a subsample covering the diameter distribution per species. Mean diameter, stand density, dominant height and stand basal area were estimated per species. There were no statistical differences between plots for each species prior to commercial thinning. As expected, after thinning statistical differences were identified in mean diameter, stand density and basal area according to Tukey contrast (Table 1).

2.2. Stem radial variation and climatic measurements

We installed band dendrometers (DB 20, EMS Brno) after thinning treatments on five trees per species and plot, according to a stratified sampling approach that took diameter distribution into account. A total of 90 dendrometer bands were installed at breast height (1.30 m) after partial bark removal (rhytidome) to reduce stem rehydration effect. The Scots pine trees selected averaged 13.8 cm (±3.2 cm standard deviation) in diameter at breast height and 11.8 m (±1.4 m sd) high, while the oaks averaged 12.0 cm (±2.8 cm sd) in diameter and 10.1 m (±1.1 m) high. There were no significant differences in height or diameter between thinning treatments for each species, but oak diameter was slightly lower than pine according to the diameter species distribution in the stand. Band dendrometers were measured to the nearest 0.1 mm every two weeks from April 2016 to December 2017. 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 following the manufacturer's instructions (11.2×10^{-6} mm∘C^{-1}). Finally, girth increment data were transformed to radial increments based on a hypothetical cylindrical tree shape.

The weather during the sampling years (2016–2017) was characterized by dry summer months (Fig. 1). However, in 2017 there was a severe drought due to scarce precipitation in early spring (March-April) as well as in fall, prolonging the drought period until the end of autumn (October). Accordingly, annual precipitation was 515 mm and 368 mm for 2016 and 2017, respectively. The average daily maximum temperatures for the warmest month were higher than mean historical records (29.6 °C and 28.6 °C for 2016 and 2017 respectively vs. 27.3 °C for 1981–2010 period). Monthly temperature and precipitation records were compiled using data from the closest AEMET automatic network station (Leon, Sahechores, 2626Y, sited at 25 km from the study site).

2.3. Data analysis

2.3.1. Intra-annual analysis at tree level

Cumulative radial increment patterns for both species showed a clear bimodal pattern, which is typical of Mediterranean environments (Albuixech et al., 2012; Aldea et al., 2017; Pacheco et al., 2018): stem growth in the spring season, contraction during the summer due to depletion of stored water (concurrent with increasing water deficit) and stem rehydration (with growth for certain species) after autumn rainfall. Because of the expected bimodal pattern, we employed a non-linear mixed model based on the sum of two Richards curves (double-Richards) to analyze the cumulative intra-annual radial increment. The first Richards curve would represent the growth pattern for the spring and the second one for the autumn. The advantage of Richards curve compared to the commonly used Logistic or Gompertz function is that a fourth parameter included in the former, allows a better and more flexible fit to the original data, avoiding convergence problems. In fact, the Logistic or Gompertz function could be considered a specific case of the Richards curve (Oswald, 2015).

Model selection was done in four steps: 1) based on extra sum of squares F-Tests and penalized root-mean-square error, different Richard curves candidates were ranked and the most parsimonious curve selected (Oswald et al., 2012). Thus, the appropriate parameterization of the double-Richards curve was chosen according to the complexity of the observed trajectories in the data (Oswald, 2015); 2) Random effects were also included in the Richards curve selected in the previous step to consider the spatial and temporal dependence of measurements. Different random structures, affecting also to different parameters, were evaluated by maximizing the restricted log-likelihood (Zuur et al., 2009) and comparing and selecting the lowest value of the Akaike information criterion (AIC); 3) Then, in order to assess their impact on the Richards curve parameters, we added species, thinning treatment, year, and diameter variables as fixed effects. We compared all possible fixed model structures including the combination of variables affecting several parameters and the interaction among them; 4) The previous models were ranked and the final model was selected according to which was the most parsimonious (lowest AIC)".

Finally, serial autocorrelation was assessed using partial autocorrelation function and their respective plots, and several serial correlation structures were evaluated (autoregressive, moving average, and a mixed autoregressive-moving average model) to model residual autocorrelation. A variance function for modeling heteroscedasticity was also used, testing among several structures (exponential, power, and constant plus power of the absolute value of the variance covariate) (Pinheiro and Bates, 2000). Model fitting was performed using the 'FlexParamCurve' (Oswald, 2015) and 'nlme' (Pinheiro et al., 2015) packages in R (R Development Core Team, 2020).

2.3.2. Inter-annual analysis of each species at stand level

The stand basal area growth for each species was estimated using the tree diameter distribution measured for each plot and applying the model fitted in the intra-annual analysis at tree level. Basal area growth
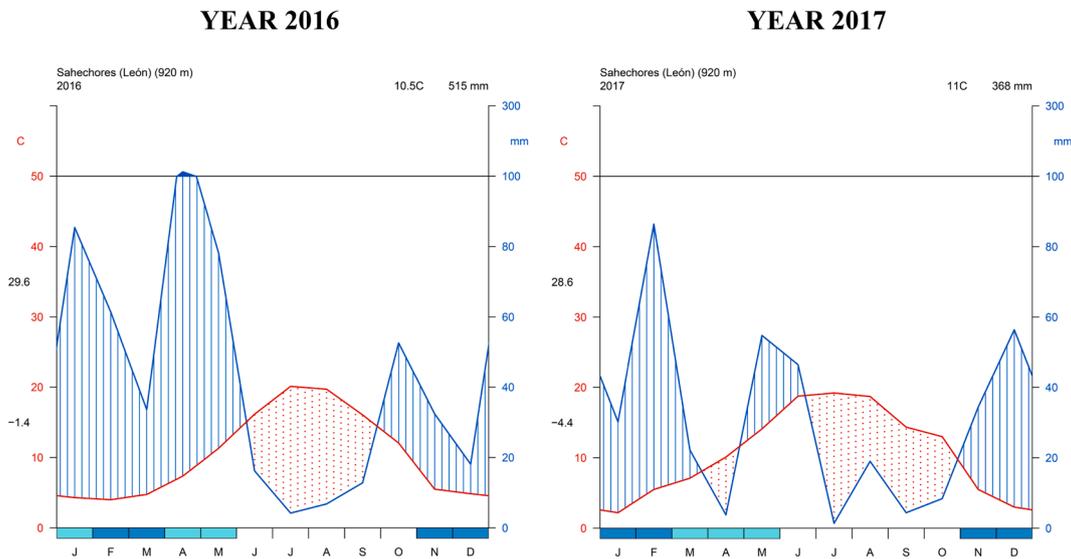

Table 1

Main stand characteristics before and after commercial thinning for each species. Data shown are mean and standard deviation values by treatment. Different letters denote significant differences after thinning at the 0.05 significance level. Ho: dominant height; dbh: mean tree diameter at breast height; BA: stand basal area; C: unthinned; MT: moderate thinning (25% BA removed); HT: heavy thinning (50% BA removed).

| Species | Treatment | H_o (m) | Before thinning | | | After thinning | | |
			Density (n·ha^{-1})	dbh (cm)	BA (m^2·ha^{-1})	Density (n·ha^{-1})	dbh (cm)	BA (m^2·ha^{-1})
Pinus sylvestris	C	12.5 ± 1.2	1,415 ± 130	12.2 ± 4.3	19.6 ± 2.3	1,415 ± 130c	12.2 ± 4.3a	19.6 ± 2.3b
	MT	10.7 ± 1.9	1,575 ± 90	12.0 ± 4.5	19.5 ± 3.9	710 ± 240b	16.0 ± 3.3b	13.7 ± 5.5b
	HT	11.7 ± 1.7	1,580 ± 130	11.8 ± 4.2	20.9 ± 3.3	390 ± 197a	15.1 ± 3.5b	9.0 ± 4.6a
Quercus pyrenaica	C	10.9 ± 1.1	2,960 ± 710	5.9 ± 3.2	12.6 ± 1.6	2,960 ± 710b	5.9 ± 3.2a	12.6 ± 1.6b
	MT	10.7 ± 0.7	2,855 ± 366	6.6 ± 3.5	12.1 ± 1.4	1,195 ± 286a	9.2 ± 4.6b	8.8 ± 1.7a
	HT	11.3 ± 1.8	2,005 ± 760	6.6 ± 4.1	8.7 ± 5.0	430 ± 427a	9.3 ± 6.3b	4.0 ± 2.9a

YEAR 2016

YEAR 2017

Fig. 1. Walter & Lieth climate diagram for sampled years. Numbers on the left side of y-axis are average daily maximum temperatures of warmest month and average daily minimum temperatures of coldest month from top to bottom respectively. .
Source: AEMET, (2018)

by species was estimated using empirical best linear unbiased predictors (EBLUPs) according to the random effects variances (tree and plot) along with different explanatory variables (i.e., species, thinning treatment, year and diameter) predicted in the previous step for all the remaining trees after thinning. The basal area value per tree, assuming a cylindrical tree shape, was aggregated for each plot to estimate the stand basal area increment and then upscaled to the hectare. The effects of the thinning treatment per species and year were then tested using "Tukey" contrasts based on global rankings, with confidence intervals and adjusted p-values. The R packages 'sae' (Molina and Marhuenda, 2015) and 'nparcomp' (Konietschke et al., 2015), were used to calculate the EBLUPs and Tukey test, respectively.

3. Results

3.1. Tree radial increment model with best structure

The best model structure was found to be a five-parameter model (all parameters from the spring and the asymptote of the autumn Richards curve) and three constant parameters (inflection point, rate and shape parameter from the autumn Richards curve). These invariable parameters adopted the mean value across all trees in the dataset, thus reducing complexity and computation, given that these parameters did not vary across group levels (trees from plots). Plot and tree (nested in plot) random effects were added to the model, affecting only the intercept of spring asymptote (A_{ij}), which turned out to be the best random structure, according to the model:

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

$$A_{ij} = \alpha_0 + \alpha_1 2017 + (\alpha_2 + \alpha_3 2017)*pine + \alpha_4 dbh + \alpha_5 MT + \alpha_6 HT + u_j + v_{ij}$$

$$I_{ij} = \beta_0 + \beta_1*pine$$

$$k_{ij} = \gamma_0 + \gamma_1*pine$$

$$m_{ij} = \tau_0$$

$$RA_{ij} = \rho_0 + \rho_1 2017$$

$$Ri_{ij} = 349$$

$$Rk_{ij} = 0.043$$

$$Rm_{ij} = 0.521$$

where y_{ij} is the cumulative radial increment for tree i in plot j; α_i, β_i, γ_i and τ_i are the asymptote, inflection point, rate and shape parameters of fixed effect variables for the spring Richards curve and ρ_i is the asymptote parameter for the autumn one (for clarification of parameters, see Figure S2); *2017* is a year dummy variable with value 0 for year 2016 and 1 for year 2017; *pine* is also a dummy variable with value 0 for oak and 1 for pine species; *dbh* is tree diameter at breast height (mm) recorded before the commercial thinning; *MT* is a dummy variable with value 1 for moderate thinning and 0 otherwise; *HT* is a dummy variable with value 1 for heavy thinning and 0 otherwise; $u_j \sim$N(0, σ_j) is the plot random effect; $v_{ij} \sim$N(0, σ_{ij}) is the tree random effect and $\varepsilon_{ij} \sim$ N(0, σ_e) is the error term. Ri_{ij}, Rk_{ij} and Rm_{ij} are the inflection point, rate and shape constant parameters from the autumn Richards curve which took the mean value from the double-Richards curve fitted for each tree (as mentioned previously).

Intra-annual cumulative radial increment patterns differed between species, thinning treatments and among years according to the observed values (Fig. 2) and the fitted double-Richards model (Table 2). Scots pine presented a higher increment rate (γ_1), but earlier inflection point (β_1) than oak, regardless of the year. The inflection point was reached on 14 May and 16 June for Scots pine and oak species, respectively. Scots pine presented a higher spring asymptotic value than oak for unthinned stands (α_3 and Fig. 3), although during 2016, the asymptote difference between species was only caused by size differences (α_2 and α_4). Year (climate) effect influenced both spring and autumn asymptotes. The spring asymptote decreased in 2017 for oak trees (α_1) due to the spring drought but increased for Scots pine (α_3) (Fig. 3). The autumn asymptote increased in 2016 but with no statistical significance (ρ_0). Both species were affected by autumn drought in 2017, so the autumn asymptotic value decreased significantly (ρ_1). Exclusively heavy thinning increased the spring asymptotic value significantly for both species (α_6) (Table 2). However, moderate thinning could also increase tree radial increment for oak compared to unthinned stands (Fig. 2), although this was not revealed in the fitted model.
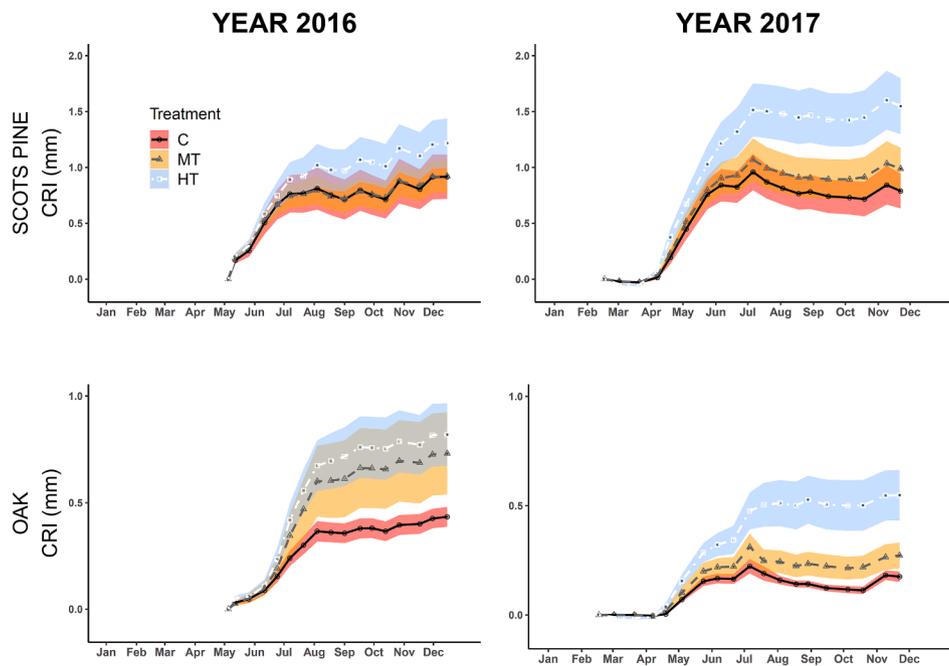
Fig. 2. Unthinned and commercial thinning treatment differences based on observed values of cumulative radial increment (CRI) patterns of each year. Circles and solid line, triangles and dashed line, and square and dot-dashed line show mean pattern for trees in unthinned, moderate and heavy thinning stands, respectively. Shaded areas denote standard error: red for unthinned, orange for moderate and blue for heavy thinning remaining trees. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Model fitted for intra-annual cumulative radial increment pattern (Eq. 1). Significant parameters are in bold. α_i, β_i, γ_i and τ_i are the asymptote, inflection point, rate and shape parameter regression of fixed effect variables for the spring and ρ_i are the asymptote parameters for the autumn Richards curve; σ_j is standard deviation for plot random effect; σ_{ij} is standard deviation for tree random effect; σ_e is standard deviation for error term; θ is the residual serial correlation parameter for moving average model MA(1); δ is function parameter used to model residual variance as a power of the absolute value of the variance covariate ($\mathbf{g_{ijk}}$):. $\mathbf{Var}(\varepsilon_{ijk}) = \sigma_e^2 (|\mathbf{g_{ijk}}|^\delta)^2$.

Parameter	Coefficient	p-value
$\alpha_0(A_{2016})$	−0.839	<0.001
$\alpha_1(A_{2017})$	−0.159	<0.001
$\alpha_2(A_{2016pine})$	0.081	0.424
$\alpha_3(A_{2017pine})$	**0.432**	**<0.001**
$\alpha_4(A_{dbh})$	**0.101**	**<0.001**
$\alpha_5(A_{MT})$	0.124	0.303
$\alpha_6(A_{HT})$	**0.374**	**0.002**
$\beta_0(I)$	**167.274**	**<0.001**
$\beta_1(I_{pine})$	**−32.592**	**<0.001**
$\gamma_0(k)$	**0.032**	**<0.001**
$\gamma_1(k_{pine})$	**0.012**	**<0.001**
$\tau_0(m)$	**0.307**	**0.032**
$\rho_0(RA_{2016})$	0.070	0.065
$\rho_1(RA_{2017})$	**−0.337**	**0.002**
$\sigma_j(A_{plot})$	$2.16 \cdot 10^{-4}$	
$\sigma_{ij}(A_{tree})$	0.409	
$\sigma_e(error)$	0.195	
δ	0.304	
θ	0.683	

3.2. Stand basal area increment for each species

The stand level analysis revealed that commercial thinning treatments resulted in the lowest basal area increment for Scots pine, regardless of the year (Fig. 4). For oak, heavy thinning led to the highest basal area increment, but with no statistical differences compared to unthinned stands. In addition, stand basal area increment for Scots pine

tended to be higher than for oak, but with no differences in the case of heavy thinning (p = 0.101). Consequently, total stand basal area increment (i.e., the sum of basal area of both species) decreased due to thinning but with no differences between the two thinning intensities applied. Stand basal increment was stable over time, i.e., no significant (p > 0.05) differences were found between years for each treatment and species.

4. Discussion

4.1. Species growth differences

No difference was observed in the asymptote parameter between species during 2016 (which can be considered a year with mean spring weather conditions), but tree size (mean diameter being greater for pine) and thinning treatment drove radial increment (Table 2). The absence of differences between species under normal weather conditions could be a consequence of both species being well adapted to the usual site conditions. However, the climatic conditions in 2017, with low precipitation in March and April (Fig. 1), resulted in a reduction in the spring asymptote for oak trees, but an increase in the case of Scots pine (Table 2 and Fig. 3). Scots pine trees were able to take advantage of soil water reserves during spring droughts due differences in leaf budburst and foliation: oak is still leafless in early spring and relies on the reserves from the previous year (Bauhus et al., 2017b; Fernández-De-Uña et al., 2017). Consequently, differences in timing with regard to water use may mean that, when photosynthesis begins in the oak, scarce water is available due to the fact that it has largely been consumed by Scots pine. As a result, oak may be more susceptible to soil water deficit in spring, while Scots pine may be more sensitive to summer drought (Fernández-De-Uña et al., 2017; Merlin et al., 2015; Steckel et al., 2020). Furthermore, both species were observed to be susceptible to dry conditions during early summer in mixed forests of Central Europe (Vospernik et al., 2023).

Drought tolerance could also underlie differences in inflection point of the species (Table 2). The tighter stomatal control and higher intrinsic
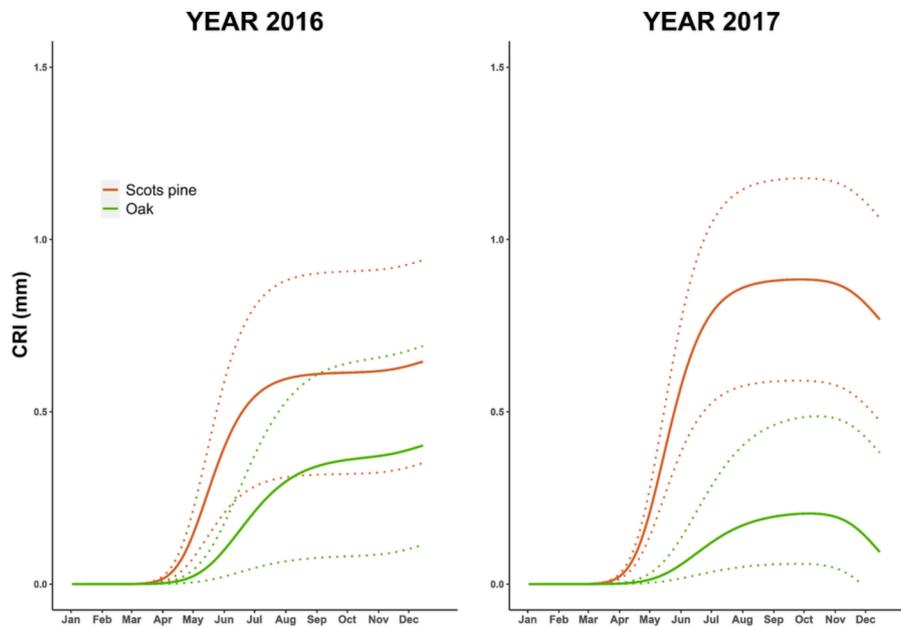
Fig. 3. Species differences in intra-annual cumulative radial increment (CRI) patterns calculated from the model predictions for the unthinned stands and both years. The thick solid lines represent double-Richards fitted models for Scots pine (red) and oak trees (green) for the species' mean diameter. The dotted lines show values for a hypothetical tree with $\pm$ 1 standard deviation from the species mean diameter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
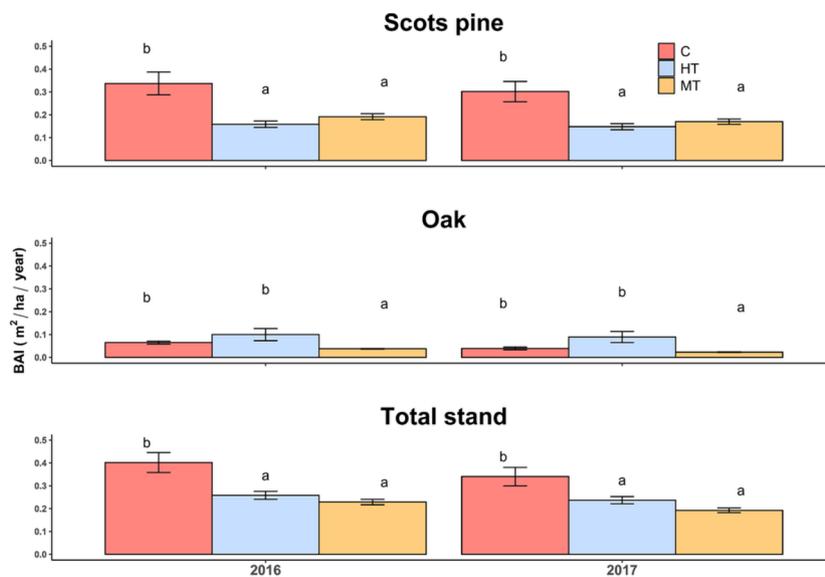

Fig. 4. Differences among unthinned plots and the two commercial thinning treatments in basal area increment at stand level for each species and year. Total stand denotes the sum of basal area increment for both species. 'C' indicates unthinned, 'MT' moderate thinning and 'HT' heavy thinning treatments. Error bars show standard error and letters indicate significant differences (p < 0.05) between treatments for each year and species.

water use efficiency of Scots pine compared to oak may restrict growth earlier (Fernández-De-Uña et al., 2017). An early inflection point for Scots pine trees could mean the need to develop riskier life strategies to capture resources (Cuny et al., 2012), although it may also be an advantage for coping with drought stress by firstly consuming the scarce supplies of soil water (Fernández-De-Uña et al., 2017).

Differences between species were also found for spring radial increment rate, with higher rates for Scots pine than oak (Table 2). Pioneer or early successional species, such as Scots pine compared to oak, have light-demanding traits which enable them to rapidly increase

radial growth (Sánchez-Costa et al., 2015). However, oak trees could utilize resources more efficiently and this may result in even higher radial increment rates (Cuny et al., 2012). Conversely, we observed a lower increment rate in the case of oak trees, which could be caused by differences in reproductive methods (seed vs. coppice). Clonal structure influences stem growth in oak coppices, so a larger individual stool (clonal clump) is less vigorous (Salomón et al., 2013), which also hampers oak coppice management (Salomón et al., 2017). In addition, over-aging could also affect growth rates and cause a severe reduction in latewood production, this being a predisposing factor in decline

episodes of oak coppice stands (Corcuera et al., 2006). Thus, radial increment is generally higher for pine than coppice oak trees in Mediterranean mixed forest (Aldea et al., 2018, 2017).

Finally, the influence of the year factor on the autumn asymptote (Table 2 and Fig. 2) suggests a probable diameter swelling/shrinkage in absence of growth. Camarero et al., (2010) and Fernández-De-Uña et al., (2017) reported that cambium reactivation, typical in Mediterranean species (Pacheco et al., 2018; Vieira et al., 2015), was commonly absent for the two species studied here. Consequently, the contraction effect during autumn 2017 was similar for both species (Table 2). The stem contraction is unusual in autumn since Mediterranean tree species generally undergo stem rehydration after summer shrinkage caused by water deficit (Albuixech et al., 2012; Sánchez-Costa et al., 2015), but September and October were extremely dry in 2017.

Overall, the differences observed between species could be caused by species-specific physiological traits resulting in temporal and spatial growth diversification, which may relax resource competition by complementary exploitation of light and water (Williams et al., 2017). Hence, pine and oak mixtures could involve niche complementarity and efficient use of resources over time by facilitation or competition reduction (Condés et al., 2023; Forrester, 2014). For example, the roots of the two species studied could occupy different depths in the soil: while the pine roots can penetrate deeper layers, *Q.pyrenaica* is characterized by a complex clonal shallow root system with most coarse roots growing horizontally within a soil layer of one-meter depth, and rare vertical roots growing below (Salomón et al., 2016). Consequently, del Río and Sterba (2009) found that Scots pine-oak mixed stands involved greater volume increment per occupied area than pure stands, as was found for Scots pine mixed with sessile oak in Central Europe (Pretzsch et al., 2020; Steckel et al., 2019).

4.2. Thinning effect at different scales

Our results showed that commercial thinning caused a clear trade-off between tree and stand growth in the short-term (1–2 years after thinning). The implementation of a given forest management practice implies the existence of trade-offs among forest functions, i.e., one specific objective may be optimized while at the same time the achievement of other objectives may be hampered or untargeted ecosystem components negatively affected (Vilà-Cabrera et al., 2018). Heavy thinning affected both species at tree level, increasing the spring asymptotic value (Table 2 and Fig. 3), with no evidence of a prolonged growing period (van der Maaten, 2013), although this finding could change at a higher temporal resolution of the measurements recorded by the continuous electronic (automatic) dendrometers. Although some studies have reported a lack of response to thinning in larger trees (Varmola et al., 2004), we observed that the effect of thinning was not dependent on tree size, probably because of the stage of the even-aged pine-oak mixed stand. We also found that heavy thinning had a positive effect at tree level regardless of year or weather conditions (Table 2). Previous research has shown that thinning reduces competition among trees, increases resource availability and consequently, promotes growth of the remaining trees of both species studied here (Cañellas et al., 2004; del Río et al., 2017a, 2008). However, the positive effect of heavy thinning compared to moderate intensity seemed to be more evident for both species during 2017 (Fig. 2). This is probably because the growth response of trees to competition reduction may be delayed (Pukkala et al., 2002) due to the large imbalance between the underground and aerial parts of the trees in the first year after thinning (Vincent et al., 2009). Thinning might encourage asymmetric competition among remaining trees and possibly promote a growth impasse by causing an abrupt change in the microenvironments of the stand (Bose et al., 2018). Therefore, thinning may also cause short-term unfavorable physiological reactions as trees adapt to new circumstances, despite the advantages of less competition (French et al., 2023). In addition, the spring drought conditions during 2017 could have affected the growth

response to thinning intensities, which is supported by several studies which point to increased availability of growing space through thinning resulting in improved drought resistance and resilience of trees reflected in height, diameter, and volume growth (D'Amato et al., 2013; Hilmers et al., 2022; Sohn et al., 2016b). Accordingly, Sohn et al., (2016a, 2016b) found that heavy thinning in Scots pine improves growth recovery following drought events and, similarly, Cotillas et al., (2009) showed that, in the case of oak, selective thinning improved tree growth in stands under conditions of reduced rainfall. Heavy thinning resulted in the greatest annual radial increment of trees in the case of pine, even during a drought event in a Mediterranean pine-oak mixed forest (Aldea et al., 2017).

The absence of differences between unthinned and moderate thinning at tree level could be due to the initial spatial heterogeneity, i.e., local-tree competition affecting target trees with band dendrometers could be similar under both treatments. The short period of time that elapsed after the commercial thinning may also explain the absence of differences between treatments. A thinning effect analysis based on intra- and inter-specific tree competition indexes and a longer time period may clarify the results obtained in this study and could provide the focus for future research. However, although not revealed by the fitted model, moderate thinning could also lead to an increase in tree radial increment for oak compared to unthinned stands (Fig. 2). Similar findings were reported by Corcuera et al., (2006), who observed that thinned oak trees formed wider tree-rings, more latewood and multiseriate tree-rings than overaged trees. On the other hand, historical oak-coppice management could cause high carbon expenditure in root respiration and aboveground development in centennial clones may be constrained, so thinning might not improve or even address physiological root-to-shoot imbalance (Salomón et al., 2017).

Our results showed that total stand basal area growth declines with commercial thinning, thus implying a loss of productivity in thinned stands in comparison to unthinned stands in the short-term period. However, there was no significant difference between the two thinning intensities, in contrast to the typical decreasing pattern associated with major reductions in stand density (del Río et al., 2017b; Pretzsch, 2020). At species level, the lower basal area increment for Scots pine in thinned stands supports findings for this species in monospecific stands (del Río et al., 2008), although the magnitude of the loss in growth depends on the region, site and stand age (del Río et al., 2017a). With regard to oak, our results show that basal area increment can remain stable or even increase with heavy thinning, but that moderate thinning would lead to a reduction in growth. Cañellas et al., (2004) reported increased tree growth after heavy thinning in monospecific oak coppice stands, although they found no differences at stand level (total basal area and biomass). The species-specific responses to thinning explain the pattern at stand level, as the greater basal area increment in oak following heavy thinning means that the difference between the control and heavy thinning treatment is reduced (Fig. 4). This suggests that the loss in productivity due to thinning may be mitigated by promoting species mixtures as opposed to monospecific stands (Thurm and Pretzsch, 2021).

In this regard, Pretzsch, (2003) reported that following stand density reduction treatments increment losses in mixed stands of Norway spruce-beech were lower than in pure stands. Primicia et al., (2016) observed that stand volume annual increments were even higher in thinned than in unthinned plots in a Scots pine-beech mixed stand where only pine trees were removed. However, at dry sites, such as that in this study, the canopy opening associated with heavy thinning may have a negative effect on stand growth by water evaporation. It is important to note that our results point to stand production decreasing with thinning intensity in the short term (Ashton and Kelty, 2018), this loss in stand growth in turn implying a reduction in carbon sequestration, resulting in decreased mitigation potential. However, tree mortality is expected to increase in the longer term due to climate change (Senf et al., 2020), especially in unmanaged forests since it is drought-density dependent

(Bradford et al., 2022). Hence, thinned stands may present higher carbon biomass stocks if harvested timber and the life span of wood products are included in the equation (Ruiz-Peinado et al., 2017). Furthermore, there is a marked trade-off between tree level and stand level growth in the short term, although the positive outcomes could offset the negative ones, depending on the target of forest management (Vilà-Cabrera et al., 2018). The greatest and most obvious positive effect of heavy thinning is that oak growth is enhanced, regardless of scale.

These structural changes could lead to a new management strategy aimed at converting overaged coppice stands into high forests (originating from seed) and achieving stand growth stability from the mixture (del Río et al., 2017b). Other ecosystem functions and services may also be favored by this approach, such as fire risk reduction, biodiversity conservation or improved conditions for oak fruiting and sexual regeneration. In addition, the size of the remaining Scots pine trees at the final harvest would increase, as the quality of the wood and therefore the value of the timber.

5. Conclusions

In this study, we have shown that although commercial thinning implies a marked trade-off between tree and stand production in the mixture at short term, oak trees responded favorably to the treatments at both scales. Furthermore, the remaining Scots pine trees would, on the one hand, benefit from reduced competition for water, in turn increasing drought resistance, and on the other, their growth would be enhanced, thus increasing the value of the timber. In short, reducing stand growth via heavy thinning in order to favor the dominated oak coppice trees may be a reasonable management proposal to ensure the stability and persistence of this type of mixture, which could play an important role in the preservation of ecosystem services under the current scenario of climate change.

CRediT authorship contribution statement

J. Aldea: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Resources. **M. del Río:** Conceptualization, Methodology, Writing – review & editing, Supervision. **N. Cattaneo:** Investigation, Writing – review & editing, Resources. **J. Riofrío:** Investigation, Writing – review & editing, Resources. **C. Ordóñez:** Investigation, Writing – review & editing, Resources. **S. Uzquiano:** Investigation, Writing – review & editing, Resources. **F. Bravo:** Investigation, Funding acquisition, Supervision, Project administration, Resources.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121462.

References

AEMET, 2018. Spanish State Meteorological Agency. Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente. Gobierno de España. [WWW Document]. Valores Clim. Norm. 1981–2010. URL www.aemet.es.

Albuixech, J., Camarero, J.J., Montserrat-Marti, G., 2012. Dinamica estacional del crecimiento secundario y anatomia del xilema en dos Quercus mediterraneos que coexisten. For. Syst. https://doi.org/10.5424/fs/2112211-12076.

Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., Del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. Agric. For. Meteorol. 237, 371–383. https://doi.org/10.1016/j.agrformet.2017.02.009.

Aldea, J., Bravo, F., Vázquez-Piqué, J., Rubio-Cuadrado, A., del Río, M., 2018. Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands. Agric. For. Meteorol. 256–257 https://doi.org/10.1016/j.agrformet.2018.03.013.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., (Ted) Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/J.FORECO.2009.09.001.

Ammer, C., 2016. Unraveling the Importance of Inter- and Intraspecific Competition for the Adaptation of Forests to Climate Change. https://doi.org/10.1007/124_2016_14.

Ashton, M.S., Kelty, M.J., 2018. The Practice of Silviculture: Applied Forest Ecology, 10th edition. ed. Irish Forestry 76.

Bauhus, J., Forrester, D.I., Pretzsch, H., Felton, A., Pyttel, P., Benneter, A., 2017c. Silvicultural options for mixed-species stands, in: Mixed-Species Forests: Ecology and Management. https://doi.org/10.1007/978-3-662-54553-9_9.

Bauhus, J., Forrester, D.I., Gardiner, B., Jactel, H., Vallejo, R., Pretzsch, H., 2017a. Ecological Stability of Mixed-Species Forests. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests. Ecology and Management. Springer Nature, Berlin, pp. 337–382. https://doi.org/10.1007/978-3-662-54553-9.

Bauhus, J., Forrester, D.I., Pretzsch, H., 2017b. From Observations to Evidence About Effects of Mixed-Species Stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests. Ecology and Management. Springer Nature, Berlin, pp. 27–72. https://doi.org/10.1007/978-3-662-54553-9.

Bose, A.K., Weiskittel, A., Kuehne, C., Wagner, R.G., Turnblom, E., Burkhart, H.E., 2018. Does commercial thinning improve stand-level growth of the three most commercially important softwood forest types in North America? For. Ecol. Manage. 409 https://doi.org/10.1016/j.foreco.2017.12.008.

Bradford, J.B., Shriver, R.K., Robles, M.D., McCauley, L.A., Woolley, T.J., Andrews, C.A., Crimmins, M., Bell, D.M., 2022. Tree mortality response to drought-density interactions suggests opportunities to enhance drought resistance. J. Appl. Ecol. 59, 549–559. https://doi.org/10.1111/1365-2664.14073.

Calama, R., Conde, M., de-Dios-García, J., Madrigal, G., Vázquez-Piqué, J., Gordo, F.J., Pardos, M., 2019. Linking climate, annual growth and competition in a Mediterranean forest: Pinus pinea in the Spanish Northern Plateau. Agric. For. Meteorol. 264 https://doi.org/10.1016/j.agrformet.2018.10.017.

Calama, R., Martínez, C., Gordo, J., Del Río, M., Menéndez-Miguélez, M., Pardos, M., 2023. The impact of climate and management on recent mortality in Pinus pinaster resin-tapped forests of inland Spain. For. An Int. J. For. Res. 2023, 1–13. https://doi.org/10.1093/FORESTRY/CPAD023.

Camarero, J.J., Olano, J.M., Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytol. https://doi.org/10.1111/j.1469-8137.2009.03073.x.

Cañellas, I., Río, M.D., Roig, S., Montero, G., 2004. Growth response to thinning in Quercus pyrenaica Willd. coppice stands in Spanish central mountain. Ann. For. Sci. 61, 243–250. https://doi.org/10.1051/forest:2004017.

Castagneri, D., Vacchiano, G., Hacket-Pain, A., DeRose, R.J., Klein, T., Bottero, A., 2022. Meta-analysis reveals different competition effects on tree growth resistance and resilience to drought. Ecosystems. https://doi.org/10.1007/s10021-021-00638-4.

Castro-Segtowich, A., Huuskonen, S., Fahlvik, N., Holmström, E., 2023. Select or not? comparing the impact of selective and schematic thinning on scots pine tree growth and stand structure. Forests 14. https://doi.org/10.3390/f14061194.

Condés, S., Pretzsch, H., del Río, M., 2023. Species admixture can increase potential tree growth and reduce competition. For. Ecol. Manage. 539, 120997 https://doi.org/10.1016/j.foreco.2023.120997.

Corcuera, L., Camarero, J.J., Sisó, S., Gil-Pelegrín, E., 2006. Radial-growth and wood-anatomical changes in overaged Quercus pyrenaica coppice stands: functional responses in a new Mediterranean landscape. Trees - Struct. Funct. https://doi.org/10.1007/s00468-005-0016-4.

Cotillas, M., Sabate, S., Gracia, C., Espelta, J.M., 2009. Growth response of mixed mediterranean oak coppices to rainfall reduction. Could selective thinning have any influence on it? For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2009.07.033.

Cuny, H.E., Rathgeber, C.B.K., Lebourgeois, F., Fortin, M., Fournier, M., 2012. Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France. Tree Physiol. https://doi.org/10.1093/treephys/tps039.

D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol. Appl. 23, 1735–1742. https://doi.org/10.1890/13-0677.1.

de-Dios-García, J., Manso, R., Calama, R., Fortin, M., Pardos, M., 2018. A new multifactorial approach for studying intra-annual secondary growth dynamics in mediterranean mixed forests: Integrating biotic and abiotic interactions. Can. J. For. Res. 48 https://doi.org/10.1139/cjfr-2017-0139.

del Río, M., Calama, R., Cañellas, I., Roig, S., Montero, G., 2008. Thinning intensity and growth response in SW-European Scots pine stands. Ann. For. Sci.

del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017a. A review of thinning effects on scots pine stands: From growth and yield to new challenges under global change. For. Syst. https://doi.org/10.5424/fs/2017262-11325.

del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Zlatanov, T.M., Bravo-Oviedo, A., 2017b. Species interactions increase the temporal stability of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. J. Ecol. https://doi.org/10.1111/1365-2745.12727.

del Río, M., Pretzsch, H., Ruiz-Peinado, R., Jactel, H., Coll, L., Löf, M., Aldea, J., Ammer, C., Avdagić, A., Barbeito, I., Bielak, K., Bravo, F., Brazaitis, G., Cerný, J., Collet, C., Condés, S., Drössler, L., Fabrika, M., Heym, M., Holm, S.O., Hylen, G., Jansons, A., Kurylyak, V., Lombardi, F., Matović, B., Metslaid, M., Motta, R., Nord-Larsen, T., Nothdurft, A., den Ouden, J., Pach, M., Pardos, M., Poeydebat, C., Ponette, Q., Pérot, T., Reventlow, D.O.J., Sitko, R., Sramek, V., Steckel, M., Svoboda, M., Verheyen, K., Vospernik, S., Wolff, B., Zlatanov, T., Bravo-Oviedo, A., 2022. Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14267.

del Río, M., Sterba, H., 2009. Comparing Volume Growth in Pure and Mixed Stands of Pinus Sylvestris and Quercus Pyrenaica. https://doi.org/10.1051/forest/2009035>.

Duchesne, L., Houle, D., 2011. Modelling day-to-day stem diameter variation and annual growth of balsam fir (Abies balsamea (L.) Mill.) from daily climate. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2011.05.027.

Felton, A., Nilsson, U., Sonesson, J., Felton, A.M., Roberge, J.M., Ranius, T., Ahlström, M., Bergh, J., Björkman, C., Boberg, J., Drössler, L., Fahlvik, N., Gong, P., Holmström, E., Keskitalo, E.C.H., Klapwijk, M.J., Laudon, H., Lundmark, T., Niklasson, M., Nordin, A., Pettersson, M., Stenlid, J., Sténs, A., Wallertz, K., 2016. Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. Ambio. https://doi.org/10.1007/s13280-015-0749-2.

Fernández-de-Uña, L., Cañellas, I., Gea-Izquierdo, G., 2015. Stand competition determines how different tree species will cope with a warming climate. PLoS One 10, e0122255.

Fernández-de-Uña, L., Rossi, S., Aranda, I., Fonti, P., González-González, B.D., Cañellas, I., Gea-Izquierdo, G., 2017. Xylem and leaf functional adjustments to drought in pinus sylvestris and quercus pyrenaica at their elevational boundary. Front. Plant Sci. https://doi.org/10.3389/fpls.2017.01200.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2013.10.003.

Forrester, D.I., 2017. Ecological and Physiological Processes in Mixed Versus Monospecific Stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests. Ecology and Management. Springer Nature, Berlin, pp. 73–116. https://doi.org/10.1007/978-3-662-54553-9.

French, K.L., Vadeboncoeur, M.A., Asbjornsen, H., Fraver, S., Kenefic, L.S., Moore, D.B., Wason, J.W., 2023. Temporary thinning shock in previously shaded red spruce. Can. J. For. Res. 53 https://doi.org/10.1139/cjfr-2022-0227.

Giuggiola, A., Bugmann, H., Zingg, A., Dobbertin, M., Rigling, A., 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. For. Ecol. Manage. 310, 827–835. https://doi.org/10.1016/j.foreco.2013.09.030.

Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytol. https://doi.org/10.1111/nph.15667.

Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M., Jactel, H., 2016. Tree diversity reduces pest damage in mature forests across Europe. Biol. Lett. https://doi.org/10.1098/rsbl.2015.1037.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. Nat. Commun. 13 https://doi.org/10.1038/s41467-022-29289-2.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., Mcdowell, N.G., Powers, J.S., Pugh, T.A.M., Ruthrof, K.X., Allen, C.D., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu. Rev. Plant Biol. https://doi.org/10.1146/annurev-arplant-102820-012804.

Hilmers, T., Schmied, G., Pretzsch, H., 2022. Legacy effects of past thinnings modulate drought stress reactions at present. Scand. J. For. Res. 37 https://doi.org/10.1080/02827581.2022.2096920.

Huuskonen, S., Domisch, T., Finér, L., Hantula, J., Hynynen, J., Matala, J., Miina, J., Neuvonen, S., Nevalainen, S., Niemistö, P., Nikula, A., Piri, T., Siitonen, J., Smolander, A., Tonteri, T., Uotila, K., Viiri, H., 2021. What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2020.118558.

Ign, 1991. Mapa geológico de España. Escala 1:50.000.Instituto Tecnológico Geominero de España. Ministerio de Fomento.

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. Curr. For. Reports. https://doi.org/10.1007/s40725-017-0064-1.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. https://doi.org/10.1111/ele.12382.

Konietschke, F., Placzek, M., Schaarschmidt, F., Hothor, L.A., 2015. nparcomp: an R software package for nonparametric multiple comparisons and simultaneous confidence intervals. J. Stat. Softw. 64, 1–17.

Linkevičius, E., Šilinskas, B., Beniušienė, L., Aleinikovas, M., Kliučius, A., 2023. The growing dynamic of pure scots pine stands using different thinning regimes in Lithuania. Forests 14, 1610. https://doi.org/10.3390/f14081610.

Magruder, M., Chhin, S., Palik, B., Bradford, J.B., 2013. Thinning increases climatic resilience of red pine. Can. J. For. Res. 43, 878–889. https://doi.org/10.1139/cjfr-2013-0088.

Martínez-Vilalta, J., Lloret, F., Breshears, D.D., 2012. Drought-induced forest decline: causes, scope and implications. Biol. Lett. https://doi.org/10.1098/rsbl.2011.1059.

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For. Ecol. Manage. 339 https://doi.org/10.1016/j.foreco.2014.11.032.

Molina, I., Marhuenda, Y., 2015. sae: An R package for small area estimation. R J. 7, 81–98.

Moreau, G., Chagnon, C., Achim, A., Caspersen, J., D'Orangeville, L., Sánchez-Pinillos, M., Thiffault, N., 2022. Opportunities and limitations of thinning to increase resistance and resilience of trees and forests to global change. For. An Int. J. For. Res. https://doi.org/10.1093/forestry/cpac010.

Navarro-Cerrillo, R.M., Sánchez-Salguero, R., Herrera, R., Ruiz, C.J.C., Moreno-Rojas, J.M., Manzanedo, R.D., López-Quintanilla, J., 2016. Contrasting growth and water use efficiency after thinning in mixed Abies pinsapo-Pinus pinaster-Pinus sylvestris forests. J. For. Sci. 62, 53–64. https://doi.org/10.17221/104/2015-JFS.

Navarro-Cerrillo, R.M., Sánchez-Salguero, R., Rodriguez, C., Duque Lazo, J., Moreno-Rojas, J.M., Palacios-Rodriguez, G., Camarero, J.J., 2019. Is thinning an alternative when trees could die in response to drought? The case of planted Pinus nigra and P. Sylvestris stands in southern Spain. For. Ecol. Manage. 433, 313–324. https://doi.org/10.1016/j.foreco.2018.11.006.

Olivar, J., Bogino, S., Rathgeber, C., Bonnesoeur, V., Bravo, F., 2014. Thinning has a positive effect on growth dynamics and growth–climate relationships in Aleppo pine (Pinus halepensis) trees of different crown classes. Ann. For. Sci. 71, 395–404. https://doi.org/10.1007/s13595-013-0348-y.

Oswald, S., 2015. FlexParamCurve: Tools to Fit Flexible Parametric Curves. Compr. R Arch, Netw.

Oswald, S.A., Nisbet, I.C.T., Chiaradia, A., Arnold, J.M., 2012. FlexParamCurve: R package for flexible fitting of nonlinear parametric curves. Methods Ecol. Evol. 3 https://doi.org/10.1111/j.2041-210X.2012.00231.x.

Pacheco, A., Camarero, J.J., Ribas, M., Gazol, A., Gutierrez, E., Carrer, M., 2018. Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2017.09.133.

Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., Calama, R., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: analysis along a climate gradient across Europe. For. Ecol. Manage. 481 https://doi.org/10.1016/j.foreco.2020.118687.

Pinheiro, J.C., Bates, D., 2000. Mixed-effects models in S and Splus. Springer, New York.

Pinheiro, J., Bates, D., DebRoy S, Sarkar, D., R Core Team, 2015. nlme: Linear and Nonlinear Mixed Effects Models.

Pretzsch, H., 2003. The elasticity of growth in pure and mixed stands of Norway spruce (Picea abies [L.] Karst.) and common beech (Fagus sylvatica L.). J. For. Sci. 49 https://doi.org/10.17221/4721-jfs.

Pretzsch, H., 2020. Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning. For. Ecol. Manage. 460 https://doi.org/10.1016/j.foreco.2020.117879.

Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehrbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K., Jansons, A., de-Dios-García, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika, M., Svoboda, M., Černý, J., Wolff, B., Ruíz-Peinado, R., del Río, M.,

2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (Matt.) Liebl.) analysed along a productivity gradient through Europe. Eur. J. For. Res. 139. https://doi.org/10.1007/s10342-019-01233-y.

Primicia, I., Artázcoz, R., Imbert, J.-B., Puertas, F., Traver, M.-C., Castillo, F.-J., 2016. Influence of thinning intensity and canopy type on Scots pine stand and growth dynamics in a mixed managed forest. For. Syst. 25, e057.

Pukkala, T., Miina, J., Palahí, M., 2002. Thinning response and thinning bias in a young Scots pine stand. Silva Fenn. 36 https://doi.org/10.14214/sf.524.

R Development Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rodríguez-Calcerrada, J., Cano, F.J., Valbuena-Carabaña, M., Gil, L., Aranda, I., 2010. Functional performance of oak seedlings naturally regenerated across microhabitats of distinct overstorey canopy closure. New For. 39, 245–259. https://doi.org/10.1007/s11056-009-9168-1.

Ruiz-Peinado, R., Bravo-Oviedo, A., López-Senespleda, E., Bravo, F., Del Rio, M., 2017. Forest management and carbon sequestration in the Mediterranean region: a review. For. Syst. 26, eR04S. https://doi.org/10.5424/fs/2017262-11205.

Saarinen, N., Kankare, V., Yrttimaa, T., Viljanen, N., Honkavaara, E., Holopainen, M., Hyyppä, J., Huuskonen, S., Hynynen, J., Vastaranta, M., 2020. Assessing the effects of thinning on stem growth allocation of individual Scots pine trees. For. Ecol. Manage. 474 https://doi.org/10.1016/j.foreco.2020.118344.

Salomón, R., Valbuena-Carabaña, M., Gil, L., González-Doncel, I., 2013. Clonal structure influences stem growth in Quercus pyrenaica Willd. coppices: bigger is less vigorous. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2013.02.011.

Salomón, R., Rodríguez-Calcerrada, J., Zafra, E., Morales-Molino, C., Rodríguez-García, A., González-Doncel, I., Oleksyn, J., Zytkowiak, R., López, R., Miranda, J.C., Gil, L., Valbuena-Carabaña, M., 2016. Unearthing the roots of degradation of Quercus pyrenaica coppices: A root-to-shoot imbalance caused by historical management? For. Ecol. Manage. 363, 200–211. https://doi.org/10.1016/j.foreco.2015.12.040.

Salomón, R., Rodríguez-Calcerrada, J., González-Doncel, I., Gil, L., Valbuena-Carabaña, M., 2017. On the general failure of coppice conversion into high forest in Quercus pyrenaica stands: a genetic and physiological approach. Folia Geobot. 52, 101–112. https://doi.org/10.1007/s12224-016-9257-9.

Sánchez-Costa, E., Poyatos, R., Sabaté, S., 2015. Contrasting growth and water use strategies in four co-occurring Mediterranean tree species revealed by concurrent measurements of sap flow and stem diameter variations. Agric. For. Meteorol. 207, 24–37. https://doi.org/10.1016/j.agrformet.2015.03.012.

Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A., Sánchez-Miranda, Á., Ballesteros-Cánovas, J.A., Alfaro-Sánchez, R., García-Cervigón, A.I., Bigler, C., Rigling, A., 2015. Disentangling the effects of competition and climate on individual tree growth: a retrospective and dynamic approach in Scots pine. For. Ecol. Manage. 358, 12–25. https://doi.org/10.1016/j.foreco.2015.08.034.

Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently linked to drought across Europe. Nat. Commun. 11 https://doi.org/10.1038/s41467-020-19924-1.

Siegmund, J.F., Sanders, T.G.M., Heinrich, I., van der Maaten, E., Simard, S., Helle, G., Donner, R.V., 2016. Meteorological drivers of extremes in daily stem radius variations of beech, oak, and pine in northeastern Germany: an event coincidence analysis. Front. Plant Sci. 7, 733. https://doi.org/10.3389/fpls.2016.00733.

Sohn, J.A., Gebhardt, T., Ammer, C., Bauhus, J., Häberle, K.-H., Matyssek, R., Grams, T. E.E., 2013. Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (Picea abies). For. Ecol. Manage. 308, 188–197. https://doi.org/10.1016/j.foreco.2013.07.048.

Sohn, J., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016a. Heavy and frequent thinning promotes drought adaptation in Pinus sylvestris forests. Ecol. Appl. 26 (7), 2190–2205.

Sohn, J., Saha, S., Bauhus, J., 2016b. Potential of forest thinning to mitigate drought stress: a meta-analysis. For. Ecol. Manage. 380, 261–273. https://doi.org/10.1016/j.foreco.2016.07.046.

Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. For. Ecol. Manage. 461. https://doi.org/10.1016/j.foreco.2020.117908.

Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J., Pretzsch, H., 2019. Transgressive overyielding in mixed compared with monospecific Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) stands – Productivity gains increase with annual water supply. For. Ecol. Manage. 439 https://doi.org/10.1016/j.foreco.2019.02.038.

Thurm, E.A., Pretzsch, H., 2021. Growth–density relationship in mixed stands – results from long-term experimental plots. For. Ecol. Manage. 483 https://doi.org/10.1016/j.foreco.2020.118909.

Toïgo, M., Vallet, P., Tuilleras, V., Lebourgeois, F., Rozenberg, P., Perret, S., Courbaud, B., Perot, T., 2015. Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea-Pinus sylvestris stands. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2015.02.019.

van der Maaten, E., 2013. Thinning prolongs growth duration of European beech (Fagus sylvatica L.) across a valley in southwestern Germany. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2013.06.030.

Varmola, M., Salminen, H., Timonen, M., 2004. Thinning response and growth trends of seeded Scots pine stands at the arctic timberline. Silva Fenn.

Vernon, M.J., Sherriff, R.L., van Mantgem, P., Kane, J.M., 2018. Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California. For. Ecol. Manage. 422 https://doi.org/10.1016/j.foreco.2018.03.043.

Vieira, J., Campelo, F., Rossi, S., Carvalho, A., Freitas, H., Nabais, C., 2015. Adjustment capacity of maritime pine cambial activity in drought-prone environments. PLoS One. https://doi.org/10.1371/journal.pone.0126223.

Vilà-Cabrera, A., Coll, L., Martínez-Vilalta, J., Retana, J., 2018. Forest management for adaptation to climate change in the Mediterranean basin: a synthesis of evidence. For. Ecol. Manage. 407, 16–22. https://doi.org/10.1016/J.FORECO.2017.10.021.

Vincent, M., Krause, C., Zhang, S.Y., 2009. Radial growth response of black spruce roots and stems to commercial thinning in the boreal forest. Forestry 82, 557–571. https://doi.org/10.1093/forestry/cpp025.

Vospernik, S., Heym, M., Pretzsch, H., Pach, M., Steckel, M., Aldea, J., Brazaitis, G., Bravo-Oviedo, A., Del Rio, M., Löf, M., Pardos, M., Bielak, K., Bravo, F., Coll, L., Černý, J., Droessler, L., Ehbrecht, M., Jansons, A., Korbouleswky, N., Jourdan, M., Nord-Larsen, T., Nothdurft, A., Ruiz-Peinado, R., Ponette, Q., Sitko, R., Svoboda, M., Wolff, B., 2023. Tree species growth response to climate in mixtures of Quercus robur/Quercus petraea and Pinus sylvestris across Europe - a dynamic, sensitive equilibrium. For. Ecol. Manage. 530, 120753 https://doi.org/10.1016/j.foreco.2022.120753.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-016-0063.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. New York. https://doi.org/10.1007/978-0-387-93837-0.