



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



Rafael M. Navarro-Cerrillo^{a,1,*}, Raúl Sánchez-Salguero^{b,1}, Carlos Rodríguez^a, Joaquín Duque Lazo^a, José M. Moreno-Rojas^c, Guillermo Palacios-Rodríguez^a, J. Julio Camarero^d

^a Depto. Ingeniería Forestal, Laboratorio de Dendrocronología, DendrodadLab- ERSAF, Universidad de Córdoba, Campus de Rabanales, Crta. IV, km. 396, E-14071 Córdoba, Spain

^b Depto. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, 41013 Sevilla, Spain

^c Area de Tecnología, Poscosecha e Industria Agroalimentaria, Instituto de Investigación y Formación Agraria y Pesquera (IFAPA), Centro "Alameda del Obispo", Avda. Menéndez Pidal, s/n, E-14004 Córdoba, Spain

^d Instituto Pirenaico de Ecología (IPE-CSIC), 50192 Zaragoza, Spain

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ABSTRACT

Previous research has provided insights into the potential response of growth and water use efficiency to thinning in Mediterranean forests, but little is known about the potential benefits of silviculture for plantations under severe drought stress. We selected two stands of *Pinus sylvestris* L. and *P. nigra* Arnold., and used dendrochronology and carbon isotopes ($\delta^{13}\text{C}$) to understand the growth and functional responses of high-density planted pine forests to thinning in drought-prone areas. Resistance, recovery, and resilience indices were calculated for each species using BAI data. We expected heavy thinning to produce stands that were more resilient to drought, particularly for the more drought-tolerant *P. nigra*. Differences in the basal area increments (BAI) and intrinsic water-use efficiency (iWUE) were found between the unthinned stand and the thinned stands, for both species. After thinning, BAI decreased as iWUE increased but this relationship was only marginally significant in *P. sylvestris*. Thinning increased growth resistance, recovery, and resilience following the severe drought of 2012. Our findings suggest that water shortage, linked to recurrent droughts, together with high tree competition, negatively affected tree growth and increased iWUE, which explains the dieback of some of these pine plantations. We evidence the vulnerability of densely planted Mediterranean pines to the forecasted warmer and drier conditions. These results show that a heavy thinning treatment (60% of basal area removed) provides a promising silvicultural framework for the adaptation of these drought-sensitive Mediterranean mountain pine forests to the potential risks of climate change.

1. Introduction

Extensive pine afforestations were highly relevant in the Mediterranean Basin during the 20th century regarding soil and water protection, but also from socioeconomic points of view (Del Lungo and Carle, 2006). For instance, ca. 3.5 million ha were reforested with pine species in Spain from the 1940s onwards, which represents 54.5% of the national area covered by conifers (Pemán García et al., 2017). These pine plantations are characterized mainly by being coetaneous and having a low degree of structural diversification and genetic composition, forming pure stands, often without an understory (Pausas et al., 2004). In general, these pine plantations are managed by protective

thinning every 20–25 years. However, forest decline and tree mortality have changed the aims of silviculture in such pine plantations; their management as a simple source of wood products has changed to sustainable and adaptive management in the face of climate change (Ameztegui et al., 2017). Drought induced forest dieback has been reported in many conifer forests in southern Europe (Linares et al., 2010; Sánchez-Salguero et al., 2012a, 2013; Camarero et al., 2015). Although the increasing impact of warmer and drier conditions is the main driver of these dieback episodes (Allen et al., 2010), land-use changes (i.e. forest expansion and lack of management) and their role in drought stress have also been widely recognized as additional factors (Martinez-Vilalta et al., 2012; Sánchez-Salguero et al., 2013; Jump et al., 2017).

* Corresponding author at: University of Cordoba, Crta. IV, km. 396, 14071 Córdoba, Spain.

E-mail addresses: rmnavarro@uco.es (R.M. Navarro-Cerrillo), rsanchez@upo.es (R. Sánchez-Salguero), josem.moreno.rojas@juntadeandalucia.es (J.M. Moreno-Rojas), jjcamarero@ipe.csic.es (J.J. Camarero).

¹ Co-first authors.

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The effects of the increase in the frequency and intensity of severe droughts in the Mediterranean Basin together with climate warming (Giorgi and Lionello, 2008) can be aggravated by a lack of management, which can increase the stand density and the competition between trees (Sánchez-Salguero et al., 2015a). Since forest dieback can cause substantial economic and environmental problems, managers have recently sought effective strategies to minimize dieback impacts, including tree mortality (Puettmann, 2011; Sohn et al., 2016). One alternative is to increase ecosystem resilience, understood as the capacity of an ecosystem to conserve the structure and functionality prior to the extreme event (i.e., drought) after some disturbance (Scheffer et al., 2001). Thinning treatments have been shown to reduce long-term stress caused by competition for water, and to reduce the vulnerability, and increase the resilience and resistance, of trees to drought (Martín-Benito et al., 2010; Linares et al., 2011; Sánchez-Salguero et al., 2012b, 2013; Navarro-Cerrillo et al., 2016; Lechuga et al., 2017). However, there are no previous studies assessing the potential of thinning regarding improving tree performance during dieback.

To address this question, we selected the southernmost European limit of Scots pine (*Pinus sylvestris* L.) and black pine (*P. nigra* Arnold.), in southern Spain, where forest dieback processes, affecting plantations, have been observed since the early 2000s (Sánchez-Salguero et al., 2012a). The lack of silviculture to reduce post-planting competition in these plantations has resulted in high-density stands vulnerable to drought-induced dieback and mortality (Martín-Benito et al., 2010; Sánchez-Salguero et al., 2013). In these plantations, thinning could enhance tree growth by decreasing the competition for water and nutrients, increasing the photosynthetic rates, and improving water use and carbon uptake (Bréda et al., 2006; McDowell, 2011). In addition, thinning alters the microclimatic conditions and consequently the forest water fluxes (Ma et al., 2010). Stable isotopes ($\delta^{13}\text{C}$) have been widely used to understand plant–environment interactions in the response to thinning (Di Matteo et al., 2017), since their measurement in tree-rings is a useful proxy that enables the inference of changes in the intrinsic water-use efficiency (iWUE), owing to the strong link between isotopic composition and water availability (McCarroll and Loader, 2004; Cernusak et al., 2013). Previous research has provided insights into the potential response of growth and iWUE in Mediterranean environments (del Río et al., 2008; Moreno-Gutiérrez et al., 2012a; Fernandes et al., 2016), although the results are contradictory. However, little is known about the potential benefits of silviculture for pine plantations under severe drought stress, in areas close to the limit of the geographical distribution of the pine species. Dendrochronological studies suggest that thinning may improve radial growth and vigor over a wide range of stand and site conditions, so it can be expected that this will also hold true for semi-arid sites prone to drought-triggered dieback (Fernandes et al., 2016). Therefore, thinning is one of the main forest management tools used to minimize forest drought vulnerability (McDowell et al., 2008). However, short-term and long-term thinning trials in xeric forests are rare and few empirical studies have evaluated the effectiveness of this approach with regard to the drought response of Mediterranean pines (but see Fernandes et al., 2016). In particular, Scots pine and black pine forests in southern Europe are expected to suffer severe water limitations and increasing temperatures (Giorgi and Lionello, 2008), and this is already leading to serious mortality processes in this type of forest (Sánchez-Salguero et al., 2012a). Therefore, it is necessary to establish experimental trials in areas close to the rear edge limit of these species, to develop silvicultural alternatives that allow urgent decisions to be taken in the field by forest managers (del Río et al., 2017).

Here, we have used dendrochronology and carbon isotopes ($\delta^{13}\text{C}$), see Cernusak and English, 2015; Di Matteo et al., 2017) to understand the growth and functional responses (changes in iWUE) of high-density planted pine forests to thinning in drought-prone areas of southern Spain. This approach is useful to evaluate whether thinning is an efficient management tool to make Mediterranean pine plantations less

vulnerable to drought-induced dieback (Sánchez-Salguero et al., 2012a; Sohn et al., 2016). For this study, we evaluated the effects of distinct thinning intensities – 0% (Control or unthinned stands), 30% (T30, 30% of basal area removed), and 60% (T60, 60% of basal area removed) – on the radial growth and iWUE of *P. nigra* and *P. sylvestris* plantations with drought-induced forest dieback symptoms (see Navarro Cerrillo et al., 2007; Sánchez-Salguero et al., 2012a,b). Our aims were: (1) to assess the growth and iWUE responses to different thinning intensities, (2) to evaluate the effects of thinning on post-drought resilience, and (3) to propose new, adaptive silviculture measures for these drought-prone Mediterranean pine plantations, based on the use of thinning to mitigate the effects of extreme droughts. We expected heavy thinning to produce stands that were more resilient to drought, particularly for the more-drought-tolerant species (*P. nigra*). The results may offer new insights into the interactive effects of drought and competition on post-drought resilience, as well as guidelines for an adaptive silviculture in the management of even-aged pine stands. The data will also allow assessment of the long-term effectiveness of thinning in the mitigation of current climate change impacts in drought-prone areas.

2. Materials and methods

2.1. Study area

The study area is located in the Sierra de los Filabres (hereafter Filabres, southern Spain, 36° 43' N, 4° 58' W; see Fig. 1a), a mountainous area situated on east-facing slopes and ranging in elevation from 1600 to 2186 m.a.s.l. The climate in the study area is continental thermo-Mediterranean with average annual rainfall of 320 mm, a mean temperature of 13.1 °C at 1000 m.a.s.l., and hot (mean maximum summer temperature is 26.3 °C) and dry summers (summer precipitation is 8.2 mm) (data correspond to Baza station, located 32 km from the study site, 37° 33' 52" N, 02° 46' 03" W, 814 m.a.s.l.) (Sánchez-Salguero et al., 2010, 2012a). A significant increase in the annual mean temperature during the 20th century (Fig. 1b) has been found in the study area, together with a significant reduction in annual precipitation. Wet periods (1950s, 1970s) have alternated with very dry periods (1980s, 1990–1994, 1999, 2005, 2012). Additionally, a long-term negative trend was detected in the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010), with increasing aridity during the second half of the 20th century as compared with the first half (Fig. 1b). The geological substrate is composed of siliceous rock with quartz micaschists, the most abundant soil types in the plantations being entisols and inceptisols. In both study sites, the slopes are steep (~25–35%). At the start of the study, the sites were covered by a 40-year-old mixed pine afforestation of *P. nigra* and *P. sylvestris* (Table 1). The forest stands contained sparse evergreen shrubs (*Adenocarpus decorticans* Boiss. *Cistus laurifolius* L.). Pine mortality was very high in this area, about 10,882 ha showing moderate or severe damage during 2002–2006 (Navarro Cerrillo et al., 2007). The study stands were planted in the 1970s using seeds from southern and central Spain. Afterwards, they were managed by thinning from below, which involved the harvesting of suppressed trees while the dominant trees were retained for future natural seeding (Serrada et al., 2008).

2.2. Experimental design

In June 2010, a thinning experiment was performed. A randomized complete block design with three blocks and three treatments was established (Quinn and Keough, 2002). Plots and blocks were located next to each other to make sure that the microclimatic and edaphic characters were analogous. The thinning treatments were carried out on nine blocks -each being 20 × 30 m with a 15-m-wide buffer strip around each block- randomly located in areas with slopes lower than 20% and a northwest exposure, considering the similarity of the canopy structural parameters, and with analogous microclimatic and edaphic

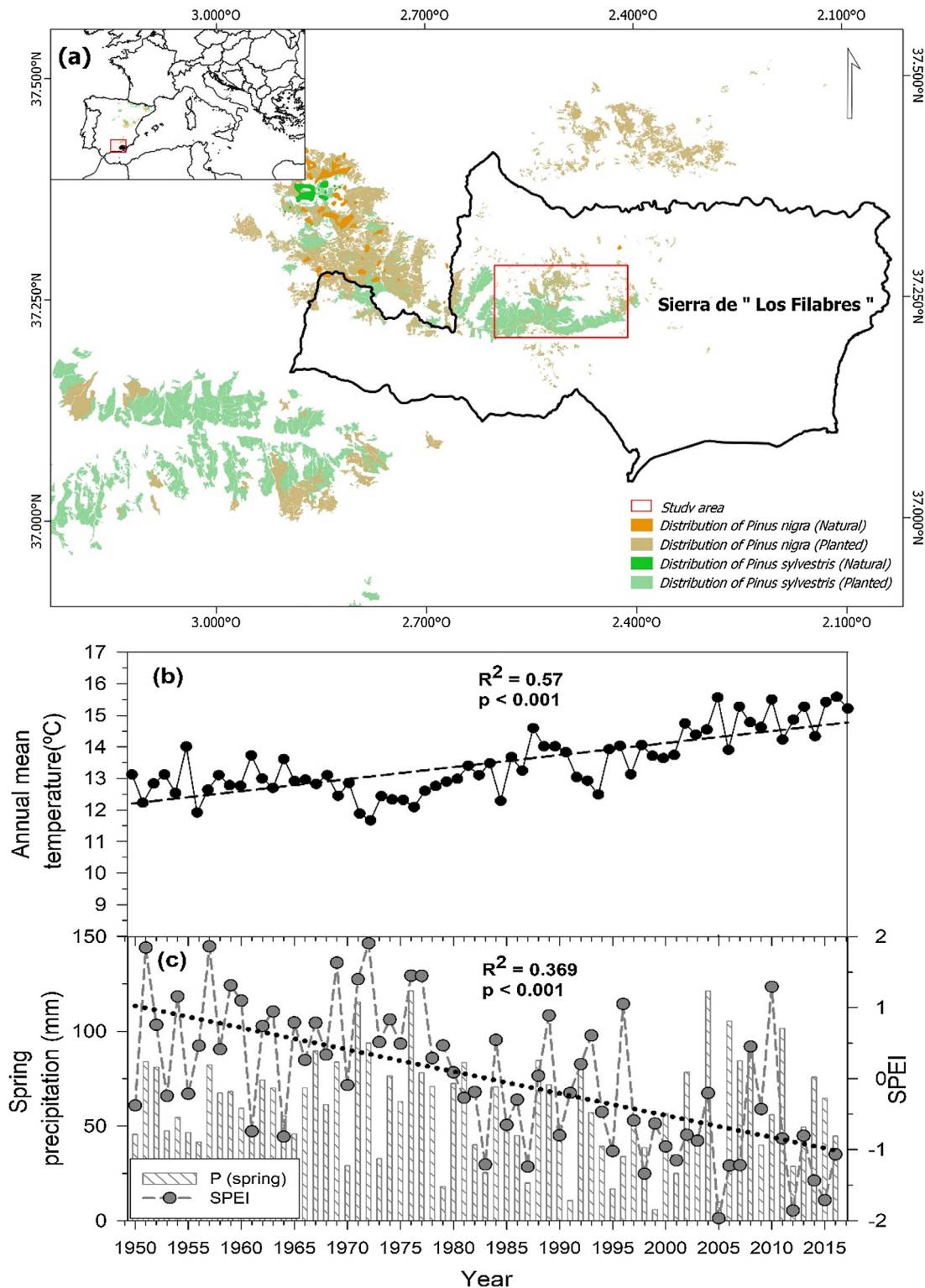


Fig. 1. (a) Site locations in Sierra de los Filabres (Andalusia, southern Spain) showing the location of experimental plots of *Pinus sylvestris* and *Pinus nigra*. (b) Climate trends considering mean annual temperature (T); (c) spring precipitation (P) and the annual Standardized Precipitation Evapotranspiration Index (SPEI) for the 1950–2016 period. The vertical black lines show extreme dry years. The displayed statistics (r^2 , P) correspond to annual temperature and the SPEI.

characters. A factorial randomized block design was used, considering three thinning intensity treatments –unthinned or control (C), intermediate thinning (T30) with removal of 30% of the initial basal area of the pines (leaving a tree basal area of $10.3 \text{ m}^2 \text{ ha}^{-1}$), and heavy thinning (T60) with removal of 60% of the initial basal area (leaving a tree basal area of $5.9 \text{ m}^2 \text{ ha}^{-1}$)- in three replicate blocks (Table 1). The

thinning treatments were applied for the primary purpose of removing overtopped, small-sized, dying, or suppressed trees, to promote future development under natural conditions with additional consideration given to uniform spacing. Thinning residues, such as slash, and stumps were removed from the treatment plots, and all remaining trees were tagged. Before thinning, the diameter at breast height (dbh, cm,

Table 1

Silvicultural characteristics of *Pinus sylvestris* and *Pinus nigra* plots according to thinning intensity (C, control or unthinned plots; T30, light thinning or 30% of basal area removed; T60, heavy thinning or 60% of basal area removed). Variables and abbreviations: D, stem density (No trees ha⁻¹); height (H, m); diameter at breast height (Dbh, cm); and basal area (G, m² ha⁻¹). Values are means ± SE.

Thinning intensity	<i>Pinus nigra</i>					<i>Pinus sylvestris</i>				
	2010		2016			2010		2016		
	D	G	H	Dbh	G	D	G	H	Dbh	G
Control	920	14.7 ± 0.8	8.2 ± 0.4	14.9 ± 0.5	16.1 ± 0.7	910	20.4 ± 0.6	7.7 ± 0.3	17.9 ± 0.6	22.9 ± 0.7
T30	644	10.3 ± 0.5	9.2 ± 0.3	15.8 ± 0.4	12.6 ± 0.5	637	14.2 ± 0.8	7.9 ± 0.4	18.3 ± 0.8	16.8 ± 0.6
T60	368	5.9 ± 0.3	9.5 ± 0.4	16.3 ± 0.4	7.7 ± 0.4	364	8.2 ± 0.3	8.6 ± 0.6	18.6 ± 0.6	9.9 ± 0.5

measured at 1.3 m above ground level) and total height (H, m) were measured with a caliper (Haglöf Mantax, Sweden) and Vertex III hypsometer (Haglöf Sweden), respectively (Table 1). No significant differences in tree density existed among the treatments within each plot before the 2010 thinning (one-way ANOVA: $F = 3.29$, $P = 0.108$, $F = 0.168$, $P = 0.849$, *P. nigra* and *P. sylvestris*, respectively).

2.3. Dendrochronological analysis and climate-growth relationships

Post-thinning sampling and field measurements were conducted in November 2016, six years after the thinning treatments. In each plot, all trees were measured (dbh, H), and five dominant trees with dbh greater than 15 cm were cored at 1.3 m with a Pressler increment borer. Two cores were sampled per tree, in the direction perpendicular to the maximum slope (Fritts, 2001). The cores were air dried, sanded with papers of progressively finer grain until the tree-rings were clearly visible, and then visually cross-dated. Individual tree-ring width series were measured to the nearest 0.01 mm with a LINTAB measuring device (Rinntech, Heidelberg, Germany). The cross-dating quality was verified using the software COFECHA (Holmes 1983), by checking the consistency of the different ring-width series among trees coexisting within the same plots. To assess the quality of the tree-ring width series, several dendrochronological statistics (Fritts, 2001) were calculated, considering the common interval after thinning, 1996–2016 (Table 1): first-order autocorrelation of raw width data (AC), mean sensitivity (MS) of indexed growth values, mean correlation between trees (Rbt), and the expressed population signal (EPS) - which measures the statistical quality of the mean site chronology as compared with a perfect, infinitely replicated chronology (Wigley et al., 1987) (Table 2). Tree age at 1.3 m was also estimated by counting the number of rings in the core, as far as the pith, or showing the innermost rings according to their curvature.

The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius was corrected by converting tree-ring widths into basal area increments (BAIs), using the formula $BAI = \pi (R^2_t - R^2_{t-1})$ where R is the radius of the tree and t is the year of tree-ring formation (Biondi and Qaedan, 2008). The growth responses of individual species to thinning were evaluated with annual series of BAI.

Table 2

Dendrochronological statistics of sampled *Pinus nigra* and *Pinus sylvestris* for the three treatments (C, control or unthinned plots; T30, light thinning or 30% of basal area removed; T60, heavy thinning or 60% of basal area removed) during the period 1996–2016. Abbreviations: BAI₂₀: mean basal area increment in the last 20 years (mean ± SD, cm² year⁻¹), Rbt, mean between-trees correlation; MS: Mean sensitivity; AC1: first-order autocorrelation; EPS, Expressed Population Signal.

Declining level	Thinning intensity	BAI ₂₀	Age (yrs.)	Rbt	MS	AC	EPS
<i>Pinus nigra</i>	C	3.6 ± 0.3	34	0.445	0.341	0.751	0.954
	T30	3.7 ± 0.3	35	0.634	0.310	0.754	0.979
	T60	3.7 ± 0.3	35	0.657	0.354	0.751	0.980
<i>Pinus sylvestris</i>	C	3.6 ± 0.3	39	0.314	0.350	0.831	0.921
	T30	4.5 ± 0.4	38	0.408	0.343	0.748	0.947
	T60	4.8 ± 0.4	39	0.389	0.345	0.756	0.943

2.4. Tree-ring isotopes analysis and intrinsic water use efficiency

To assess the responses of the two pine species to thinning intensity and climate, one core per tree was used for C isotope analysis, thereby providing a useful estimation of the long-term effects of thinning on iWUE (McCarroll and Loader, 2004). We analyzed δ¹³C in climatically contrasting years: unfavorable years (i.e., years with a combination of low precipitation and high temperatures: 1995, 2005, 2012) and favorable years (i.e., years with a combination of high precipitation and moderate temperatures: 1993, 2003, 2013) (Fig. 1). The selected years included periods before (1993, 1995, 2003, 2005) and after (2012, 2013) the thinning treatments, to explore the effects of management on iWUE. Complete dated rings (including both early and late wood) were carefully separated into sections corresponding to specific growth years using a razor blade, under a stereomicroscope. Samples were ground to a fine powder using a ball mill (Spex 5300, Metuchen, NJ, USA) and 400–600 μg of milled wood were weighed in tin cups for carbon isotopes (δ¹³C) analysis. Isotope subsamples were combusted in an elemental analyzer (Thermo Fisher, Germany) and the resulting gases were analyzed in an isotope ratio mass spectrometer (IRMS; Thermo-Fisher Delta V Advanced, Germany) located at the LISEEM laboratory (IFAPA, Cordoba, Spain). The carbon isotope discrimination (δ¹³C; ‰ enrichment relative to the international standard, Vienna Pee Dee Belemnite) and the iWUE (μmol mol⁻¹) were calculated according to standard methodologies and formulae (see Farquhar and Richards, 1984 for details).

2.5. Climatic data

The availability of data from a weather station close to the study site is limited due to the length of the observation period and gaps in local climatic data (Calar Alto meteorological station, 37° 13' 25" N, 02° 32' 46" W; 2168 m.a.s.l., which covers the period 1990–2016, is located less than 3 km from the study area, <http://www.caha.es/es/observaci%C3%B3n/meteorolog%C3%ADa>). Therefore, we used 0.25°-gridded monthly data for the mean temperature and total precipitation, available for the period 1954–2016 from the E-OBS climate data set (Haylock et al., 2008). We obtained the July SPEI indices at scales of 6 (SPEI₆) and 12 months (SPEI₁₂), to evaluate drought severity (Vicente-

Serrano et al., 2010). Negative SPEI values correspond to dry conditions and would be related to a decline in growth, whereas positive SPEI values indicate wet conditions, which should correspond to enhanced growth (Pasho et al., 2011). The SPEI indices were used to select the four most intense droughts in the study area for the period 1975–2016 (see Fig. 1).

2.6. Growth resilience indices

To quantify the response of tree growth to selected extreme droughts before (1995, 2005) and after (2012) the thinning treatments, three resilience indices (CR) were calculated for each species, using BAI data and following Lloret et al. (2011):

- The resistance index (CR_T), which quantifies the growth of the tree during the drought (D_t) with respect to the previous growth ($PreD_t$):

$$CR_T = D_t / PreD_t \quad (1)$$

- The recovery index (CR_S), which is the response of the growth after the drought ($PostD_t$), compared with D_t :

$$CR_S = PostD_t / D_t \quad (2)$$

- The resilience index (CR_C), which is the ratio of the growth values measured after ($PostD_t$) and before ($PreD_t$) the drought:

$$CR_C = PostD_t / PreD_t \quad (3)$$

Higher values of CR_T , CR_S , and CR_C indicate greater growth resistance, resilience, and recovery, respectively. The pre- and post-drought periods were 3-years long, to avoid drought overlap and because growth has been shown to recover to normal values after this period (Gazol et al., 2017).

2.7. Statistical analyses

To understand how the tree growth responses to climate were influenced by the thinning treatments, the unit of replication for each treatment was the block ($n = 3$), considering two thinning intensities (T30 and T60) and a control (C) for each pine species. Pairwise comparisons of the treatments were made using the Tukey-Kramer multiple comparison test. For statistical analysis, the BAI and iWUE measurements were examined for normality and homoscedasticity; when the variables were not normal, the data were normalized using a Box-Cox transformation. The relationships between BAI and iWUE were explored by linear regressions. For calculation of the BAI trends, the analyses were performed on log-transformed values to normalize the variable. To evaluate the short-term responses of BAI to thinning, we applied a repeated measures analysis of variance (one-way ANOVA), selecting periods of equal length, defined as pre-treatment (1984–2009) and post-treatment (2010–2016). Then, we calculated the mean BAI series for these periods, which were used as within-subjects factors

Table S1

Mean values (\pm SE) of basal area increment (BAI) and intrinsic water-use efficiency (iWUE) for each species and thinning treatment (C, control or unthinned plots, T30, light thinning or 30% of basal area removed; T60, heavy thinning or 60% of basal area removed). Different letters indicate significant differences ($P < 0.05$) between treatments in a repeated measures ANOVA Tukey's test for the same period.

	Thinning intensity	BAI ($\text{cm}^2 \text{year}^{-1}$)		iWUE ($\mu\text{mol mol}^{-1}$)	
		<i>Pinus nigra</i>	<i>Pinus sylvestris</i>	<i>Pinus nigra</i>	<i>Pinus sylvestris</i>
Pre-thinning (1984–2009)	C	4.57 \pm 0.36 ^a	3.86 \pm 0.35 ^a	100.75 \pm 1.62 ^a	104.01 \pm 1.37 ^a
	T30	4.89 \pm 0.49 ^a	3.47 \pm 0.27 ^a	101.05 \pm 1.64 ^a	103.95 \pm 1.83 ^a
	T60	4.63 \pm 0.44 ^a	3.75 \pm 0.28 ^a	99.84 \pm 1.52 ^a	105.58 \pm 1.40 ^a
Post-thinning (2010–2016)	C	2.64 \pm 0.24 ^a	3.10 \pm 0.31 ^a	110.28 \pm 2.43 ^b	115.55 \pm 2.28 ^a
	T30	4.67 \pm 0.41 ^b	4.67 \pm 0.54 ^b	102.49 \pm 2.59 ^a	113.81 \pm 2.20 ^a
	T60	5.56 \pm 0.51 ^b	4.88 \pm 0.41 ^b	101.54 \pm 2.45 ^a	114.13 \pm 2.90 ^a

(Table 3).

The differences among the three resilience indices (CR_T , CR_S , and CR_C) calculated for the selected droughts (1995, 2005, and 2012) and among the values of growth (mean BAI data) for the period 1996–2016 (BAI_{20}) were compared using analyses of variance (ANOVAs). Prior to statistical analysis, we examined all the resilience indices for normality and homoscedasticity. When the variables were not normal, the data were subjected to a Box-Cox transformation. Differences among the treatments were considered significant at a level of $P = 0.05$. The dplR package was used to calculate tree-ring statistics and all statistical analyses were performed using the R software, version 3.4.0 (R Core Development Team, 2018).

3. Results

3.1. Radial growth and iWUE responses to thinning

The growth patterns were similar for both pine species and all thinning intensities, and they were characterized by noticeable growth reductions in dry periods (1990–1995, 2005, and 2012) and growth increases during wet periods (1993, 1997, and 2013; see Fig. 2). The lowest annual growth rates (ca. $3.0 \text{ cm}^2 \text{ year}^{-1}$) occurred in the driest years (2012 and 2016). After thinning, BAI recovered in the stands at both thinning intensities, but faster in T60 stands (the mean BAI values for the 2009–2016 period were 3.7 and $4.8 \text{ cm}^2 \text{ year}^{-1}$ in *P. nigra* and *P. sylvestris*, respectively) than in T30 stands (the mean BAI values for the 2009–2016 period were 3.7 and $4.5 \text{ cm}^2 \text{ year}^{-1}$, respectively). The thinning effect on growth seems to have been transitory since *P. sylvestris* trees from the C and T30 stands showed similar BAI values (ca. $2.0 \text{ cm}^2 \text{ year}^{-1}$).

The inter-tree synchrony of the growth series (Rbt and EPS statistics) was higher for *P. nigra* than for *P. sylvestris* and increased with the intensity of thinning for *P. nigra*, with the lowest common coherence in growth corresponding to unthinned (C trees) stands (Fig. 2; Table 2). The year-to-year growth persistence (AC) and the variability between consecutive rings (MS) were similar for the two species (Table 2).

During the 1980–2016 period, *P. nigra* showed the highest average BAI, both before ($4.69 \text{ cm}^2 \text{ year}^{-1}$) and after ($4.29 \text{ cm}^2 \text{ year}^{-1}$) the 2010 thinning, with the BAI values being lowest, significantly so ($P < 0.001$), in the control plot ($2.64 \text{ cm}^2 \text{ year}^{-1}$) and increasing as thinning intensity increased (Table 3; Fig. 2). In contrast, *P. sylvestris* had the lowest BAI values before ($3.69 \text{ cm}^2 \text{ year}^{-1}$) and after ($4.21 \text{ cm}^2 \text{ year}^{-1}$) thinning, with significant differences in BAI among thinning intensities ($P < 0.001$) (Table 3). The post-thinning BAI values were significantly higher than the pre-thinning values, for both species (data not included).

The iWUE increased significantly after thinning, for both species, although *P. sylvestris* experienced a relative increase (+9.5%) that was significantly higher ($P < 0.05$, Fig. 2) than for *P. nigra* (+4.2%, Fig. 2). *Pinus sylvestris* showed the highest iWUE values before ($104.51 \mu\text{mol mol}^{-1}$) and after ($114.49 \mu\text{mol mol}^{-1}$) thinning, with the

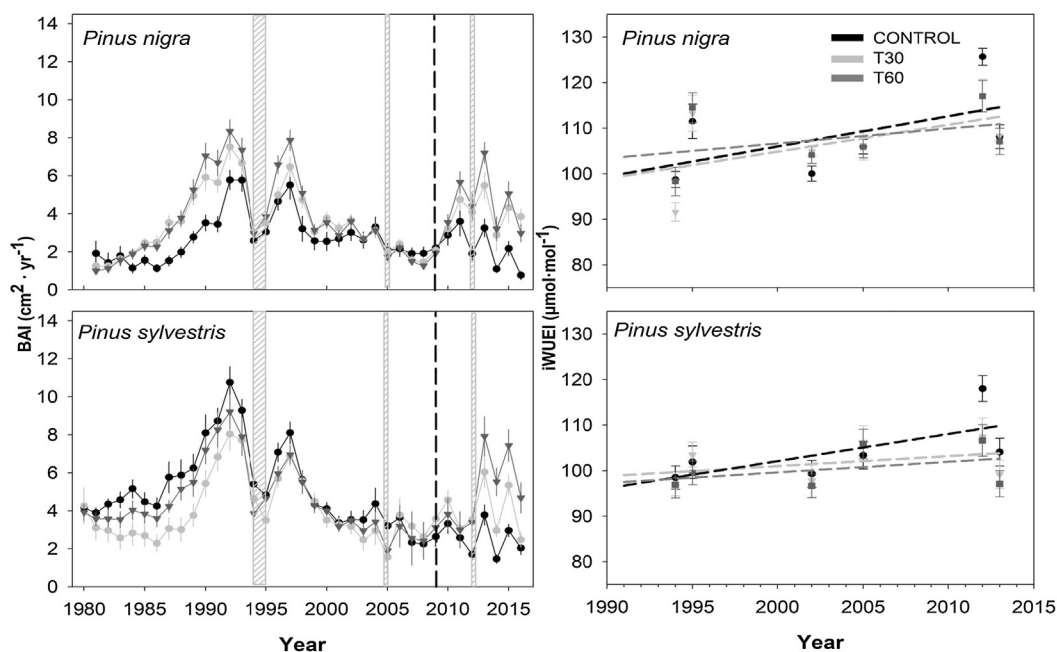


Fig. 2. Basal area increment (BAI) mean series and intrinsic water-use efficiency (iWUE) of *Pinus nigra* and *Pinus sylvestris* according to thinning intensity (C, Control or unthinned plots; T30, light thinning, 30% basal area removed; T60, heavy thinning, 60% of basal area removed). iWUE trends are calculated for wet (1993, 2002, 2013) and dry (1995, 2005, 2012) years. In the BAI plots the vertical dashed line corresponds to the 2010 thinning treatment and vertical grey areas correspond to the 1994–1995, 2005 and 2012 drought (see Fig. 1).

lowest values occurring in the T30 stands (Table 3; Fig. 2). In contrast, *P. nigra* showed the lowest values before ($100.54 \mu\text{mol mol}^{-1}$) and after ($104.77 \mu\text{mol mol}^{-1}$) thinning, with iWUE decreasing as thinning intensity increased (Table 3, Fig. 2). After thinning, there were significant differences in the iWUE values between the two species ($F = 1.20$; $P < 0.001$). In addition, the values differed significantly among the treatments for *P. sylvestris* ($F = 3.44$; $P < 0.05$), but not for *P. nigra* ($F = 0.84$; $P = 0.43$).

3.2. Relationships between iWUE and BAI

The relationships between BAI and iWUE were similar for both species and for the different thinning intensities but had different magnitudes (Fig. 3). We observed no significant relationships between BAI and iWUE before thinning (Fig. 3). After thinning, BAI decreased as iWUE increased but this relationship was only marginally significant in *P. sylvestris* ($P = 0.059$). The BAI decrease was greater for *P. sylvestris* than for *P. nigra* and differed between the thinning intensities (Fig. 3). Furthermore, we did not find an overall strengthening of the associations between BAI and iWUE with increasing thinning intensity.

The post-thinning changes in iWUE and BAI during climatically unfavorable (dry) and favorable (wet) years highlight a consistent response among the pine species and treatments (Fig. 4). After thinning, the maximum BAI values for the two species were observed in wet years, although this increase in the growth rate was related to the intensity of thinning. *Pinus sylvestris* showed a reduction in BAI (and an increase in iWUE) with increasing thinning intensity (Fig. 4). In *P. nigra* the most pronounced differences in BAI were observed during unfavorable years for the heavy-thinning treatment (T60), *P. nigra* being less responsive during climatically favorable years. The BAI of *P. sylvestris* showed the greatest response to heavy thinning (T60), in both unfavorable and favorable years, with higher sensitivity to the thinning treatment than *P. nigra* (Fig. 4).

3.3. Post-drought growth resilience indices

The growth resistance (CR_T) to drought before thinning (1995 and

2005) did not show significant differences between years. However, thinning increased the CR_T , growth recovery (CR_S), and growth resilience (CR_C) in relation to the severe 2012 drought (Fig. 5 and Table 3). *Pinus sylvestris* showed the highest increase after thinning, the lowest values occurring in the unthinned stands (Fig. 5), but significant differences among the treatments were found for CR_T ($F = 8.70$; $P < 0.001$) and CR_S ($F = 12.14$; $P < 0.001$). In contrast, after thinning, *P. nigra* showed lower CR_T and CR_S values than *P. sylvestris* (Table S1; Fig. 5), the values of all three indices increasing significantly with the intensity of the thinning (CR_T $F = 15.60$; $P < 0.001$; CR_C $F = 2.91$; $P < 0.05$; CR_S $F = 20.43$; $P < 0.001$).

4. Discussion

The growth and iWUE of the *P. sylvestris* and *P. nigra* stands varied significantly under the different thinning treatments. Our data suggest that the regulation of pine stocking will permit a more plastic response to drought through faster recovery of growth and increases in iWUE, particularly in the case of *P. nigra*. The variation in growth among the thinning treatments was linked to changes in iWUE.

Water availability is a major limitation to forest productivity in Mediterranean ecosystems (David et al., 2016). Therefore, changes in the water availability induced by reducing the competition between trees for water and nutrients in densely planted afforestations might be a major factor in the stability of drought-prone forests (Sánchez-Salguero et al., 2013). The experimental design of the thinning performed here contributes to novel strategies for adaptation to climate change focused on improving ecosystem resilience in the long-term for drought-prone plantations. A few studies have quantified the effects of thinning, by combining analyses of tree-rings stable isotopes and growth productivity, in drought-prone *P. sylvestris* and *P. nigra* forests (Martín-Benito et al., 2010; Sohn et al., 2016). In accordance with our hypothesis, our study focused on the effects of silvicultural treatment and provides evidences that intense thinning has the effect of reducing iWUE (assuming the assimilation rate remains constant). The use of stable C isotopes indicated that the iWUE of both *Pinus* species decreased when BAI increased. However, previous studies have shown

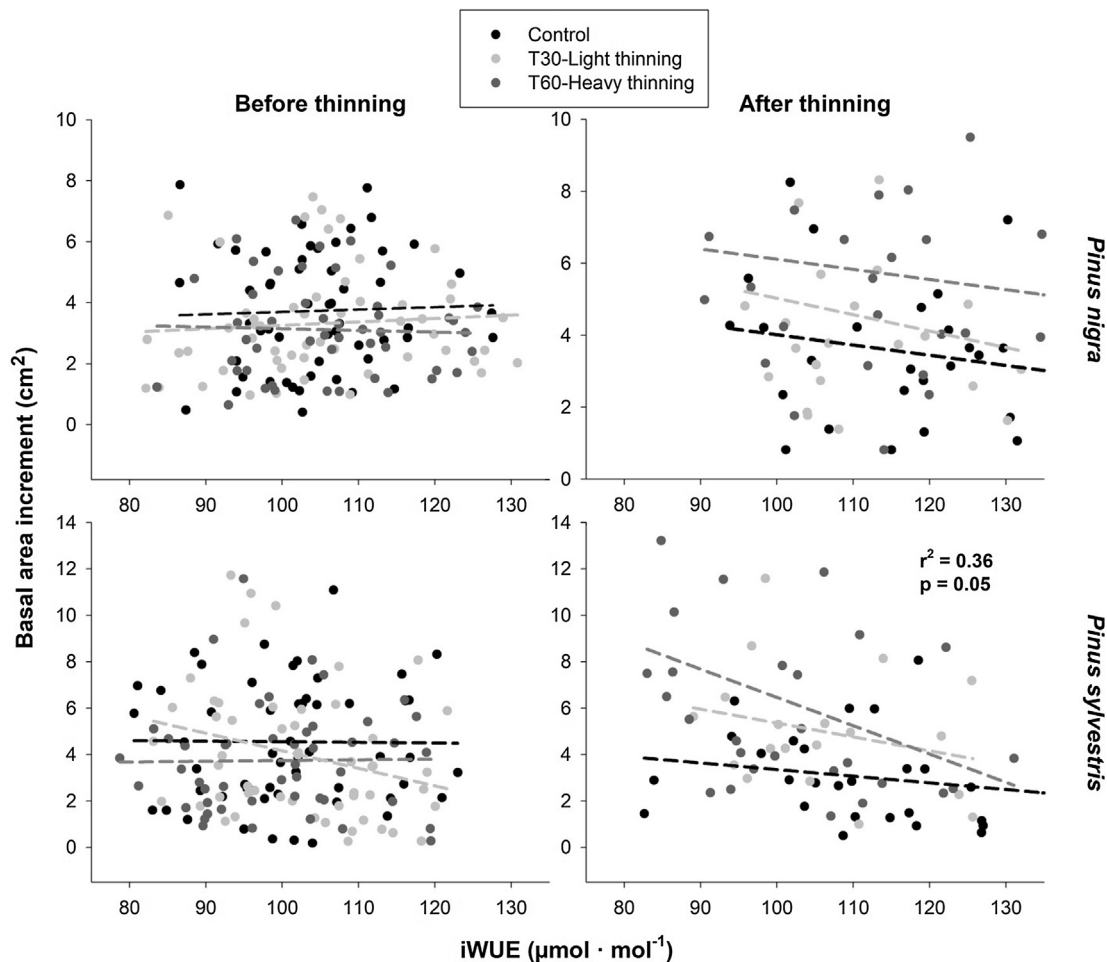


Fig. 3. Relationship between intrinsic water-use efficiency (iWUE) and basal area increment (BAI) of *Pinus nigra* and *Pinus sylvestris* before (1984–2009) and after (2010–2016) thinning (C, control or unthinned plots; T30, light thinning, 30% of basal area removed; T60, heavy thinning, 60% of basal area removed).

contradictory responses of iWUE to thinning treatments in *Pinus* species to explain physiological mechanisms underlying differences in growth patterns (Moreno-Gutiérrez et al., 2012a,b; Fernandes et al. 2016; Navarro-Cerrillo et al., 2016).

4.1. Effects of thinning on radial growth

In general, water availability is the major limiting factor for tree growth in xeric sites (Giuggiola et al., 2016). Here, the growth increment in both species was more pronounced in the heavily thinned stands (T60), in accordance with previous studies on several pine species (e.g., Mäkinen and Isomäki, 2004; Martín-Benito et al., 2010; Del Campo et al., 2014). However, the similar growth increments in the lightly (T30) and heavily (T60) thinned stands for *P. nigra* might be due to its higher drought tolerance, relative to *P. sylvestris*, in high-density stands (Sánchez-Salguero et al., 2012a,b).

Our results agree with other studies suggesting that *P. sylvestris* and *P. nigra* are drought-sensitive species susceptible to both rising temperatures and decreasing precipitation, but we found that the resilience of these species to drought is lower in unthinned than in heavily thinned stands. In addition, lower growth rates in dense and unthinned stands make these forests prone to drought-induced dieback and mortality (Sánchez-Salguero et al., 2012b).

The positive effect of thinning on tree growth has been reported for different *P. nigra* and *P. sylvestris* forests across Spain (e.g., Martín-Benito et al., 2010; Moreno-Fernández et al., 2014; del Río et al., 2017). Tree-level responses to the removal of competition are grounded on limiting-resources ecological theory (Ford et al., 2017). For trees

subjected to low competition the soil water content, soil-to-canopy hydraulic conductance, stomatal conductance, and photosynthetic rates are often higher than for trees subjected to high competition (Bréda et al., 2006). The growth increase and the reductions in water use efficiency (iWUE), for both species, after thinning (Fig. 3) indicate that water shortage due to competition limited the growth enhancement of these plantations (Moreno-Gutiérrez et al., 2012b). The differing behaviors of the thinned and control stands may be due to short-term effects of thinning (e.g. reduction of stand transpiration, interception of precipitation and competition, both aboveground and belowground), resulting in a soil water content increase (Bréda et al., 2006; Sohn et al., 2016). It is possible that the remaining trees had access to more water sources, as already shown in other thinning studies (see del Río et al., 2017 for a review). However, the long-term potential effects of thinning (e.g. increased water demand of exposed trees due to their enlarged foliage area, increased transpiration of the remaining trees, the development of understory vegetation) may reduce soil water availability because of an increased water demand of exposed trees having a greater area of foliage (Sohn et al., 2016).

However, the increase in soil temperature in thinned plots might have enhanced both evaporation and transpiration, amplifying the drought stress and making the trees more sensitive to the climate, compared to the trees located in closed, unthinned stands (Bréda et al., 2006). In turn, the management of the stand structure may be able to modulate such climate-related drivers (Sohn et al., 2016). Our results show that thinning represents a potential strategy for the minimization of climate change effects on drought-sensitive pine species, by improving the availability of resources to the remaining trees.

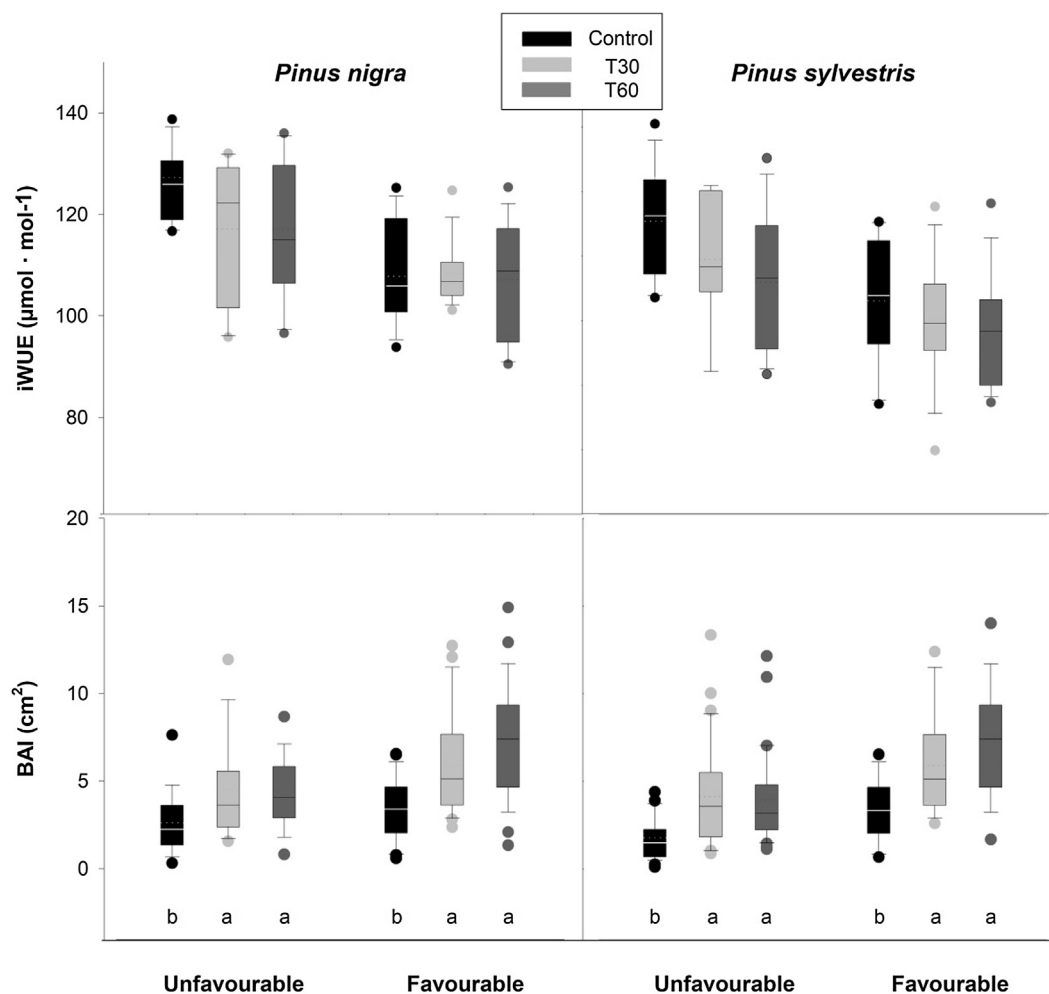


Fig. 4. Responses of intrinsic water use efficiency (iWUE) and basal area increment (BAI) for *Pinus nigra* and *Pinus sylvestris* for climatically unfavourable (dry) (1995, 2005, 2012) and favourable (wet) years (1993, 2002, 2013) considering different thinning treatments (C, control or unthinned plots; T30, light thinning, 30% of basal area removed; T60, heavy thinning, 60% of basal area removed). Different letters indicate significant differences ($P < 0.05$) between treatments within each climate condition.

Nevertheless, growth rates are affected not only by water supply and temperature, but also by nutrient limitation, microclimate acclimation, and reallocation of carbohydrates after thinning treatments controlling long-term acclimation to environmental conditions (Peñuelas et al., 2011). Previous studies have shown the positive effects of logging residues on the availability of nutrients for growth and leaf production (De las Heras et al., 2012). However, Forrester et al. (2005) found that the leaf nutrient content and foliar nutrient resorption efficiency decreased with tree age in plantations. These results suggest that the nutrient use efficiency of the remaining trees in thinned stands increases with rising resource availability (Matsushima and Chang, 2007).

4.2. Thinning as a tool to optimize the competition for water

The relative improvement of the supply of water and light caused by thinning determines its effects on iWUE. In general, thinning enhances WUE in light- (Martín-Benito et al., 2010) and water-limited environments (Moreno-Gutiérrez et al., 2011; Giuggiola et al., 2016).

After thinning, there was a negative correlation between BAI and iWUE, for both pine species and all treatments, indicating alterations in either the photosynthetic rate or the stomatal conductance (Seibt et al., 2008). However, due to the similar slopes of the regression lines, this relationship was only marginally significant in *P. sylvestris* but it was not significant in *P. nigra* when comparing all thinning treatments

(Fig. 3). These findings are consistent with an expected growth decrease in a context of climatic stress, due to limitation of photosynthesis, thus resulting in a reduction of CO_2 uptake (Granda et al., 2014). In addition, the negative relationship between BAI and iWUE after thinning suggests that increasing iWUE over time may limit growth. Similar results have been reported for *P. sylvestris* (Voltas et al., 2013; Hereş et al., 2014) and *P. nigra* (Martín-Benito et al., 2010). However, our results showed a nonsignificant effect of thinning on WUEi in the short term, in concordance with previous studies for Aleppo pine (Moreno-Gutiérrez et al., 2012b; Fernandes et al., 2016) and black pine (Martín-Benito et al., 2010).

Trees subjected to low competition often maintain more favorable water status and rates of gas-exchange and photosynthesis than trees subjected to highly competitive stress (Bréda et al., 2006). Trees subjected to low competition are more sensitive to water availability, likely because they allocate more resources to above and below-ground growth (Gleason et al., 2017). We found that iWUE was significantly lower in the thinned stands, for both species, suggesting that thinning reduced drought stress as a consequence of delayed stomatal closure or reduced photosynthesis rates under drought. However, since growth increased, the most likely explanation is that the stomatal conductance rates increased (Fernandes et al., 2016). Previous studies showed similar responses of iWUE to thinning treatments for several Mediterranean pine species, suggesting a more conservative water use strategy at high densities for these species (Martín-Benito et al., 2010, 2017;

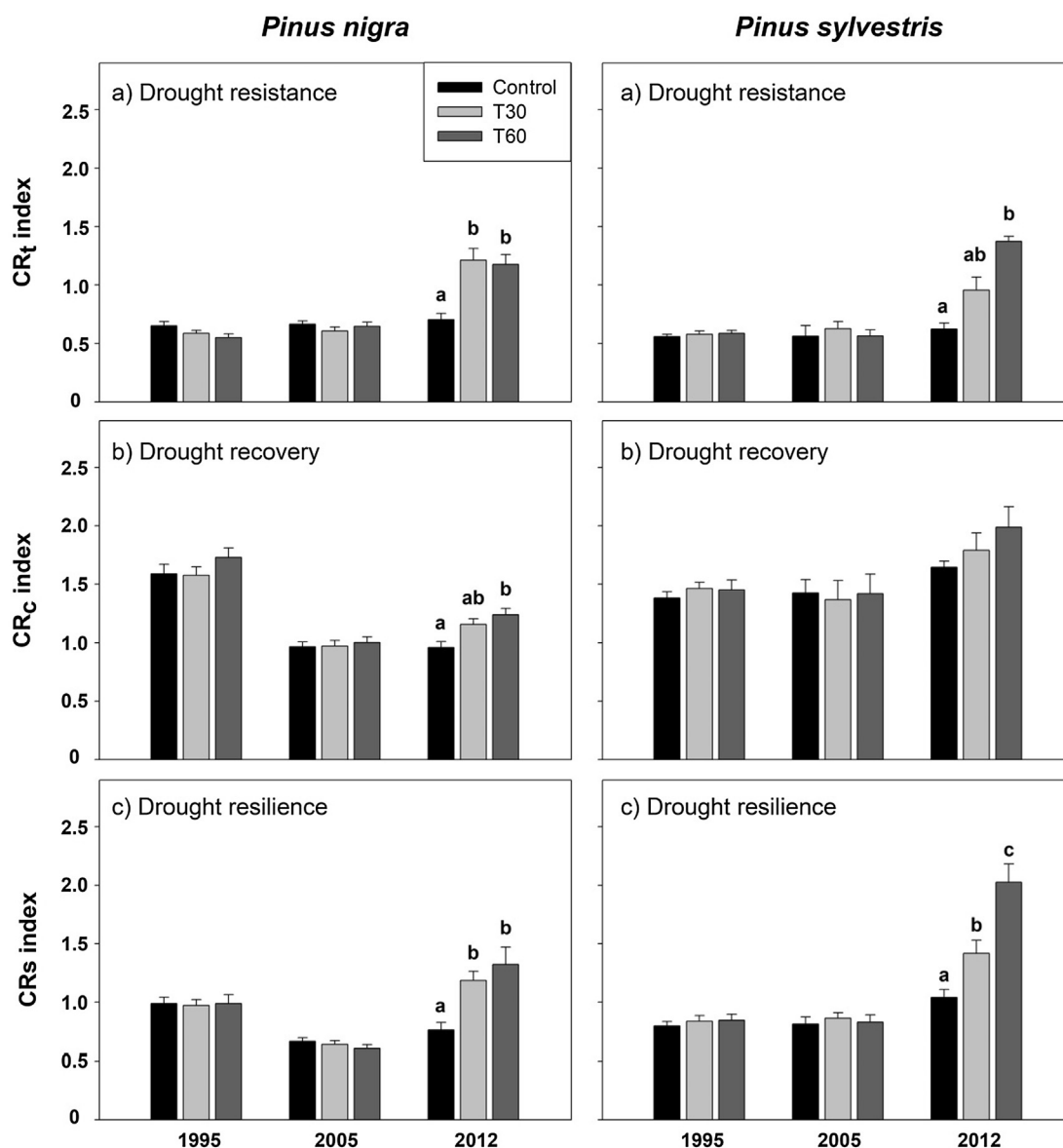


Fig. 5. Resistance (CR_T), resilience (CR_C), and recovery (CR_R) growth indices calculated for *Pinus sylvestris* and *P. nigra* during the extreme dry years (see Fig. 1) before (1995 and 2005) and after (2012) the thinning treatment (C-Control-0%, T30, moderate thinning or 30% of basal area removed; T60, heavy thinning or 60% of basal area removed). Different letters indicate significant differences ($P < 0.05$) between treatments within each year. Values are means \pm SD. See Table S1. The thinning was carried out in 2010.

Moreno-Gutiérrez et al., 2012a,b). The response was more pronounced in *P. nigra*, the species more tolerant of drought, a possible consequence of a hydraulic strategy that led to a greater overall assimilation capacity through better stomatal control of water losses than in *P. sylvestris* (Martínez-Vilalta et al., 2012; Fernández-de-Uña et al., 2015). The heavy thinning (T60) resulted in the highest growth rates for both species, although the change in the iWUE values induced by thinning was greater in *P. sylvestris* than in *P. nigra*, which only showed a slight increase in iWUE. Similar results were reported by Eilmann et al. (2010) for a *P. sylvestris* forest showing dieback. Thus, water shortage seems to be the main cause of the greater growth reductions and elevated mortality rates of *P. sylvestris* stands in these drought-prone plantations (Sánchez-Salguero et al., 2012b).

The water-spending behavior of *P. sylvestris* – leading to higher photosynthetic and growth rates under favorable environmental conditions, as reflected in its growth trajectory – also has risks attached, since increasing water loss might represent a threat to plant survival in dry years. This contrasting response might also imply different levels of

resistance to xylem embolism and a higher risk of hydraulic failure in stands according to the thinning intensity. Increases in radial growth, and expansion of conductive elements, lead to major gains in hydraulic conductivity (Domec and Gartner, 2002) but may also imply higher vulnerability to hydraulic failure (McDowell, 2011). Meanwhile, continued metabolic demand for carbohydrates and increasing respiration rates, linked to a rise in temperature, increase the likelihood of carbon starvation (Adams et al., 2009).

Our results suggest that the improved secondary growth of the remaining trees within the thinned stands may rely on carbon sources stored as reserves, decreasing their vulnerability (McDowell et al., 2008). This hypothesized allocation of carbon to secondary growth as a response to reduced competition may be linked to fall and winter photosynthesis prior to the growing season; the greater availability of light caused by thinning may allow replacement of the photosynthates used in growth processes (Lechuga et al., 2017).

4.3. Thinning modifies resilience to drought

The increased frequency of extreme drought events observed in recent decades is the most likely factor that has led to recent and widespread defoliation, dieback, and tree mortality in pine plantations in southern Spain and elsewhere (Navarro Cerrillo et al., 2007; Carnicer et al., 2011; Sánchez-Salguero et al., 2012a,b). These events might lead to chronic stress and ultimately to the severe decline of forest productivity and tree death (Petrucco et al., 2017). Despite small differences in the resilience indices prior to thinning, the *P. sylvestris* and *P. nigra* stands showed strong growth responses to drought after thinning, with the control plots showing the lowest values of growth resistance, recovery, and resilience. The forests studied here also showed a marked growth reduction during the droughts occurring before (1995, 2005) and after (2012) the thinning treatments. However, while all individuals were able to recover their pre-drought growth levels in 2012, individuals in thinned stands showed better growth improvement afterwards. This evidences the greater recovery capacity of thinned stands under xeric conditions (Millar et al., 2007). However, this short-term growth response may not imply a long-term reduction in vulnerability (see, for instance, Lechuga et al., 2017).

In particular, *P. sylvestris* showed great sensitivity to thinning in terms of its resistance (CR_r) and resilience (CR_c), independently of the treatment intensity, although its recovery (CR_s) was less responsive. For *P. nigra*, the resilience capacity and growth were sensitive to the thinning intensity. This is in line with the long-term trend of growth, which showed a partial recovery after 2012 but not after previous droughts (1995, 2005) (Sánchez-Salguero et al., 2013). This also agrees with previous anatomical studies (e.g., Pellizzari et al., 2016; Petrucco et al., 2017) in which wider cells with thinner walls were found in *P. sylvestris* trees that were constantly exposed to drought; this risky strategy was a response to the need to optimize water uptake efficiency under water shortage.

The increase in resilience observed after thinning was expected, although the persistent growth reduction during the following years suggests that the carbon pools and/or carbon uptake capacity were not fully restored (Hartmann et al., 2015). Although single extreme droughts had a short-term and reversible effect on tree growth (e.g., 1995), multi-year droughts induced prolonged periods of growth suppression and enhanced the long-term risk of tree death (Sánchez-Salguero et al., 2012a; Camarero et al., 2015). These responses suggest that the physiological mechanisms triggered by thinning, and influenced by the climatic conditions, are indeed similar for both pine species studied here.

5. Conclusions

One of the main problems faced by forest plantations in southern Europe, and in other areas of the Mediterranean Basin, is the mortality processes related to climate change, and in particular to severe drought. Different authors have highlighted the importance of thinning in the adaptation of this type of artificial forest to the new climatic conditions. In this work, we contribute to this field with a new example of the advantages provided by this silvicultural strategy. Water shortage, linked to recurrent droughts, together with high competition among trees, negatively affected growth and increased iWUE, which potentially explains the dieback of some pine plantations. However, for plantations of species at the limit of their distribution, as in the case of Scot Pine and black pine in the south of the Iberian Peninsula, it is possible that thinning benefits are simply a transitory solution that partially mitigates the effect of the drought but does not prevent the disappearance of these plantations in the medium and long term. However, our results show two important findings. Firstly, the differing responses of Scots pine and black pine imply the need for different thinning strategies. Trees from thinned stands showed a more plastic response to drought, recovering their growth more quickly and

increasing iWUE, particularly in the case of *P. nigra*. Secondly, this type of silvicultural practice is convenient, although its effect is limited, since it allows progressive adaptation of the forest structure, particularly at low or very low densities, in an economically viable manner, avoiding sudden mortality processes that produce irreversible damage and strong social alarm. Growth in dense, unthinned stands experiences more inertia in response to climate variation than that in thinned stands, and this may explain the higher vulnerability and the lower resilience to drought in *P. sylvestris*, relative to *P. nigra*. With these findings, we evidence the vulnerability of densely planted Mediterranean pines to the forecasted warmer and drier conditions. Therefore, this work is a new contribution that shows the need for forest managers to take urgent measures that will help drought-sensitive Mediterranean pine plantations adapt to the risks associated with climate warming, thereby avoiding their irreversible loss while other actions should be performed to change the species composition of those plantations to maintain ecosystem function and services in the long-term

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.006>.

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