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3

4 **Is thinning an alternative when trees could die in response to**
5 **drought? The case of planted *Pinus nigra* and *P. sylvestris* stands**
6 **in southern Spain**

7

8 Rafael M. NAVARRO-CERRILLO^{1*†}, Raúl SÁNCHEZ-SALGUERO^{2†}, Carlos
9 RODRIGUEZ¹, Joaquín DUQUE LAZO¹, José M MORENO-ROJAS³, Guillermo
10 PALACIOS-RODRIGUEZ¹, J. Julio CAMARERO⁴

11 ¹*Depto. Ingeniería Forestal, Laboratorio de Dendrocronología. DendrodatLab- ERSAF.*
12 *Universidad de Córdoba. Campus de Rabanales, Crta. IV, km. 396, E-14071 Córdoba. Spain. E-*
13 *mail: rmnavarro@uco.es*

14 ²*Depto. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, 41013 Sevilla,*
15 *Spain E-mail: rsanchez@upo.es*

16 ³*Area de Tecnología, Poscosecha e Industria Agroalimentaria. Instituto de Investigación y*
17 *Formación Agraria y Pesquera (IFAPA). Centro "Alameda del Obispo". Avda. Menéndez Pidal,*
18 *s/n. E-14004. Córdoba, Spain. E-mail: josem.moreno.rojas@juntadeandalucia.es*

19 ⁴*Instituto Pirenaico de Ecología (IPE-CSIC), 50192 Zaragoza, Spain E-mail:*
20 *jjcamarero@ipe.csic.es*

21 † Co-first authors.

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23 Running-title: *Pinus nigra* and *P. sylvestris* response to drought and thinning

24 *To whom correspondence may be addressed.

25 *Rafael M. Navarro-Cerrillo*

26 *University of Cordoba*

27 *Crta. IV, km. 396, 14071*

28 *Córdoba, Spain*

29 *E-mail: rmnavarro@uco.es Phone: +34 957218657*

31 **Abstract**

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

54 **Key words:** Climate change, Mediterranean climate; forest dieback; drought
55 stress, pine plantation management; thinning.

57 **1. Introduction**

58 Extensive pine afforestations were highly relevant in the Mediterranean Basin
59 during the 20th century regarding soil and water protection, but also from
60 socioeconomic points of view (Del Lungo and Carle, 2006). For instance, ca. 3.5
61 million ha were reforested with pine species in Spain from the 1940s onwards,
62 which represents 54.5% of the national area covered by conifers (Pemán et al.,
63 2017). These pine plantations are characterized mainly by being coetaneous and
64 having a low degree of structural diversification and genetic composition, forming
65 pure stands, often without an understory (Pausas et al., 2004). In general, these
66 pine plantations are managed by protective thinning every 20–25 years. However,
67 forest decline and tree mortality have changed the aims of silviculture in such pine
68 plantations; their management as a simple source of wood products has changed
69 to sustainable and adaptive management in the face of climate change (Ameztegui
70 et al., 2017). Drought induced forest dieback has been reported in many conifer
71 forests in southern Europe (Linares et al., 2010; Sánchez-Salguero et al., 2012a,
72 2013; Camarero et al., 2015). Although the increasing impact of warmer and drier
73 conditions is the main driver of these dieback episodes (Allen et al., 2010), land-
74 use changes (i.e. forest expansion and lack of management) and their role in
75 drought stress have also been widely recognized as additional factors (Martinez-
76 Vilalta et al., 2012; Sánchez-Salguero et al., 2013; Jump et al., 2017).

77 The effects of the increase in the frequency and intensity of severe
78 droughts in the Mediterranean Basin together with climate warming (Giorgi and
79 Lionello, 2008) can be aggravated by a lack of management, which can increase

80 the stand density and the competition between trees (Sánchez-Salguero et al.,
81 2015a). Since forest dieback can cause substantial economic and environmental
82 problems, managers have recently sought effective strategies to minimize dieback
83 impacts, including tree mortality (Puettmann, 2011; Sohn et al., 2016). One
84 alternative is to increase ecosystem resilience, understood as the capacity of an
85 ecosystem to conserve the structure and functionality prior to the extreme event
86 (i.e., drought) after some disturbance (Scheffer et al., 2001). Thinning treatments
87 have been shown to reduce long-term stress caused by competition for water, and
88 to reduce the vulnerability, and increase the resilience and resistance, of trees to
89 drought (Martín-Benito et al., 2010; Linares et al., 2011; Sánchez-Salguero et al.,
90 2012b, 2013; Navarro-Cerrillo et al., 2016; Lechuga et al., 2017). However, there
91 are no previous studies assessing the potential of thinning regarding improving
92 tree performance during dieback.

93 To address this question, we selected the southernmost European limit of
94 Scots pine (*Pinus sylvestris* L.) and black pine (*P. nigra* Arnold.), in southern
95 Spain, where forest dieback processes, affecting plantations, have been observed
96 since the early 2000s (Sánchez-Salguero et al., 2012a). The lack of silviculture to
97 reduce post-planting competition in these plantations has resulted in high-density
98 stands vulnerable to drought-induced dieback and mortality (Martín-Benito et al.,
99 2010; Sánchez-Salguero et al., 2013). In these plantations, thinning could enhance
100 tree growth by decreasing the competition for water and nutrients, increasing the
101 photosynthetic rates, and improving water use and carbon uptake (Bréda et al.,
102 2006; McDowell, 2011). In addition, thinning alters the microclimatic conditions

103 and consequently the forest water fluxes (Ma et al., 2010). Stable isotopes ($\delta^{13}\text{C}$)
104 have been widely used to understand plant–environment interactions in the
105 response to thinning (Di Matteo et al., 2017), since their measurement in tree-
106 rings is a useful proxy that enables the inference of changes in the intrinsic water-
107 use efficiency (iWUE), owing to the strong link between isotopic composition and
108 water availability (McCarroll and Loader, 2004; Cernusak et al., 2013). Previous
109 research has provided insights into the potential response of growth and iWUE in
110 Mediterranean environments (del Río et al., 2008; Moreno-Gutierrez et al., 2012a;
111 Fernandes et al., 2016), although the results are contradictory. However, little is
112 known about the potential benefits of silviculture for pine plantations under severe
113 drought stress, in areas close to the limit of the geographical distribution of the
114 pine species. Dendrochronological studies suggest that thinning may improve
115 radial growth and vigor over a wide range of stand and site conditions, so it can be
116 expected that this will also hold true for semi-arid sites prone to drought-triggered
117 dieback (Fernandes et al., 2016). Therefore, thinning is one of the main forest
118 management tools used to minimize forest drought vulnerability (McDowell et al.,
119 2006). However, short-term and long-term thinning trials in xeric forests are rare
120 and few empirical studies have evaluated the effectiveness of this approach with
121 regard to the drought response of Mediterranean pines (but see Fernandes et al.,
122 2016). In particular, Scots pine and black pine forests in southern Europe are
123 expected to suffer severe water limitations and increasing temperatures (Giorgi
124 and Lionello, 2008), and this is already leading to serious mortality processes in
125 this type of forest (Sánchez-Salguero et al., 2012a). Therefore, it is necessary to

126 establish experimental trials in areas close to the rear edge limit of these species,
127 to develop silvicultural alternatives that allow urgent decisions to be taken in the
128 field by forest managers (del Río et al., 2017).

129 Here, we have used dendrochronology and carbon isotopes ($\delta^{13}\text{C}$, see
130 Cernusak and English, 2015; Di Matteo et al., 2017) to understand the growth and
131 functional responses (changes in iWUE) of high-density planted pine forests to
132 thinning in drought-prone areas of southern Spain. This approach is useful to
133 evaluate whether thinning is an efficient management tool to make Mediterranean
134 pine plantations less vulnerable to drought-induced dieback (Sánchez-Salguero et
135 al., 2012a; Sohn et al. 2016). For this study, we evaluated the effects of distinct
136 thinning intensities - 0% (Control or unthinned stands), 30% (T30, 30% of basal
137 area removed), and 60% (T60, 60% of basal area removed) - on the radial growth
138 and iWUE of *P. nigra* and *P. sylvestris* plantations with drought-induced forest
139 dieback symptoms (see Navarro-Cerrillo et al., 2006; Sánchez-Salguero et al.,
140 2012a, b). Our aims were: (1) to assess the growth and iWUE responses to
141 different thinning intensities, (2) to evaluate the effects of thinning on post-
142 drought resilience, and (3) to propose new, adaptive silviculture measures for
143 these drought-prone Mediterranean pine plantations, based on the use of thinning
144 to mitigate the effects of extreme droughts. We expected heavy thinning to
145 produce stands that were more resilient to drought, particularly for the more-
146 drought-tolerant species (*P. nigra*). The results may offer new insights into the
147 interactive effects of drought and competition on post-drought resilience, as well
148 as guidelines for an adaptive silviculture in the management of even-aged pine

149 stands. The data will also allow assessment of the long-term effectiveness of
150 thinning in the mitigation of current climate change impacts in drought-prone
151 areas.

152

153 **2. Materials and Methods**

154 *2.1. Study area*

155 The study area is located in the Sierra de los Filabres (hereafter Filabres, southern
156 Spain, 36° 43' N, 4° 58' W; see Fig. 1a), a mountainous area situated on east-
157 facing slopes and ranging in elevation from 1600 to 2186 m.a.s.l. The climate in
158 the study area is continental thermo-Mediterranean with average annual rainfall of
159 320 mm, a mean temperature of 13.1 °C at 1000 m.a.s.l., and hot (mean maximum
160 summer temperature is 26.3 °C) and dry summers (summer precipitation is 8.2
161 mm) (data correspond to Baza station, located 32 km from the study site, 37° 33'
162 52" N, 02° 46' 03" W, 814 m.a.s.l.) (Sánchez-Salguero et al., 2010, 2012a). A
163 significant increase in the annual mean temperature during the 20th century (Fig.
164 1b) has been found in the study area, together with a significant reduction in
165 annual precipitation. Wet periods (1950s, 1970s) have alternated with very dry
166 periods (1980s, 1990-1994, 1999, 2005, 2012). Additionally, a long-term negative
167 trend was detected in the Standardized Precipitation Evapotranspiration Index
168 (SPEI; Vicente-Serrano et al., 2010), with increasing aridity during the second
169 half of the 20th century as compared with the first half (Fig. 1b). The geological
170 substrate is composed of siliceous rock with quartz micaschists, the most
171 abundant soil types in the plantations being entisols and inceptisols. In both study

172 sites, the slopes are steep (~25-35%). At the start of the study, the sites were
173 covered by a 40-year-old mixed pine afforestation of *P. nigra* and *P. sylvestris*
174 (Table 1). The forest stands contained sparse evergreen shrubs (*Adenocarpus*
175 *decorticans* Boiss. *Cistus laurifolius* L.). Pine mortality was very high in this area,
176 about 10,882 ha showing moderate or severe damage during 2002–2006
177 (Navarro-Cerrillo et al., 2006). The study stands were planted in the 1970s using
178 seeds from southern and central Spain. Afterwards, they were managed by
179 thinning from below, which involved the harvesting of suppressed trees while the
180 dominant trees were retained for future natural seeding (Serrada et al., 2008).

181

182 2.2. Experimental design

183 In June 2010, a thinning experiment was performed. A randomized complete
184 block design with three blocks and three treatments was established (Quinn and
185 Keough, 2002). Plots and blocks were located next to each other to make sure that
186 the microclimatic and edaphic characters were analogous. The thinning treatments
187 were carried out on nine blocks -each being 20 × 30 m with a 15-m-wide buffer
188 strip around each block- randomly located in areas with slopes lower than 20%
189 and a northwest exposure, considering the similarity of the canopy structural
190 parameters, and with analogous microclimatic and edaphic characters. A factorial
191 randomized block design was used, considering three thinning intensity treatments
192 –unthinned or control (C), intermediate thinning (T30) with removal of 30% of
193 the initial basal area of the pines (leaving a tree basal area of 10.3 m² ha⁻¹), and
194 heavy thinning (T60) with removal of 60% of the initial basal area (leaving a tree

195 basal area of 5.9 m² ha⁻¹)- in three replicate blocks (Table 1). The thinning
196 treatments were applied for the primary purpose of removing overtopped, small-
197 sized, dying, or suppressed trees, to promote future development under natural
198 conditions with additional consideration given to uniform spacing. Thinning
199 residues, such as slash, and stumps were removed from the treatment plots, and all
200 remaining trees were tagged. Before thinning, the diameter at breast height (dbh,
201 cm, measured at 1.3 m above ground level) and total height (H, m) were measured
202 with a caliper (Haglöf Mantax, Sweden) and Vertex III hypsometer (Haglöf
203 Sweden), respectively (Table 1). No significant differences in tree density existed
204 among the treatments within each plot before the 2010 thinning (one-way
205 ANOVA: $F = 3.29$, $P = 0.108$, $F = 0.168$, $P = 0.849$, *P. nigra* and *P. sylvestris*,
206 respectively).

207

208 *2.3. Dendrochronological analysis and climate-growth relationships*

209 Post-thinning sampling and field measurements were conducted in November
210 2016, six years after the thinning treatments. In each plot, all trees were measured
211 (dbh, H), and five dominant trees with dbh greater than 15 cm were cored at 1.3 m
212 with a Pressler increment borer. Two cores were sampled per tree, in the direction
213 perpendicular to the maximum slope (Fritts, 2001). The cores were air dried,
214 sanded with papers of progressively finer grain until the tree-rings were clearly
215 visible, and then visually cross-dated. Individual tree-ring width series were
216 measured to the nearest 0.01 mm with a LINTAB measuring device (Rinntech,
217 Heidelberg, Germany). The cross-dating quality was verified using the software

218 COFECHA (Holmes 1983), by checking the consistency of the different ring-
219 width series among trees coexisting within the same plots. To assess the quality of
220 the tree-ring width series, several dendrochronological statistics (Fritts, 2001)
221 were calculated, considering the common interval after thinning, 1996-2016
222 (Table 1): first-order autocorrelation of raw width data (AC), mean sensitivity
223 (MS) of indexed growth values, mean correlation between trees (Rbt), and the
224 expressed population signal (EPS) - which measures the statistical quality of the
225 mean site chronology as compared with a perfect, infinitely replicated chronology
226 (Wigley et al., 1987) (Table 2). Tree age at 1.3 m was also estimated by counting
227 the number of rings in the core, as far as the pith, or showing the innermost rings
228 according to their curvature.

229 The trend due to the geometrical constraint of adding a volume of wood to
230 a stem of increasing radius was corrected by converting tree-ring widths into basal
231 area increments (BAIs), using the formula $BAI = \pi (R^2_t - R^2_{t-1})$ where R is the
232 radius of the tree and t is the year of tree-ring formation (Biondi and Qaedan,
233 2008). The growth responses of individual species to thinning were evaluated with
234 annual series of BAI.

235

236 *2.4. Tree-ring isotopes analysis and intrinsic water use efficiency*

237 To assess the responses of the two pine species to thinning intensity and climate,
238 one core per tree was used for C isotope analysis, thereby providing a useful
239 estimation of the long-term effects of thinning on iWUE (McCarroll and Loader,
240 2004). We analyzed $\delta^{13}C$ in climatically contrasting years: unfavorable years (i.e.,

241 years with a combination of low precipitation and high temperatures: 1995, 2005,
242 2012) and favorable years (i.e., years with a combination of high precipitation and
243 moderate temperatures: 1993, 2003, 2013) (Fig. 1). The selected years included
244 periods before (1993, 1995, 2003, 2005) and after (2012, 2013) the thinning
245 treatments, to explore the effects of management on iWUE. Complete dated rings
246 (including both early and late wood) were carefully separated into sections
247 corresponding to specific growth years using a razor blade, under a
248 stereomicroscope. Samples were ground to a fine powder using a ball mill (Spex
249 5300, Metuchen, NJ, USA) and 400-600 μg of milled wood were weighed in tin
250 cups for carbon isotopes ($\delta^{13}\text{C}$) analysis. Isotope subsamples were combusted in
251 an elemental analyzer (Thermo Fisher, Germany) and the resulting gases were
252 analyzed in an isotope ratio mass spectrometer (IRMS; ThermoFisher Delta V
253 Advanced, Germany) located at the LISEEM laboratory (IFAPA, Cordoba,
254 Spain). The carbon isotope discrimination ($\delta^{13}\text{C}$; ‰ enrichment relative to the
255 international standard, Vienna Pee Dee Belemnite) and the iWUE ($\mu\text{mol mol}^{-1}$)
256 were calculated according to standard methodologies and formulae (see Farquhar
257 and Richards, 1984 for details).

258

259 *2.5. Climatic data*

260 The availability of data from a weather station close to the study site is limited
261 due to the length of the observation period and gaps in local climatic data (Calar
262 Alto meteorological station, 37° 13' 25" N, 02° 32' 46" W; 2,168 m.a.s.l., which
263 covers the period 1990-2016, is located less than 3 km from the study area,

264 <http://www.caha.es/es/observaci%C3%B3n/meteorolog%C3%ADa>). Therefore,
265 we used 0.25°-gridded monthly data for the mean temperature and total
266 precipitation, available for the period 1954–2016 from the E-OBS climate data set
267 (Haylock et al., 2008). We obtained the July SPEI indices at scales of 6 (SPEI₆)
268 and 12 months (SPEI₁₂), to evaluate drought severity (Vicente-Serrano et al.,
269 2010). Negative SPEI values correspond to dry conditions and would be related to
270 a decline in growth, whereas positive SPEI values indicate wet conditions, which
271 should correspond to enhanced growth (Pasho et al., 2010). The SPEI indices
272 were used to select the four most intense droughts in the study area for the period
273 1975-2016 (see Fig. 1).

274

275 2.6. Growth resilience indices

276 To quantify the response of tree growth to selected extreme droughts before
277 (1995, 2005) and after (2012) the thinning treatments, three resilience indices
278 (CR) were calculated for each species, using BAI data and following Lloret et al.
279 (2011):

- 280 • The resistance index (CR_T), which quantifies the growth of the tree
281 during the drought (D_r) with respect to the previous growth ($PreD_r$):

$$282 \quad CR_T = D_r / PreD_r \quad (1)$$

- 283 • The recovery index (CR_S), which is the response of the growth after the
284 drought ($PostD_r$), compared with D_r :

$$285 \quad CR_S = PostD_r / D_r \quad (2)$$

286 • The resilience index (CR_C), which is the ratio of the growth values
287 measured after (PostD_r) and before (PreD_r) the drought:

$$288 \quad CR_C = \text{PostD}_r / \text{PreD}_r \quad (3)$$

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

293

294 *2.7. Statistical analyses*

295 To understand how the tree growth responses to climate were influenced by the
296 thinning treatments, the unit of replication for each treatment was the block (n =
297 3), considering two thinning intensities (T30 and T60) and a control (C) for each
298 pine species. Pairwise comparisons of the treatments were made using the Tukey-
299 Kramer multiple comparison test. For statistical analysis, the BAI and iWUE
300 measurements were examined for normality and homoscedasticity; when the
301 variables were not normal, the data were normalized using a Box-Cox
302 transformation. The relationships between BAI and iWUE were explored by
303 linear regressions. For calculation of the BAI trends, the analyses were performed
304 on log-transformed values to normalize the variable. To evaluate the short-term
305 responses of BAI to thinning, we applied a repeated measures analysis of variance
306 (one-way ANOVA), selecting periods of equal length, defined as pre-treatment
307 (1984–2009) and post-treatment (2010–2016). Then, we calculated the mean BAI
308 series for these periods, which were used as within-subjects factors (Table 3).

309 The differences among the three resilience indices (CR_T , CR_S , and CR_C) calculated
310 for the selected droughts (1995, 2005, and 2012) and among the values of growth
311 (mean BAI data) for the period 1996-2016 (BAI_{20}) were compared using analyses
312 of variance (ANOVAs). Prior to statistical analysis, we examined all the resilience
313 indices for normality and homoscedasticity. When the variables were not normal,
314 the data were subjected to a Box-Cox transformation. Differences among the
315 treatments were considered significant at a level of $P = 0.05$. The dplR package
316 was used to calculate tree-ring statistics and all statistical analyses were
317 performed using the R software, version 3.4.0. (R Core Development Team,
318 2018).

319

320 **3. Results**

321 *3.1. Radial growth and $iWUE$ responses to thinning*

322 The growth patterns were similar for both pine species and all thinning intensities,
323 and they were characterized by noticeable growth reductions in dry periods (1990-
324 1995, 2005, and 2012) and growth increases during wet periods (1993, 1997, and
325 2013; see Fig. 2). The lowest annual growth rates (ca. $3.0 \text{ cm}^2 \text{ year}^{-1}$) occurred in
326 the driest years (2012 and 2016). After thinning, BAI recovered in the stands at
327 both thinning intensities, but faster in T60 stands (the mean BAI values for the
328 2009-2016 period were 3.7 and $4.8 \text{ cm}^2 \text{ year}^{-1}$ in *P. nigra* and *P. sylvestris*,
329 respectively) than in T30 stands (the mean BAI values for the 2009-2016 period
330 were 3.7 and $4.5 \text{ cm}^2 \text{ year}^{-1}$, respectively). The thinning effect on growth seems to

331 have been transitory since *P. sylvestris* trees from the C and T30 stands showed
332 similar BAI values (ca. 2.0 cm² year⁻¹).

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

339 During the 1980-2016 period, *P. nigra* showed the highest average BAI,
340 both before (4.69 cm² year⁻¹) and after (4.29 cm² year⁻¹) the 2010 thinning, with
341 the BAI values being lowest, significantly so ($P < 0.001$), in the control plot (2.64
342 cm² year⁻¹) and increasing as thinning intensity increased (Table 3; Fig. 2). In
343 contrast, *P. sylvestris* had the lowest BAI values before (3.69 cm² year⁻¹) and after
344 (4.21 cm² year⁻¹) thinning, with significant differences in BAI among thinning
345 intensities ($P < 0.001$) (Table 3). The post-thinning BAI values were significantly
346 higher than the pre-thinning values, for both species (data not included).

347 The iWUE increased significantly after thinning, for both species,
348 although *P. sylvestris* experienced a relative increase (+9.5%) that was
349 significantly higher ($P < 0.05$, Fig. 2) than for *P. nigra* (+4.2%, Fig. 2). *Pinus*
350 *sylvestris* showed the highest iWUE values before (104.51 μmol mol⁻¹) and after
351 (114.49 μmol mol⁻¹) thinning, with the lowest values occurring in the T30 stands
352 (Table 3; Fig. 2). In contrast, *P. nigra* showed the lowest values before (100.54
353 μmol mol⁻¹) and after (104.77 μmol mol⁻¹) thinning, with iWUE decreasing as

354 thinning intensity increased (Table 3, Fig. 2). After thinning, there were
355 significant differences in the iWUE values between the two species ($F = 1.20$; $P <$
356 0.001). In addition, the values differed significantly among the treatments for *P.*
357 *sylvestris* ($F = 3.44$; $P < 0.05$), but not for *P. nigra* ($F = 0.84$; $P = 0.43$).

358

359 3.2. Relationships between iWUE and BAI

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

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

377 showed the greatest response to heavy thinning (T60), in both unfavorable and
378 favorable years, with higher sensitivity to the thinning treatment than *P. nigra*
379 (Fig. 4).

380

381 3.3. Post-drought growth resilience indices

382 The growth resistance (CR_T) to drought before thinning (1995 and 2005) did not
383 show significant differences between years. However, thinning increased the CR_T ,
384 growth recovery (CR_S), and growth resilience (CR_C) in relation to the severe 2012
385 drought (Fig. 5 and Table 3). *Pinus sylvestris* showed the highest increase after
386 thinning, the lowest values occurring in the unthinned stands (Fig. 5), but
387 significant differences among the treatments were found for CR_T ($F = 8.70$; $P <$
388 0.001) and CR_S ($F = 12.14$; $P < 0.001$). In contrast, after thinning, *P. nigra*
389 showed lower CR_T and CR_S values than *P. sylvestris* (Table 4; Fig. 5), the values
390 of all three indices increasing significantly with the intensity of the thinning (CR_T
391 $F = 15.60$; $P < 0.001$; CR_C $F = 2.91$; $P < 0.05$; CR_S $F = 20.43$; $P < 0.001$).

392

393 4. Discussion

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

400 Water availability is a major limitation to forest productivity in
401 Mediterranean ecosystems (David et al., 2016). Therefore, changes in the water
402 availability induced by reducing the competition between trees for water and
403 nutrients in densely planted afforestations might be a major factor in the stability
404 of drought-prone forests (Sánchez-Salguero et al., 2013). The experimental design
405 of the thinning performed here contributes to novel strategies for adaptation to
406 climate change focused on improving ecosystem resilience in the long-term for
407 drought-prone plantations. A few studies have quantified the effects of thinning,
408 by combining analyses of tree-rings stable isotopes and growth productivity, in
409 drought-prone *P. sylvestris* and *P. nigra* forests (Martín-Benito et al., 2010; Song
410 et al., 2016). In accordance with our hypothesis, our study focused on the effects
411 of silvicultural treatment and provides evidences that intense thinning has the
412 effect of reducing iWUE (assuming the assimilation rate remains constant). The
413 use of stable C isotopes indicated that the iWUE of both *Pinus* species decreased
414 when BAI increased. However, previous studies have shown contradictory
415 responses of iWUE to thinning treatments in *Pinus* species to explain
416 physiological mechanisms underlying differences in growth patterns (Perez de Lis
417 et al. 2011; Moreno-Gutiérrez et al. 2012; Fernandes et al. 2016; Navarro-Cerrillo
418 et al., 2016).

419

420 *4.1. Effects of thinning on radial growth*

421 In general, water availability is the major limiting factor for tree growth in xeric
422 sites (Giuggiola et al., 2016). Here, the growth increment in both species was

423 more pronounced in the heavily thinned stands (T60), in accordance with previous
424 studies on several pine species (e.g., Mäkinen and Isomäki, 2004a, b; Martín-
425 Benito et al., 2010; Del Campo et al., 2014). However, the similar growth
426 increments in the lightly (T30) and heavily (T60) thinned stands for *P. nigra*
427 might be due to its higher drought tolerance, relative to *P. sylvestris*, in high-
428 density stands (Sánchez-Salguero et al., 2012a, 2012b).

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

435 The positive effect of thinning on tree growth has been reported for
436 different *P. nigra* and *P. sylvestris* forests across Spain (e.g., Martín-Benito et al.,
437 2010; Moreno-Fernández et al., 2014; del Río et al., 2017). Tree-level responses
438 to the removal of competition are grounded on limiting-resources ecological
439 theory (Ford et al., 2017). For trees subjected to low competition the soil water
440 content, soil-to-canopy hydraulic conductance, stomatal conductance, and
441 photosynthetic rates are often higher than for trees subjected to high competition
442 (Breda et al., 2006). The growth increase and the reductions in water use
443 efficiency (iWUE), for both species, after thinning (Fig. 3) indicate that water
444 shortage due to competition limited the growth enhancement of these plantations
445 (Moreno-Gutiérrez et al., 2012b). The differing behaviors of the thinned and

446 control stands may be due to short-term effects of thinning (e.g. reduction of stand
447 transpiration, interception of precipitation and competition, both aboveground and
448 belowground), resulting in a soil water content increase (Bréda et al., 2006; Sohn
449 et al., 2016). It is possible that the remaining trees had access to more water
450 sources, as already shown in other thinning studies (see del Río et al., 2017 for a
451 review). However, the long-term potential effects of thinning (e.g. increased water
452 demand of exposed trees due to their enlarged foliage area, increased transpiration
453 of the remaining trees, the development of understory vegetation) may reduce soil
454 water availability because of an increased water demand of exposed trees having a
455 greater area of foliage (Sohn et al., 2016).

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

464 Nevertheless, growth rates are affected not only by water supply and
465 temperature, but also by nutrient limitation, microclimate acclimation, and
466 reallocation of carbohydrates after thinning treatments controlling long-term
467 acclimation to environmental conditions (Peñuelas et al., 2011). Previous studies
468 have shown the positive effects of logging residues on the availability of nutrients

469 for growth and leaf production (De las Heras et al., 2012). However, Forrester et
470 al. (2005) found that the leaf nutrient content and foliar nutrient resorption
471 efficiency decreased with tree age in plantations. These results suggest that the
472 nutrient use efficiency of the remaining trees in thinned stands increases with
473 rising resource availability (Matsushima and Chang, 2007).

474

475 *4.2. Thinning as a tool to optimize the competition for water*

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

480 After thinning, there was a negative correlation between BAI and iWUE,
481 for both pine species and all treatments, indicating alterations in either the
482 photosynthetic rate or the stomatal conductance (Seibt et al., 2008). However, due
483 to the similar slopes of the regression lines, this relationship was only marginally
484 significant in *P. sylvestris* but it was not significant in *P. nigra* when comparing
485 all thinning treatments (Figure 3). These findings are consistent with an expected
486 growth decrease in a context of climatic stress, due to limitation of
487 photosynthesis, thus resulting in a reduction of CO₂ uptake (Granda et al. 2014).
488 In addition, the negative relationship between BAI and iWUE after thinning
489 suggests that increasing iWUE over time may limit growth. Similar results have
490 been reported for *P. sylvestris* (Voltas et al. 2013; Hereş et al. 2014) and *P. nigra*
491 (Martín-Benito et al., 2010). However, our results showed a nonsignificant effect

492 of thinning on WUE_i in the short term, in concordance with previous studies for
493 Aleppo pine (Moreno-Gutiérrez et al. 2012b; Fernandes et al 2016) and black pine
494 (Martín-Benito et al. 2010).

495 Trees subjected to low competition often maintain more favorable water
496 status and rates of gas-exchange and photosynthesis than trees subjected to highly
497 competitive stress (Bréda et al., 2006). Trees subjected to low competition are
498 more sensitive to water availability, likely because they allocate more resources to
499 above and below-ground growth (Gleason et al., 2017). We found that iWUE was
500 significantly lower in the thinned stands, for both species, suggesting that thinning
501 reduced drought stress as a consequence of delayed stomatal closure or reduced
502 photosynthesis rates under drought. However, since growth increased, the most
503 likely explanation is that the stomatal conductance rates increased (Fernandes et
504 al., 2016). Previous studies showed similar responses of iWUE to thinning
505 treatments for several Mediterranean pine species, suggesting a more conservative
506 water use strategy at high densities for these species (Martín-Benito et al., 2010,
507 2017; Moreno-Gutiérrez et al. 2012a, b). The response was more pronounced in *P.*
508 *nigra*, the species more tolerant of drought, a possible consequence of a hydraulic
509 strategy that led to a greater overall assimilation capacity through better stomatal
510 control of water losses than in *P. sylvestris* (Martinez-Vilalta et al., 2012;
511 Fernandez-de-Uña et al., 2015). The heavy thinning (T60) resulted in the highest
512 growth rates for both species, although the change in the iWUE values induced by
513 thinning was greater in *P. sylvestris* than in *P. nigra*, which only showed a slight
514 increase in iWUE. Similar results were reported by Eilmann et al. (2010) for a *P.*

515 *sylvestris* forest showing dieback. Thus, water shortage seems to be the main
516 cause of the greater growth reductions and elevated mortality rates of *P. sylvestris*
517 stands in these drought-prone plantations (Sánchez-Salguero et al., 2012b).

518 The water-spending behavior of *P. sylvestris* - leading to higher
519 photosynthetic and growth rates under favorable environmental conditions, as
520 reflected in its growth trajectory - also has risks attached, since increasing water
521 loss might represent a threat to plant survival in dry years. This contrasting
522 response might also imply different levels of resistance to xylem embolism and a
523 higher risk of hydraulic failure in stands according to the thinning intensity.
524 Increases in radial growth, and expansion of conductive elements, lead to major
525 gains in hydraulic conductivity (Domec and Gartner, 2002) but may also imply
526 higher vulnerability to hydraulic failure (McDowell, 2011). Meanwhile, continued
527 metabolic demand for carbohydrates and increasing respiration rates, linked to a
528 rise in temperature, increase the likelihood of carbon starvation (Adams et al.,
529 2009).

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

537

538 5.3. *Thinning modifies resilience to drought*

539 The increased frequency of extreme drought events observed in recent decades is
540 the most likely factor that has led to recent and widespread defoliation, dieback,
541 and tree mortality in pine plantations in southern Spain and elsewhere (Navarro-
542 Cerrillo et al., 2006; Carnicer et al., 2011; Sánchez-Salguero et al., 2012a, b).
543 These events might lead to chronic stress and ultimately to the severe decline of
544 forest productivity and tree death (Petrucco et al., 2017). Despite small differences
545 in the resilience indices prior to thinning, the *P. sylvestris* and *P. nigra* stands
546 showed strong growth responses to drought after thinning, with the control plots
547 showing the lowest values of growth resistance, recovery, and resilience. The
548 forests studied here also showed a marked growth reduction during the droughts
549 occurring before (1995, 2005) and after (2012) the thinning treatments. However,
550 while all individuals were able to recover their pre-drought growth levels in 2012,
551 individuals in thinned stands showed better growth improvement afterwards. This
552 evidences the greater recovery capacity of thinned stands under xeric conditions
553 (Millar et al., 2007). However, this short-term growth response may not imply a
554 long-term reduction in vulnerability (see, for instance, Lechuga et al., 2017).

555 In particular, *P. sylvestris* showed great sensitivity to thinning in terms of
556 its resistance (CR_T) and resilience (CR_C), independently of the treatment intensity,
557 although its recovery (CR_S) was less responsive. For *P. nigra*, the resilience
558 capacity and growth were sensitive to the thinning intensity. This is in line with
559 the long-term trend of growth, which showed a partial recovery after 2012 but not
560 after previous droughts (1995, 2005) (Sánchez-Salguero et al., 2013). This also

561 agrees with previous anatomical studies (e.g., Pellizzari et al., 2016; Petrucco et
562 al., 2017) in which wider cells with thinner walls were found in *P. sylvestris* trees
563 that were constantly exposed to drought; this risky strategy was a response to the
564 need to optimize water uptake efficiency under water shortage.

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

574

575 **5. Conclusions**

576 One of the main problems faced by forest plantations in southern Europe, and in
577 other areas of the Mediterranean Basin, is the mortality processes related to
578 climate change, and in particular to severe drought. Different authors have
579 highlighted the importance of thinning in the adaptation of this type of artificial
580 forest to the new climatic conditions. In this work, we contribute to this field with
581 a new example of the advantages provided by this silvicultural strategy . Water
582 shortage, linked to recurrent droughts, together with high competition among
583 trees, negatively affected growth and increased iWUE, which potentially explains

584 the dieback of some pine plantations. However, for plantations of species at the
585 limit of their distribution, as in the case of Scot Pine and black pine in the south of
586 the Iberian Peninsula, it is possible that thinning benefits are simply a transitory
587 solution that partially mitigates the effect of the drought but does not prevent the
588 disappearance of these plantations in the medium and long term. However, our
589 results show two important findings. Firstly, the differing responses of Scots pine
590 and black pine imply the need for different thinning strategies. Trees from thinned
591 stands showed a more plastic response to drought, recovering their growth more
592 quickly and increasing iWUE, particularly in the case of *P. nigra*. Secondly, this
593 type of silvicultural practice is convenient, although its effect is limited, since it
594 allows progressive adaptation of the forest structure, particularly at low or very
595 low densities, in an economically viable manner, avoiding sudden mortality
596 processes that produce irreversible damage and strong social alarm. Growth in
597 dense, unthinned stands experiences more inertia in response to climate variation
598 than that in thinned stands, and this may explain the higher vulnerability and the
599 lower resilience to drought in *P. sylvestris*, relative to *P. nigra*. With these
600 findings, we evidence the vulnerability of densely planted Mediterranean pines to
601 the forecasted warmer and drier conditions. Therefore, this work is a new
602 contribution that shows the need for forest managers to take urgent measures that
603 will help drought-sensitive Mediterranean pine plantations adapt to the risks
604 associated with climate warming, thereby avoiding their irreversible loss while
605 other actions should be performed to change the species composition of those
606 plantations to maintain ecosystem function and services in the long-term

607

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624

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Figure 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.

Figure 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)

Figure 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).

Figure 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

Figure 5. Resistance (CR_T), resilience (CR_C), and recovery (C_S) 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.

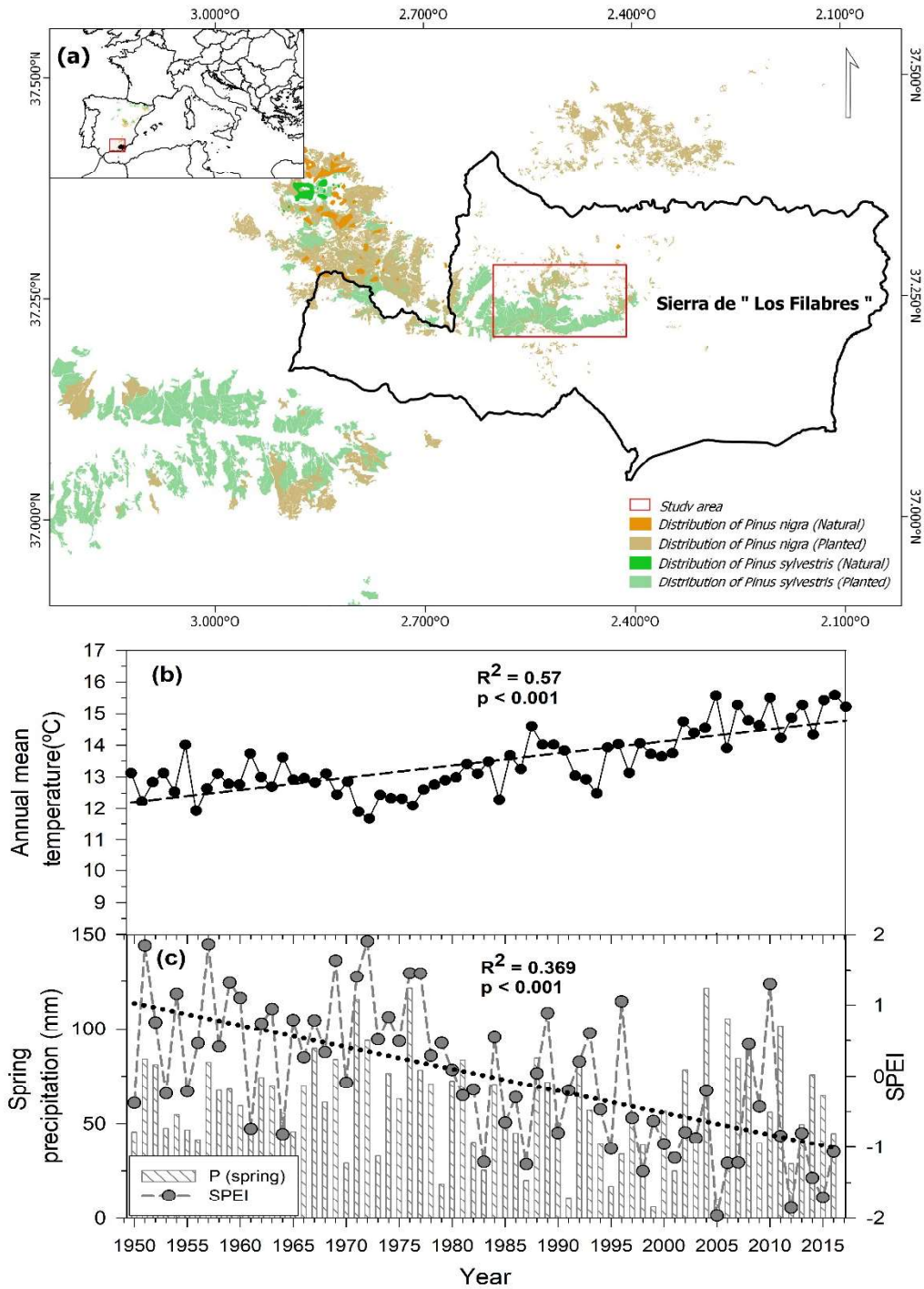


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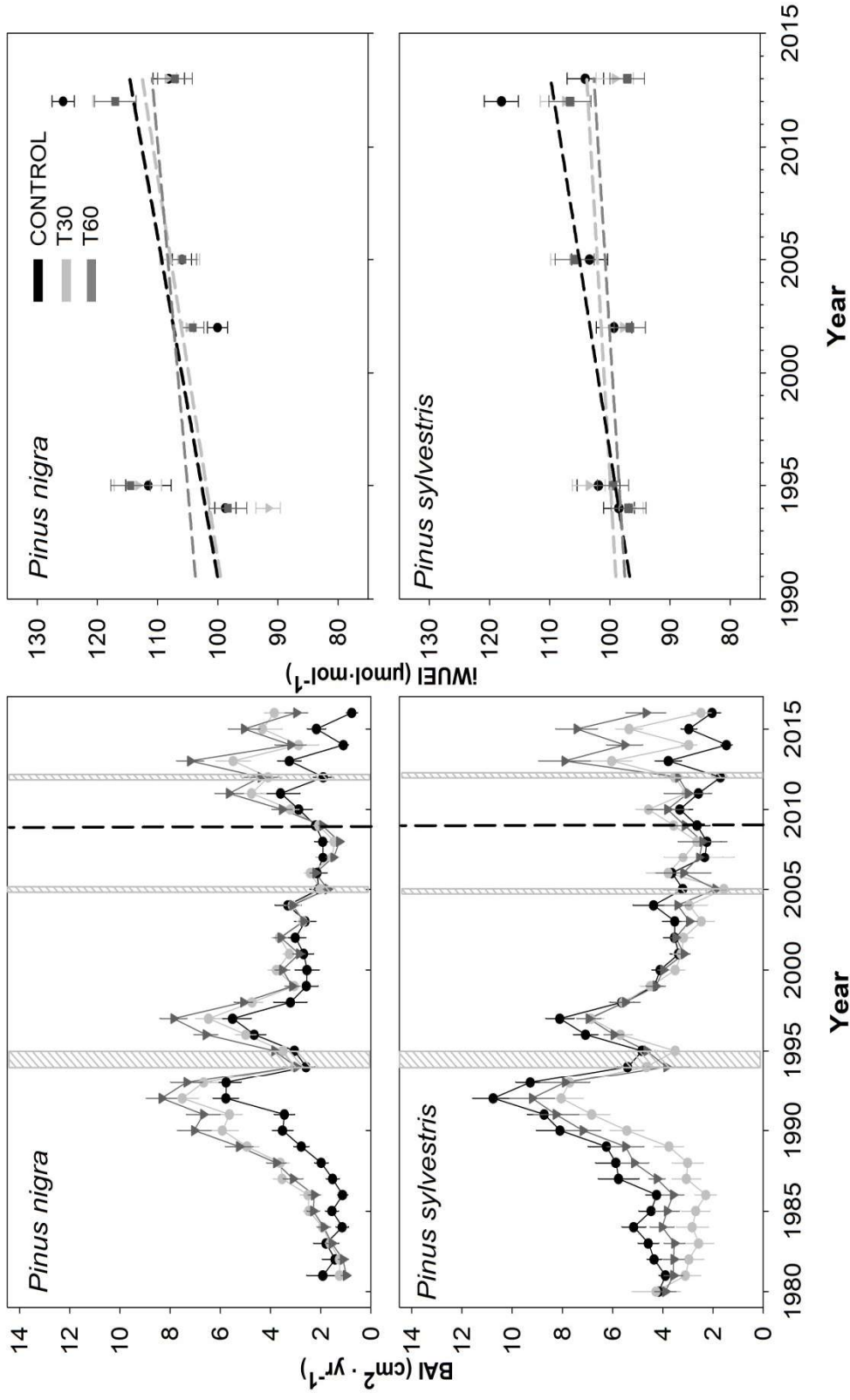


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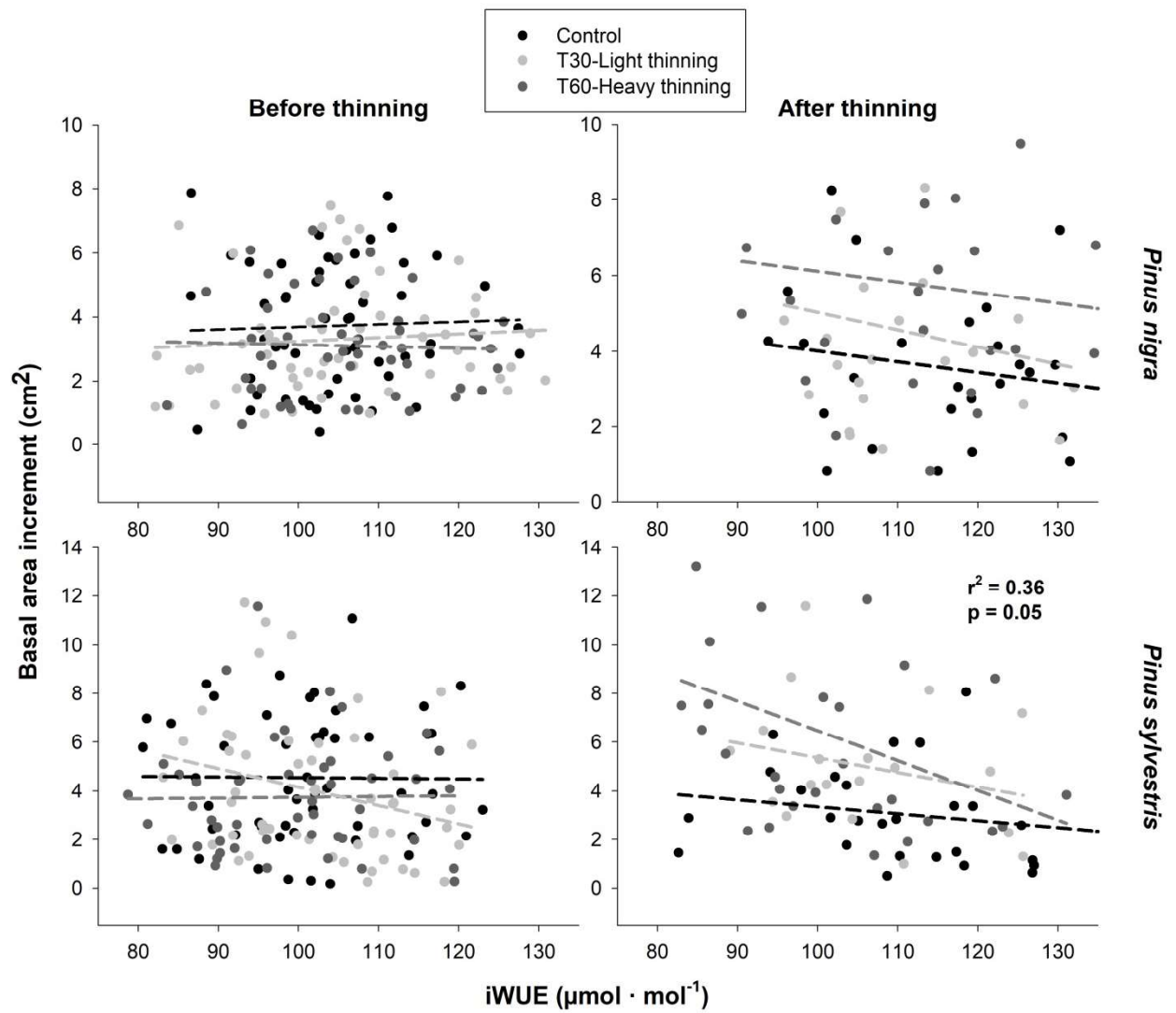


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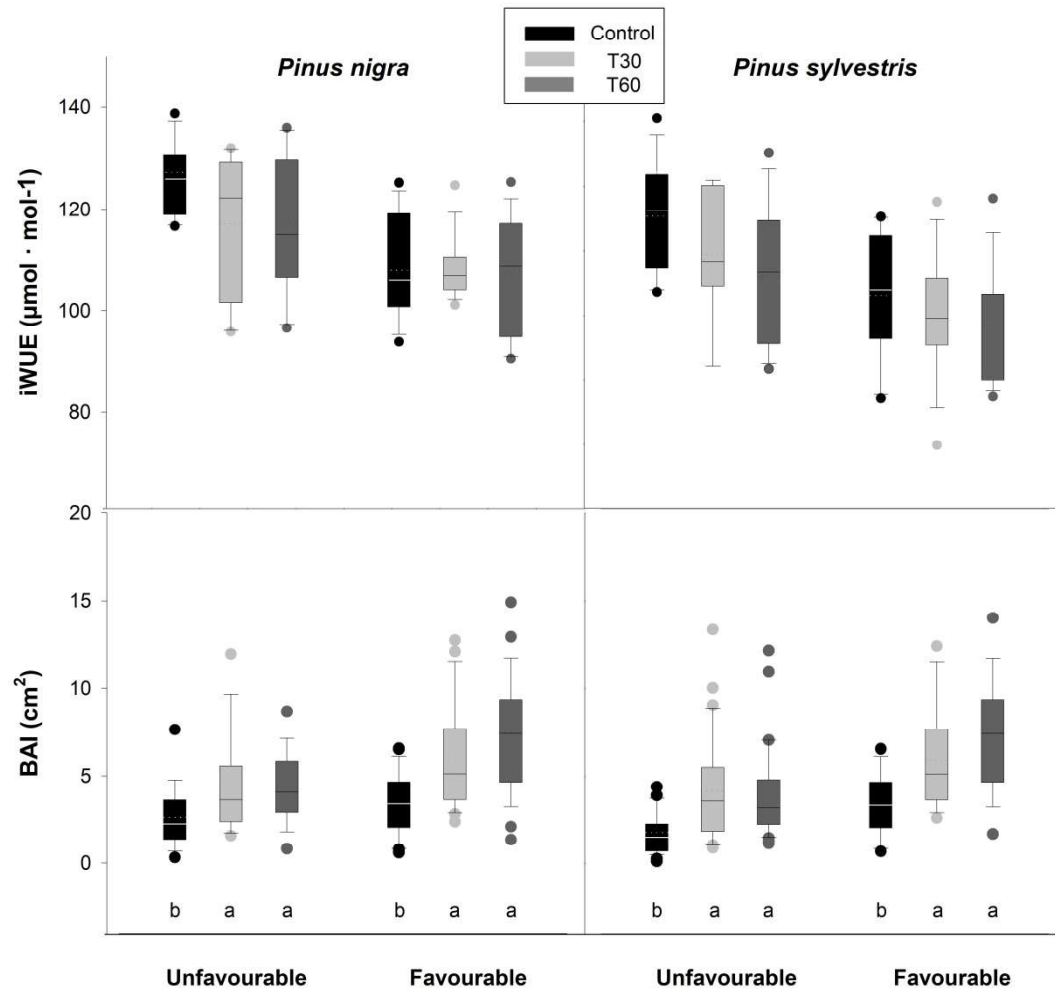


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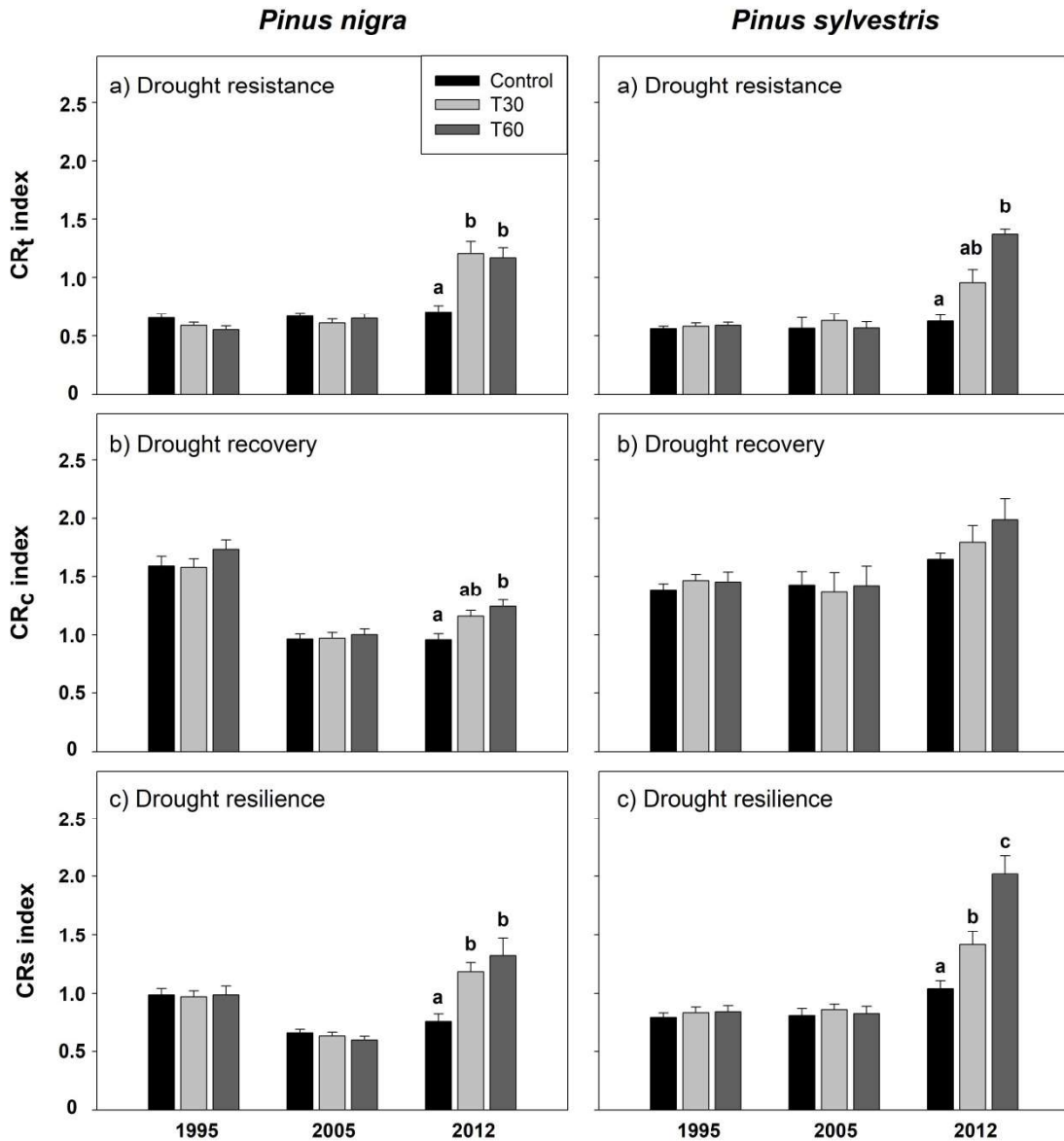


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Table 1.- Silvicultural characteristics of *Pinus sylvestris* and *Pinus nigra* plots according to thinning intensity (C, control or unthinned plots; T30, light thinning or 30% of basal area removed; T60, heavy thinning or 60% of basal area removed). 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

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 \pm SD, cm² year⁻¹), Rbt, mean between-trees correlation; MS: Mean sensitivity; AC1: first-order autocorrelation; EPS, Expressed Population Signal

Declining level	Thinning intensity	BAI₂₀	Age (yrs.)	Rbt	MS	AC	EPS
<i>Pinus nigra</i>	C	3.6 \pm 0.3	34	0.445	0.341	0.751	0.954
	T30	3.7 \pm 0.3	35	0.634	0.310	0.754	0.979
	T60	3.7 \pm 0.3	35	0.657	0.354	0.751	0.980
<i>Pinus sylvestris</i>	C	3.6 \pm 0.3	39	0.314	0.350	0.831	0.921
	T30	4.5 \pm 0.4	38	0.408	0.343	0.748	0.947
	T60	4.8 \pm 0.4	39	0.389	0.345	0.756	0.943

Table 3.- 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 (cm ² year ⁻¹)		iWUE (μ 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