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Thinning improves growth and resilience after severe droughts in *Quercus subpyrenaica* coppice forests in the Spanish Pre-Pyrenees

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12   **Abstract**

13   During the past years, growth and productivity of different oak species have been constrained by

14   water shortage in seasonally dry regions such as the Mediterranean Basin. Thinning could improve

15   oak radial growth in these drought-prone regions through the reduction of tree competition for soil

16   water in summer. However, we still lack adequate, long-term assessments on how lasting are thinning

17   treatments effects and to what extent they contribute to oak growth recovery after drought. Here we

18   aim: (i) to study the radial growth sensitivity to drought of *Quercus subpyrenaica* in the Spanish Pre-

19   Pyrenees, and (ii) to verify if thinning represents a suitable option to enhance growth resistance to

20   drought and post-drought growth recovery. We analysed basal area increment (BAI) trends in the

21   period 1960-2020 of formerly coppiced oak stands thinned in 1984 and compared them with

22   unthinned plots and also with coexisting Scots pine (*Pinus sylvestris*) growing in thinned plots. We

23   used the Standardized Precipitation Evapotranspiration Index (SPEI) to estimate the severity of

24   droughts and we also assessed climate-growth relationships. Oaks in thinned plots showed higher

25   BAI (369 mm^2) than those in unthinned plots (221 mm^2). Growth rates remained higher in thinned

26   than in unthinned plots also under severe drought stress. A severe summer drought in 1986 caused

27   abrupt BAI reductions in both oaks (- 40.5%) and pines (- 40.1%). The positive effect of thinning on

28   growth lasted for over 20 years and slightly declined as canopies closed. In the thinned plots, trees

29   with smaller diameter showed the greatest growth release. Oaks in unthinned plots and Scots pine

30   were more sensitive to short-term droughts in terms of growth reduction than oaks in thinned plots,

31   while long term droughts have similar effects on oaks from both thinned and unthinned plots. Oaks

32   were resilient to drought, showing recovery periods lasting from 1 to 2 years in both thinned and

33   unthinned plots. However, intense and prolonged droughts could strongly reverse the expected

34   growth enhancement of thinned plots, and a greater frequency of droughts would limit coppice growth

35   and productivity thus lengthening the rotation periods.

36   **Key words**: Mediterranean oaks, dendroecology, SPEI, release, resilience.

1. Introduction

Under a climate warming scenario, there is a greater likelihood of air temperatures and evapotranspiration rate exceeding the optimum range for many tree species, leading to range contractions in drought-prone regions (Thuiller 2004, Wang et. Al 2018). In seasonally dry Mediterranean regions, models predict greater susceptibility to climate warming and drought for winter deciduous, ring-porous oaks, often dominant in mesic sites (Benito Garzón et al. 2008, de Dios et al. 2009, Acácio et al. 2017, Vila-Viçosa et al. 2020). However, we lack field data to test these predictions and to assess the sensitivity to drought of oaks given their ecological and socio-economic relevance in Mediterranean regions.

In recent years, dieback and mortality related to drought events have been reported in southern European deciduous oak forests, mainly in Spain and Italy (Amorini et al. 1996, Camarero et al. 2016, Colangelo et al. 2017, Gentilesca et al. 2017, Lloret et al. 2022). Under drought stress, deciduous, ring-porous oaks may osmotically adjust their tissues to continue to draw water into the leaves and keep high photosynthesis rates (anisohydry), increasing the risk of damage due to hydraulic failure since most of the stem conductivity depends on vessels located in the last-formed ring (Novick et al. 2022, Kaproth and Cavender-Bares 2016). In these species, stem radial increment is reduced in drought years, as well as mean lumen area of earlywood vessels thus decreasing hydraulic conductivity (Eilmann et al. 2006).

The effects of drought events on trees and forests can be assessed through the analysis of resilience components, and tree-ring data constitute one of the main valuable proxies for this purpose (Lloret et al 2011). Resilience is defined as the capacity of ecosystems, communities, or individuals to recover after disturbance and regain its pre-disturbance structure and function (Scheffer et al. 2001, Folke et al. 2004). Several dendroecological studies have shown how drought severity is the major factor influencing radial growth resilience to drought (e.g., Gazol et al. 2018). How oaks respond to climate (drought) also depend on both, external and internal constraints. For example, site characteristics may modify soil water availability resulting in a persisting environmental constraint for tree growth, as demonstrated in *Quercus pubescens* Willd on limestone bedrock (Vodnik et al. 2019). In addition, the risk of drought-induced dieback may be size-dependent, with canopy defoliation and mortality risk increasing with decreasing height and radial growth rate as found in *Quercus faginea* Lam. (Camarero et al. 2016). Drought-induced dieback leads to cascading effects on oak forests and associated species because it not only reduces tree growth but vitality since it may also increase tree vulnerability to biotic stressors such as insect defoliators and fungal pathogens (Wargo 1996; Thomas et al. 2002; Canelo et al. 2021).

In Spain, winter-deciduous oaks such as *Q. faginea*, *Q. pubescens* and *Quercus pyrenaica* Willd. dominate many formerly coppiced forests, which comprise about 20% of the total forest area (Serrada et al. 1992, Cañellas et al. 2004). In the past, these oak coppices played relevant socio-economic roles in Mediterranean countries, primarily providing firewood and charcoal but also ensuring grazing for livestock in wood-pasture mixed systems. However, the withdrawal of these traditional uses and of regular coppicing has reduced stem radial growth rate making these overaged stands prone to drought-induced dieback (Corcuera et al. 2006). The management of such coppice forests is a key forestry issue, especially in the Mediterranean countries where scenarios of warmer and drier climate conditions are forecasted (Vila-Viçosa et al. 2020).

Thinning could reduce the impact of drought in coppiced forests that enter the stem exclusion stage, reducing intra- and inter-species competition between trees for water (Cabon et al. 2018; Gavinet et al. 2020). Canopy openings following thinning improve light conditions and enhance coppice above-ground growth with an abrupt increase in tree growth (Müllerová et al. 2016; Hepner et al. 2020). Furthermore, comparing growth responses to climate variability between thinned and unthinned stands would provide a reliable assessment on post-thinning resilience to drought. However, we still lack suitable assessments of post-drought growth responses after thinning and drought to discern if post-thinning growth enhancement is transitory and linked to drought alleviation.

In this work we aimed: (*i*) to evaluate the effects of thinning on radial growth in treated and untreateded *Q. subpyrenaica* formerly coppiced stands; and (*ii*) to assess if thinning can enhance growth and improve resilience by alleviating drought stress. Our hypothesis is that thinning can increase resistance to drought impact and improve resilience (post-drought recovery) of trees to severe water deficit by reducing tree-to-tree competition for soil water and light. We compared oak growth responses to thinning and drought and used as reference Scots pine (*Pinus sylvestris* L) trees inhabiting thinned and unthinned stands.

2. Material and methods

2.1 Study area and species

In North-eastern Spain, *Q. pubescens* and *Q. faginea* form a major biogeographic transition between the northern Eurosiberian and southern Mediterranean regions subjected to seasonal summer drought (Loidi and Herrera 1990). *Q. pubescens* is a sub-Mediterranean species present in sites with summer precipitation higher than 150 mm and altitude range between 400 and 1500 m (Ruiz de la Torre and Ceballos 1979). *Q. faginea* is a Mediterranean oak restricted to Morocco and Iberian Peninsula, mostly in sites with basic soils, summer precipitation higher than 100 mm and altitudes between 600-1200 m a.s.l. (Ruiz de la Torre and Ceballos 1979). The contact areas between both species allowed their mixing and the resulting hybrid was named *Quercus subpyrenaica* E.H. del Villar (Amaral

Franco 1990), which may be also regarded as a *Q. pubescens* subspecies (Govaerts and Frodin 1998). Currently, *Q. subpyrenaica* populations are mainly found in the Central and Western Spanish Pre-Pyrenees, where usually form mixed forests with Scots pine.

The study site is located in one of these Spanish Pre-Pyrenean ranges (Sierra de Luesia-Sto. Domingo) near the "Puy Moné" peak (1302 m a.s.l.), Aragón region (**Fig. 1a**). The main forest type is a *Q. subpyrenaica* (*Qs*) mixed forest, whit *Acer campestris* L., *Acer opalus* Mill., *Pinus sylvestris* L. and *Fagus sylvatica* L. in the most mesic sites (valley bottoms, N-oriented slopes) and *Arbutus unedo* L. in warm-dry sites (S-oriented slopes). Other less abundant woody species are among trees *Ilex aquifolium* L., *Crataegus monogyna* Jacq., *Sorbus torminalis* L., among shrubs *Buxus sempervirens* L. and *Juniperus communis* L., and the vine *Amelanchier ovalis* Medik. Bioclimate in this region is temperate oceanic (Sub-Mediterranean variant). The mean annual temperature is 10.4 °C whereas mean annual precipitation is 795 mm, with a mean annual water balance of -16 mm (Spanish Meteorological Agency AEMET, period 1961-2020 period). Weekly values of the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2017), calculated on 48-month long scales, were high in 1978–1985 and low in 1985–1996 indicating wet and dry conditions, respectively (**Fig .1b**).
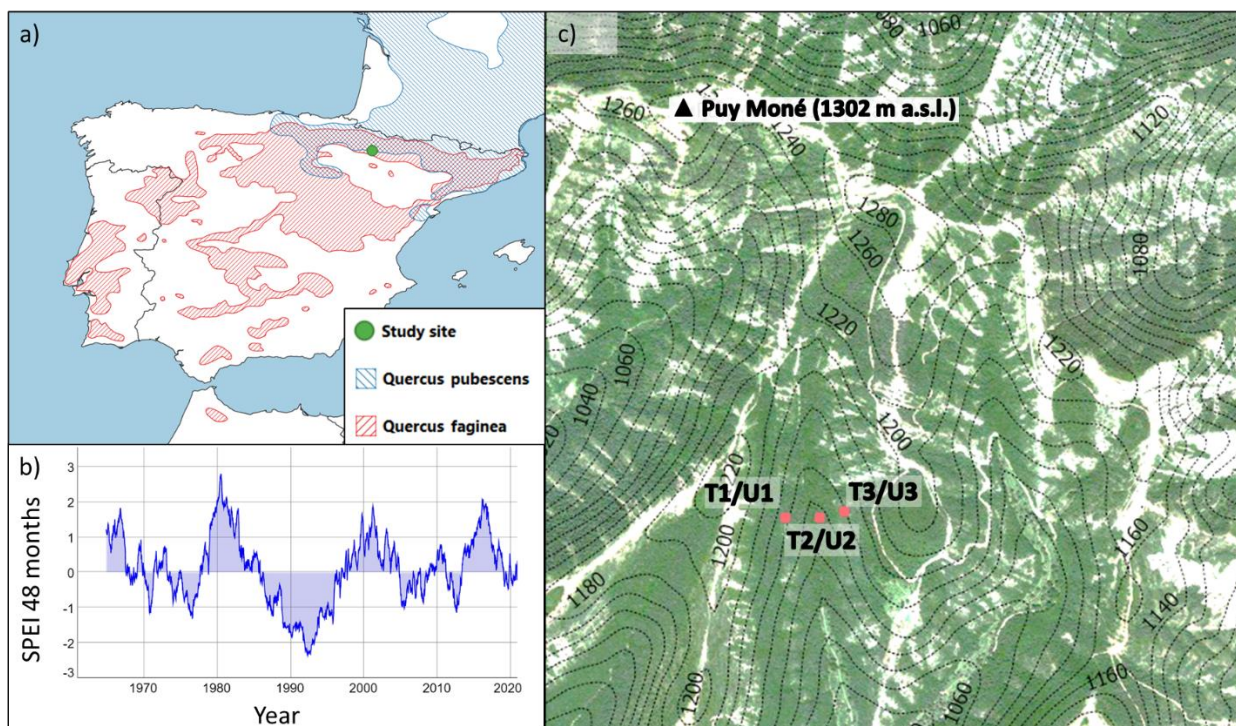
Figure 1. (a) Location of the study site and distribution range of *Q. pubescens* and *Q. faginea* in the Iberian Peninsula (Caudullo et al. 2017). (b) SPEI calculated on 48-month scale in study site area (Vicente-Serrano et al. 2017). (c) Location of sampled plots: east-facing side (T1/U1), valley floor (T2/U2) and west-facing side (T3/U3).

2.2 Field sampling

Thinning was carried out in 1984 on three squared plots of 100 m² in *Q. subpyrenaica* coppice stands. The basal area percentage removed in the thinning was 50%, corresponding to about 20-30 m² ha⁻¹. The three thinned plots have different topographic features within the study area slope (SE and SW aspects, valley floor). In each thinned plot (T1, T2 and T3) structural parameters (dbh, diameter at breat height; height) were measured, and tree increment cores were collected. Cores and measurements were also collected in nearby unthinned plots (U1, U2, U3) of the same size and with similar topographic features than T1, T2 and T3, respectively. Sampling with the same protocol was repeated at all plots in 2003/2004 and 2021, except for the T3 plot which was surveyed only in 2003.

For each plot and woody species, we calculated mean dbh and height, tree density and total basal area (**Table 1**). We also calculated species richness (S) and species diversity (Shannon H' index) considering all woody plant species sampled within each plot.

2.3 Tree-ring data processing

All *Q. subpyrenaica* trees inside each plot were cored using a 0.5-mm increment borer (Haglof, Sweden). For each tree, 2 cores were extracted at breast height (1.3 m) from the thickest stems of each multi-stemmed individual. Additional cores were also collected from *P. sylvestris* trees located in T1. In total, we sampled 145 oaks (71 trees in thinned plots and 74 trees in unthinned plots) and 12 pines. We considered the Scots pine series because pines were present in formerly thinned plots and could be used as a reference growth data to detect post-thinning growth enhancements.

We mounted all cores on wooden supports after air drying and polished them with progressively finer sandpapers. We visually cross-dated each core and then measured ring widths using a semi-automatic system (LINTAB-TSAP, Rinntech, Germany) at 0.01 mm accuracy. We used the COFECHA software to check the visual cross-dating (Holmes 1983). Next, tree-ring width series measured from the same tree were transformed into basal area increment (BAI) series and averaged for each tree using the *bai.in* function contained in *dplR* package (Bunn 2008) of R software (R Development Core Team, 2020).

2.4 Growth release detection

To detect potential growth releases following the 1984 thinning, BAI series were analysed. The 95% confidence interval of mean BAI series in thinned and unthinned plots was calculated using 1000 bootstrap resampling. Growth release following canopy opening in 1984 was estimated by calculating the percentage of BAI change (BC). For each individual tree, the BC was calculated comparing mean BAI values in the 1981−1984 and 1985−1988 periods using the equation [1] where

157   M1 is the 4-year mean BAI including the thinning year (period 1981−1984) and M2 is the following

158   4-year mean (1985−1988 period).

$$BC = [(M2−M1) / M1] \times 100 \qquad [1]$$

160   This approach is similar to the growth averaging method (Nowacki and Abrams 1997) based on

161   comparing running 10-year ring-width means and used to detect growth releases or suppressions.

162   **Table 1.** Topographic and structural characteristics of thinned (T1, T2 and T3) and unthinned (U1, U2 and
163   U3) sampled plots. Woody species abbreviations: *Ac, Acer campestre; Ao, Acer opalus; Au, Arbutus unedo;*
164   *Av, Amelanchier ovalis; Bs, Buxus sempervirens; Cm, Crataegus monogyna; Ia, Ilex aquifolium; Jc, Juniperus*
165   *communis; Ps, Pinus sylvestris; Qi, Quercus ilex; Qs, Quercus subpyrenaica.* Variables' abbreviations: S,
166   species richness; H', diversity.

Plot	Elevation (m a.s.l.)	Slope (°)	Aspect	Density (No. stems ha⁻¹)	Qs density (No. stems ha⁻¹)	Total basal area (m²ha⁻¹)	Qs basal area (m²ha⁻¹)	Qs mean diameter (cm)	Qs dominant height (m)	Woody species	S	H'
T1	1150	25	SE	3200	1800	44.35	41.74	17.2	13.5	Qs, Bs, Av, St, Ia, Ac, Ps	7	1.33
T2	1110	6	S	5900	1500	91.19	63.47	23.2	21.5	Qs, Bs, Ao, Ia, Fs	5	1.29
T3	1140	20	SW	2800	1500	21.75	14.31	11.0	14.0	Qs, Qi, Au, Cm	4	1.44
U1	1150	25	SE	7300	4400	56.92	53.45	12.4	11.0	Qs, Bs, Jc, Cm, Ia	5	0.82
U2	1110	6	S	6900	3200	52.78	48.15	13.8	12.0	Qs, Bs, Jc, Ps	4	0.87
U3	1140	20	SW	5900	3300	31.76	22.78	9.4	11.5	Qs, Qi, Au, Cm	4	1.6

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169   **2.5 Growth responses to drought**

170   To analyse growth responses to drought we compared detrended BAI series and the SPEI drought

171   index. First, the BAI series were detrended by fitting cubic spline functions to remove the age-, size-

172   and disturbance-related trends and to emphasize the high-frequency growth variability (Cook et al.

173   1990). We set the smoothing spline rigidity at 10 years and its wavelength cut-off value at 50%. We

174   detrended all measured series dividing observed by fitted values to obtain dimensionless BAI indices.

175   Three mean site chronologies were developed with a minimum sample depth of 10 series: (i) a *Q.*

176   *subpyrenaica* chronology in thinned plots, (ii) a *Q. subpyrenaica* chronology in unthinned plots, and

177 (iii) a *P. sylvestris* chronology. Mean standard chronologies were obtained averaging individual BAI

178 indexed series using a bi-weight robust method (Fritts 1976).

179   For climate-growth analyses we used mean standard chronologies and monthly SPEI indices

180 calculated on 1-, 3-, 6- and 9-months. SPEI data correspond to the 1.1-km^2 gridded SPEI dataset for

181 Spain (Vicente-Serrano et al. 2017). Correlation values were calculated between monthly SPEI and

182 indexed BAI for all the months of the vegetative period, April to November, in the post-thinning,

183 common period 1984–2020. The stability of the strongest climate signals detected in this analysis

184 was assessed by calculating moving response coefficients using 30-year moving windows and a 1-

185 year offset. Function parameters were bootstrapped to calculate their significance and confidence

186 intervals. This analysis was done using the treeclim R package (Zang and Biondi 2015).

187   Finally, potential severe drought events were detected based on a SPEI threshold of −1.28 (Agnew,

188 2000). For these years (1967, 1986, 1989, 1995 and 2012) the Lloret resilience components (Lloret

189 et al. 2011), i.e. resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience (RRs) indices,

190 and the growth recovery time (GRT, Thurm et al. 2016) were calculated on individual detrended BAI

191 series using the "*res.comp*" fuction in "*pointRes*" R package (van der Maaten-Theunissen et al. 2015).

192 We considered 4 years of pre- and post-disturbance for calculating resilience components and

193 considered the maximum length of the recovery period equal to 10 years.

2.6 Variability of resilience components

195 Components of oak trees resilience (Rt, Rc, Rs and RRs) relative to drought events were used as

196 response variables for each Generalized Linear Mixed-Effects (GLME) model applied, using the

197 following predictors as fixed effects: (i) tree age, (ii) tree dbh, (iii) mean ring-width increment (RW),

198 (iv) mean sensitivity (MS), a measure of the relative change in width between consecutive rings (Fritts

199 1976), and (v) individual climate-growth correlation values (CorrSPEI). Treatment (unthinned

200 /thinned) was used as dummy variable to search for response differences. Then, separate models for

201 thinned and unthinned plots were fitted. Parameters (i), (ii), (iii) and (iv) refer to reconstructed values

202 at the date of each drought events, based on ring-width measurements. MS was calculated using

203 "*sens1*" function of the "*dplR*" R package (Bunn 2008). CorrSPEI is to the correlation value between

204 each tree indexed BAI series and the SPEI within the common period 1984–2002 using the Pearson's

205 coefficient. This 19-year interval follows the thinning and was selected to include most of the BAI

206 series from trees sampled in 2003. To avoid multicollinearity between predictors, we considered only

207 a specific period for the SPEI computation, choosing the months that returned greater significance

208 based on the results of the previous analysis (chapter 2.5). The Variance Inflation Factor (VIF) was

209 used to detect multicollinearity among predictors considering a threshold of VIF > 5 for presence of

210 multicollinearity. All predictors were standardized to account for differences in measurement units.

The plot aspect was considered as random effect. Since the response variable (tree growth resistance) did not satisfy the normal distribution criterion (Shapiro–Wilk test), the gamma family was set in the GLMEs (**Fig. S1**). This analysis was carried out using the *glmer* function of the *lme4* R package (Bates et al. 2007). Marginal and conditional R^2 values (R^2m and R^2c, respectively), accounting for the variability due to fixed and fixed plus random factors, respectively, of fitted models were computed using "*r2_nakagawa*" function of the "*performance*" R package (Lüdecke et al. 2021). VIF was calculated using the *vif* function in the *car* R package (Fox et al. 2007).

3. Results

3.1 Quantification of release events in thinned plots

Sampled oak trees were relatively young, with a mean age of 43 years in thinned plots and of 51 years in unthinned ones. In both cases, oaks presented both positive trends of mean BAI series up to the 1970s, representing the vigorous juvenile phase of growth during a wet-cool decade (**Fig. 2**). Scots pines showed higher growth rates than oaks, but also more interannual variability, with an exceptional BAI reduction in years 1992-1993 (**Fig. 2b**). In 1989, both species and plots featured a drop in BAI due to an exceptional dry year.

After 1984, oaks in thinned plots showed a growth release. For the following years, up to 2004 the oaks BAI values remained higher in thinned plots. The mean BAI change (BC) of oaks in 1984 for thinned plots was 100%, but close to 0% for Scots pines and oaks in unthinned plots (**Fig. 3a**). The differences between the first and third quartiles in BC values were much larger in the thinned plots suggesting greater individual variability following the treatment. Trees featuring higher release levels were the ones which, at the date of thinning, had smaller diameters (**Fig. 3b**). Trees DBH in 1984 and BC were negatively related in thinned plots ($r = -0.63$, $p < 0.05$).
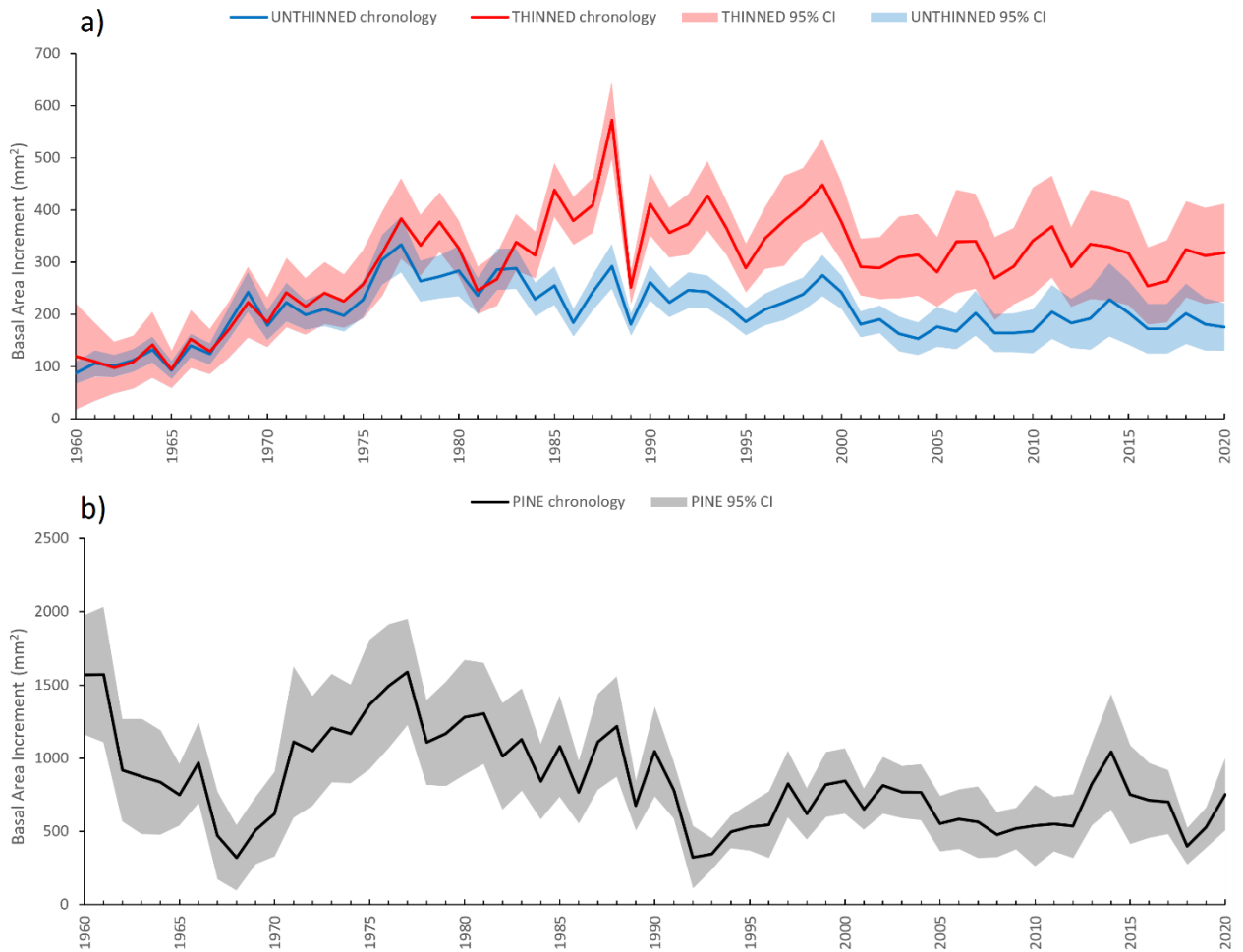
Figure 2. a) Basal area increment (BAI) chronologies of oaks in thinned (red line) and unthinned (blue line) plots and bootstrapped confidence intervals (95% CIs). b) BAI chronology of Scots pines and bootstrapped confidence intervals (95% CIs).
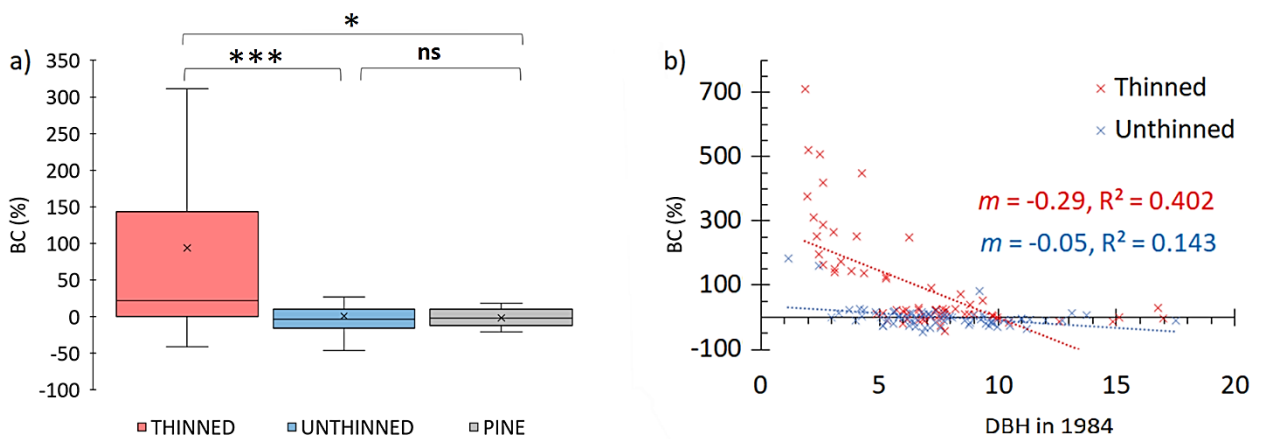
Figure 3: (a) Box plots of basal area increment (BAI) change (BC) after the thinning in 1984 in thinned and unthinned oak plots and in *P. sylvestris* (pine) series. Significant differences in BC (%) between groups were tested with paired two-sided Student's t-Test. Significance levels: ns (not significant) $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. (b) Scatter plot relating oak diameter (DBH) in 1984 with BAI change (BC) in thinned (red cross) and unthinned (blue cross) plots; the slope of the lines is denoted by the letter *m*.
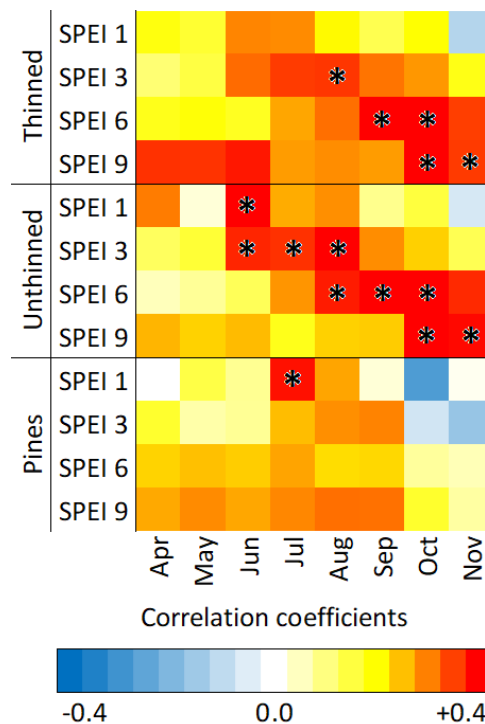
3.2 Growth response to drought events

In the post thinning interval (1984–2020), we found a significant BAI response to the 1-month SPEI values for June in unthinned plots, whereas no significant correlation was found for thinned plots indicating a low responsiveness to short term changes in soil water availability (**Fig. 4**). The highest and significant correlation coefficients in *P. sylvestris* trees were found between indexed BAI and July 1-month SPEI, indicating a higher sensitivity to shorter drought events than oaks in thinned plots and a more similar response to oaks without thinning. The 3-month (June, July, and August) SPEI showed positive relationships with oak BAI for unthinned plots and only in August for thinned plots. Correlation coefficients for oaks in thinned and unthinned plots were high and significant for October 6- and 9-month long SPEIs. The moving correlation analyses revealed a progressive loss of significance of the correlations with the June 1-month SPEI in thinned plots, while the values remained higher and significant in the unthinned plots. However, no difference between thinned and unthinned plots for 6- and 9-month long SPEIs was found in moving correlation analyses (**Figs. 5** and **S3**).

Exceptional dry growing seasons, with SPEI below the threshold of -1.28, occurred in 1967, 1986, 1989, 1995 and 2012 (**Fig. S2**). In terms of resistance, the 1989 drought affected more severely studied trees, causing abrupt BAI growth reductions in both oaks (-40.5%) and pines (-40.1%). On the other hand, the 2012 drought event did not severely reduce growth of oaks and had a low effect on pines. *P. sylvestris* series showed remarkable differences with oaks in 1967 and 1995 (**Fig. 6**), when their resistance to drought was lower and higher than oaks, respectively.

Generally, oaks and pines have high recovery rates (Rc>1) after drought (**Fig. 6**). Consequently, four years after the drought events BAI values were close to pre-disturbance levels, with resilience values close to one. On average, recovery periods for both pines and oaks occurred in one or two years, with exception of the 1967 drought when pines required four years and the ones in1989 and 1995 when most oaks needed more than two years to recover. Relative resilience indices showed distributions similarly to recovery indices (**Figs. 6** and **S4**), and they were inversely proportional to the resistance index.
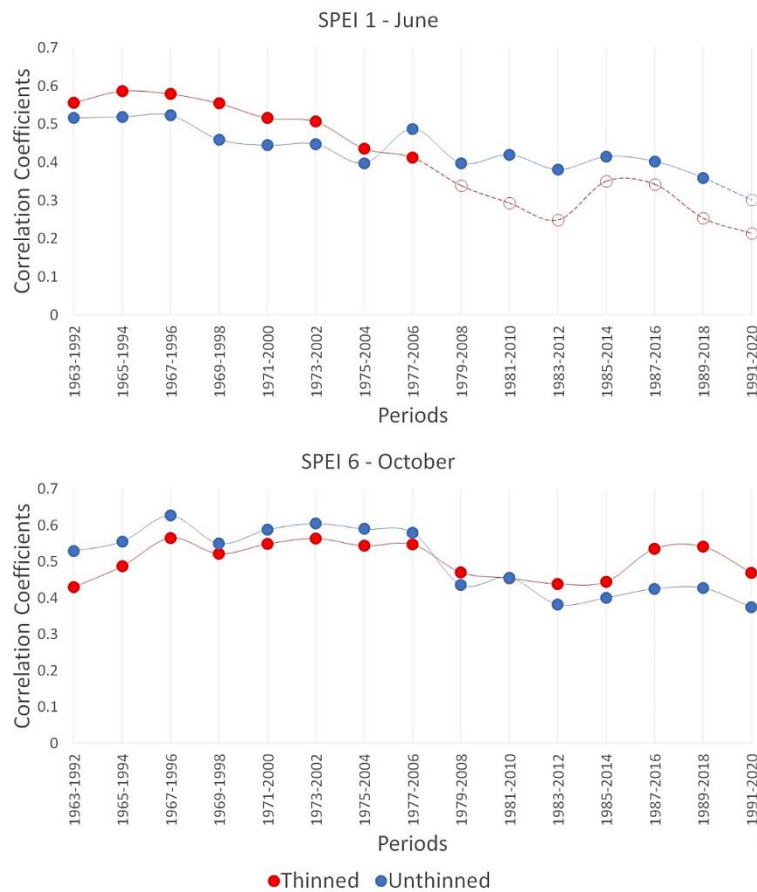
Figure 5. Pearson's correlation coefficients calculated using 30-year moving windows between mean indexed BAI standard chronologies and June 1-month SPEI index and October 6-month SPEI. Filled dots for significant 95% bootstrap confidence interval. Period of analysis is 1963-2020. All results are plotted in Figure S3.
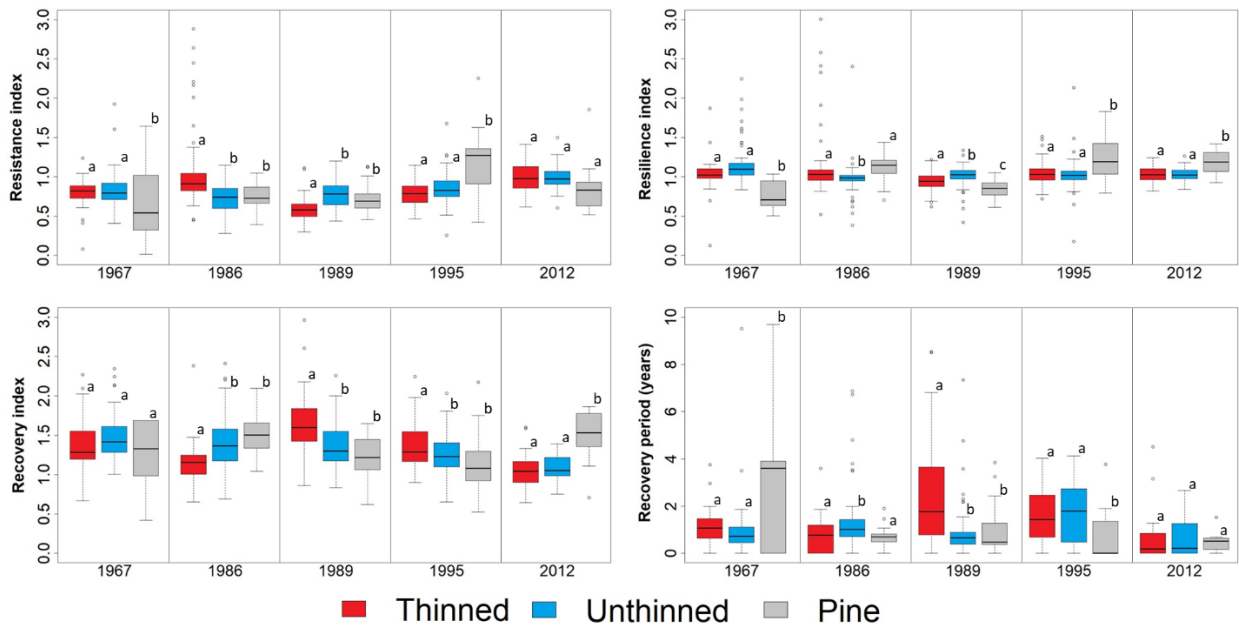
Figure 6. Boxplots showing resistance, recovery and resilience indices and recovery period (years) of *Q. subpyrenaica* trees in thinned (red) and unthinned (blue) plots and *P. sylvestris* trees (grey) for drought events of the years 1967, 1986, 1989, 1995 and 2012 (see also Fig. S2). Relative resilience indices calculated in *Q. subpyrenaica* trees in thinned and unthinned plots are plotted in Figures S4. Significant differences between groups (paired two-sided Student's t-Test with α=0.05) were represented by overhead letters.

3.3 Variability of resilience components

The October 9-month SPEI index was selected as a main drought driver of oak growth for the computation of climate growth correlation at individual tree level in the common period 1984−2002 (CorrSPEI). Within this time interval, we analyzed three exceptional droughts (1986, 1989 and 1995; cf. **Fig. S2**) using GLMEs.

Generally, thinned plots showed higher resistance values in 1986 and lower in 1989 than unthinned plots (**Table 2**). In 1986 and 1989, RW had a significant negative effect over resistance in unthinned stands. In the second event, MS and CorrSPEI parameters presented negative influences on growth resistance, especially for thinned plots. In the 1995 drought, there was not significant difference among thinned and unthinned plots, resistance was negatively related to RW and MS. For the same event, the only parameter with significant weight was the correlation coefficient between SPEI and BAI in unthinned plots (**Table 2**).

Thinned plots showed a significantly lower resilience after the 1986 severe drought. However, larger oaks from thinned plots showed lower levels of relative resilience in the 1989 and higher in the 1995 drought. Mean sensitivity had a significant positive (1986) and negative (1989) weight on resilience, especially for thinned stands. CorrSPEI was often positively related to resilience, especially in 1989 and 1995. Finally, the relative resilience was not influenced by either tree DBH or

305 tree age, but it depended more on CorrSPEI (positive relationship) and slightly on ring width and
306 mean sensitivity (**Table 2**).

307   In all models performed, slope aspect always explained a very little portion of the variance.
308 Moreover, the values of conditional and marginal R^2 were similar indicating that most variability in
309 growth resistance to drought was accounted for by fixed factors (**Table 2**).

310 **Table 2.** Summary statistics (*t* values) of Generalized Linear Mixed-Effects models fitting tree growth resistance, recovery, resilience and relative resilience in
311 the three drought years studied (1986, 1989 and 1995). Variables are abbreviated as: dbh, diameter at breath height; RW, mean ring width; MS, mean sensitivity;
312 CorrSPEI, correlation coefficients of October 9-month SPEI index and the BAI chronology. In the case of fixed factors, NA indicates the parameter not included
313 in the model, whereas in the case of the random factor (slope aspect) NA was used when the calculation of the conditional R^2 (R^2c) was not possible due to
314 variance equal to 0. Bold values are statistically significant. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
315

Resistance	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	**+8.73***	**+11.15***	**+5.59***	**+15.51***	**+9.29***	**+11.16***	**+12.10***	**+11.16***	**+7.89***
Age	*NA*	*NA*	+0.31	*NA*	*NA*	-1.81	*NA*	*NA*	+0.28
dbh	-1.26	-1.36	NA	**-2.15***	-0.18	NA	+1.00	**+2.04***	NA
RW	-0.81	-0.38	**-1.99***	-0.19	-0.83	**-2.30***	**-2.21***	**-2.92****	-0.99
MS	+0.40	+0.01	-0.44	**-3.65***	**-3.07****	-1.36	**-4.05***	**-3.81***	-0.92
CorrSPEI	-0.33	-1.12	+0.37	**-2.75****	-1.69	**-2.60****	-1.43	-0.39	-1.85
Thinning (dummy)	**+3.31***	*NA*	*NA*	**-5.47***	*NA*	*NA*	*-0.72*	*NA*	*NA*
Slope aspect variance	<0.01	0	<0.01	<0.01	0.01	0	<0.01	<0.01	<0.01
R²m	0.07	0.04	0.03	0.18	0.05	0.15	0.13	0.21	0.06
R²c	0.09	*NA*	0.07	0.19	0.07	*NA*	0.14	0.26	0.09

Recovery	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	**+9.36***	**+8.50***	**+5.79***	**+8.082***	**+7.67***	**+5.69***	**+8.52***	**+9.72***	**+5.93***
Age	*NA*	*NA*	*NA*	*NA*	*NA*	+0.18	*NA*	*NA*	-0.73
dbh	+0.45	*+0.91*	+0.53	*-0.16*	-0.41	*NA*	-1.69	-1.13	*NA*
RW	-1.61	-1.67	-1.56	+1.25	+1.33	+0.57	**+2.19***	**+1.99***	+0.07
MS	+0.06	-0.50	+0.52	+1.13	+0.43	+0.93	**+3.62***	**+2.95****	+1.49
CorrSPEI	+1.28	+0.98	+1.37	**+3.43***	+1.62	**+2.89***	**+6.06***	**+2.45***	**+5.62***
Thinning (dummy)	**-4.41***	*NA*	*NA*	**+3.31***	*NA*	*NA*	-0.18	*NA*	*NA*
Slope aspect variance	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.00	<0.01
R²m	0.268	0.107	0.090	0.426	0.247	0.189	0.446	0.457	0.352
R²c	0.334	0.259	0.175	0.448	0.303	0.247	0.462	*NA*	0.410

Resilience	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	**+8.01*****	**+6.01*****	**+7.35*****	**+18.35*****	**+19.00*****	**+11.44*****	**+11.74*****	**+11.76*****	**+8.64*****
Age	*NA*	*NA*	*NA*	*NA*	*NA*	-1.63	*NA*	*NA*	-1.07
dbh	**-2.35***	*-1.25*	+1.29	**-2.92****	-1.94	*NA*	-1.61	1.85	*NA*
RW	+1.91	+1.66	**-2.26***	+0.75	+1.93	**-2.10***	-0.11	-0.04	**-2.34***
MS	**+3.77*****	**+2.36***	+0.32	**-2.27***	**-3.28****	+0.72	-0.22	+0.04	-0.16
CorrSPEI	+0.71	-0.60	**+2.12***	**+2.28***	**+1.99***	+1.73	**+4.38*****	**+2.16***	**+3.88*****
Thinning (dummy)	+0.47	*NA*	*NA*	**-2.65****	*NA*	*NA*	+0.53	*NA*	*NA*
Slope aspect variance	0.00	<0.01	<0.01	<0.01	0.00	<0.01	<0.01	<0.01	0.00
R^2m	0.293	0.319	0.106	0.176	0.188	0.147	0.147	0.129	0.243
R^2c	*NA*	0.336	0.140	0.185	*NA*	0.185	0.165	0.205	*NA*

Relative resilience	1986			1989			1995		
	All	Thinned	Unthinned	All	Thinned	Unthinned	All	Thinned	Unthinned
Intercept	**+20.00*****	**+15.42**	**+13.73*****	**+21.72*****	**+18.49*****	**+13.53*****	**+21.72*****	**+13.69*****	**+13.84*****
Age	*NA*	*NA*	*NA*	*NA*	*NA*	-0.37	*NA*	*NA*	-0.39
dbh	+0.06	+0.28	+1.26	-1.48	-1.32	*NA*	*-1.48*	-0.85	*NA*
RW	-1.43	-0.76	**-2.37***	+1.72	+1.76	-1.69	1.72	**+2.23***	*-0.87*
MS	+1.29	+0.36	+1.00	**+3.28****	-0.86	1.05	**+3.28****	**+2.18***	+1.88
CorrSPEI	+1.70	+0.84	**+2.08***	**+6.67*****	1.65	**+3.12****	**+6.67*****	**+2.87****	**+5.77*****
Thinning (dummy)	**-3.10****	*NA*	*NA*	0.05	*NA*	*NA*	0.05	*NA*	*NA*
Slope aspect variance	<0.00	<0.01	<0.01	<0.01	0.00	<0.01	<0.01	0.00	<0.01
R^2m	0.169	0.024	0.219	0.176	0.188	0.147	0.529	0.484	0.503
R^2c	0.231	0.152	0.226	0.185	*NA*	0.185	0.530	*NA*	*0.505*

4. Discussion

4.1 Effects of thinning on oak radial growth

Thinning enhanced radial growth in *Q. subpyrenaica* trees, an effect lasted for over 20 years and slightly decreasing probably in relation to canopies closure. Other studies on other oak species confirm the lasting duration of the positive effect of thinning on growth (Cutter et al. 1991; Mayor et al. 1993; Cañellas et al 2004). The *Q. subpyrenaica* response after these treatments depended on stem diameter, with smaller stems featuring more plastic response and showing a higher relative growth improvement than larger individuals. This could be related to the suppressed position of the dominated layer that promptly enhanced radial growth after the canopy opened by thinning. The larger trees, which had already reached a dominant or codominant position within the stand, exhibited fewer release effects. This response could be due to higher competition among stems of the same individual, as reported by Corcuera et al. (2006) for multi-stemmed *Quercus pyrenaica* coppice trees. Juodvalkis et al. (2005) also reported similar results demonstrating that an increase of tree volume could be achieved only when thinning 10-30 years-old oak (*Quercus robur*) stands, whereas at older ages the positive effect of thinning is buffered by overaging. On the other hand, the larger trees were the most favoured by thinning due to their greater capacity of resource uptake (soil water and nutrients) and allocation occurring after thinning in a study on *Q. pyrenaica* coppice stands in central Spain (Cañellas et al 2004). However, an imbalance between stem diameter and parent root system size could occur after a thinning treatment in coppice stands, resulting in smaller trees not necessarily suppressed in root water uptake by bigger individuals.

4.2 Effects of thinning on climate-growth relationships

Since *Q. subpyrenaica* has shown a wide range of ecophysiological adjustments in response to drought stress in experiments based on seedlings, even wider than their parental taxa (Himrane et al. 2004), it is important to assess the growth responses to water shortage of adult trees inhabiting formerly coppiced forests as has been done in *Q. faginea* (Alla and Camarero 2012). In our study, climate-growth analysis confirmed the key role of water availability in limiting tree stem growth, in line with other studies on Mediterranean deciduous oaks (Corcuera et al. 2004, Camarero et al. 2016, Martínez-Sancho et al. 2021). Growth and productivity of oaks was linked to more consistently to longer (i.e 6 to 9 months) droughts. However, in unthinned plots growth was linked to early summer (June) drought conditions, similarly to what Di Filippo et al. (2010) found in Turkey oak (*Quercus cerris* L.). Moving windows analysis revealed that this effect was also significant in oaks located in thinned plots, but it lost its significance following the thinning treatment. Correlations values between oak growth and longer droughts (6- to 9-month SPEIs) did not show differences between thinned and unthinned plots and remained stable even after treatment.

351   Scots pine growth exhibited positive correlations to 1-month July SPEI, therefore being more

352   sensitive to short-term droughts than *Q. subpyrenaica* in thinned plots. The different ecophysiological

353   strategies of coexisting pines and oaks to withstand summer drought were well described by Martín-

354   Gómez et al. (2017). They found that the anisohydric oaks presented a faster recovery of predawn

355   water potential after summer drought than the pines. This is probably associated with more accessible

356   and deeper soil water tables which could explain specific response to longer droughts. These authors

357   also reported a stronger negative effect of drought stress on long-term growth in pines, relying on

358   shallower soil water tables, compared with oaks.

359   In our study, the exceptional growth reduction featured in Scots pine in 1992-1993 period (**Fig.**

360   **2b**) was not related to severe drought conditions, suggesting an impact of other abiotic or biotic

361   disturbances such as the defoliator pine processionary moth, *Thaumetopoea pityocampa* (Camarero

362   et al. 2022). In addition, cold winter conditions (January and February were cold in 1992) could also

363   have contributed to the sharp decrease in Scots pine growth (Matisons et al. 2019).

364   **4.3 Impact of severe droughts on growth resilience**

365   The oak *Q. subpyrenaica* is a ring-porous species with anisohydric behavior, maintaining higher

366   transpiration and physiological activity under mild-to moderate drought conditions (Corcuera et al.

367   2004, Himrane et al. 2004, Tognetti et al. 2007). However, during very dry summer conditions, *Q.*

368   *subpyrenaica* reduces transpiration rates showing high recovery rates after the first seasonal

369   precipitation in early fall (Martín-Gómez et al. 2017). The exceptionally and successive droughts

370   detected in the study site from the 1980s onwards, also investigated by other authors for nearby

371   forested areas in Spain (Camarero et al. 2015, 2016, 2018; Manrique-Alba et al. 2022), could explain

372   an intensification of the coupling between oak growth and water deficit. Differently from *Q. ilex and*

373   *Q. faginea* mixed coppice forests in a drier area of eastern Spain (Camarero et al. 2016), *Q.*

374   *subpyrenaica* in our study site proved highly resistant to the 2012 drought event in both thinned and

375   unthinned plots, perhaps because it was less severe in the Spanish Pre-Pyrenees. The other selected

376   drought events affected differently studied plots: the 1967 and 1995 ones produced similar effects

377   regardless of thinnings, whereas in 1986 and 1989 the resistance values differed between thinned and

378   unthinned plots. Specifically, in 1986 the growth reduction on thinned oak plots was mitigated by the

379   release of the post-thinning phase. In 1989 drought induced a more pronounced growth reduction in

380   oaks of thinned plots. Nevertheless, also in concomitance of severe droughts events absolute BAI

381   values in thinned plots were significantly higher than those recorded in unthinned plots, in line with

382   the results obtain by Aldea et al. (2017) in thinned, mixed pine-oak stands.

383   Most trees recovered pre-disturbance growth levels within one or two years, confirming global

384   analyses of post-drought growth recovery (Anderegg et al. 2015), with wider interquartile ranges for

the recovery periods after the 1989 drought, when some oaks and pines took up to six years to fully recover growth levels.

The fitted GLMEs confirmed the opposite influence of thinning on resilience components (Rs, Rc, Rs and RR) in oak trees during the 1986 and 1989 droughts, while in 1995 the differences between thinned and unthinned plots were not significant. Tree-level drought sensitivity assessed with CorrSPEI generally had a higher weight than structural (DBH and age) and growth (RW and MS) parameters on resilience components. As expected, CorrSPEI was negatively related to drought Rs but positively related to Rc, Rs and RR. Oaks trees with larger DBH feature higher resilience against severe droughts and shorten the time to regian pre-drought growth rates (Camarero et al., 2016; Colangelo et al. 2017, González de Andrés et al. 2021). However, we are not able to claim a clear role of stem diameter on resilience components, with an opposite effect during 1995 drought as compared to 1986 and 1989 droughts.

Inter-annual growth variability estimated with mean sensitivity statistics (MS) is negatively related with drought resistance only in thinned plots and for the 1989 and 1995 events. The growth release following the thinning enhanced the MS in oaks trees making drought influence on growth more noticeable. Instead, competition in unthinned plots explains the production of complacent growth series and the lack of significance of MS in GLMs.

Soil and topographic features such as aspect and/or relative position of forest along the slope could also influence the effect of drought on tree growth (Lloret et al 2004). In our study case, little differences of slope aspects did not change oaks resilience components, with no differences detected by GLMEs in sensitivity between SE- and wetter SW-oriented slopes. A larger number of plots distributed at different aspects could help for better investigating this aspect.

Our results are supported by the outcomes of a recent meta-analysis showing a high variability of stand competition influence over tree growth resilience after drought (Castagneri et al. 2022). Our initial hypothesis of greater resistance and resilience of thinned plots oaks cannot be always confirmed but only for the first severe drought occurred after the treatment. A possible explanation is that forest management strategies such as thinning induce only short-term benefits but may not result in long-term adaptation to global change, that could be achieved promoting changes in species or genetic composition (Vilà-Cabrera et al. 2018).

5. Conclusions

Q. subpyrenaica stem radial growth showed a moderate post-thinning release especially in trees with lower DBH. Thinning induced long-lasting growth increase, reversed only by severe droughts. Following drought events reducing the amount of stored wood biomass, could lengthen the post-drought recovery time (usually 1-2 years), postpone the turnover cycle and the timing of other silvicultural treatments. At the same time, thinning could reduce competition between individuals for soil water, causing dieback, especially in overaged coppice stands. We argue that future studies should carefully plan and monitor thinning treatments in similar seasonally dry oak coppices which probably respond more positively to thinning treatments carried out during wetter decades and in regular intervals shorter than 20 years.

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