



Thinning increases tree growth by delaying drought-induced growth cessation in a Mediterranean evergreen oak coppice

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ABSTRACT

The Mediterranean evergreen oak coppices of Southern Europe are increasingly vulnerable to drought because of both the ongoing climate change that increases drought length and intensity, and the lack of forest management that induces a structural aging of the stands. Decreasing stand density through thinning has been widely regarded as a means to improve the resistance of evergreen oak forests to climate change by decreasing the competition for water amongst the remaining stems.

Data from a 30-years thinning experiment, that includes a control and four thinning intensity treatments (from 25% to 80% of basal area removed), in a coppiced holm oak (*Quercus ilex* L.) forest of southern France, was used to quantify the effects of thinning on stem growth. Building on the 'sink limitation' paradigm, which proposes that tree growth is controlled by phenology and climatic constraints and decoupled from carbon assimilation, we investigated if the effect of thinning on stem growth was explained by a delayed drought-induced growth cessation. Using a water balance model, we simulated the date of drought-induced growth cessation, previously found to correspond to the day of the year when water potential drops below a threshold of -1.1 MPa, and used it to predict growth in the different treatments of the thinning experiment.

Thinning increased long-term growth at the stem level but decreased the wood biomass at the stand level. Decreasing stem density, and hence the leaf area index, was simulated to delay the date of drought-induced growth cessation. A growth model based on the date of growth cessation explained 85% of the effect of thinning on stem growth over the 30-year period of the study, and 95% for the first five years after thinning.

The canopy density for which the effect of thinning is the most beneficial was found to maximize the growth duration without lifting completely the water limitation in summer. Moderate thinning had a sustained beneficial effect on the growth of all stem size classes, whereas stronger thinning intensities increased the size asymmetry of competition and their overall effect dropped faster. Our simple predictive model based on the simulation of the water balance as a function of stand density opens the way to providing management guidelines for the optimization of tree density as a function of water limitation in Mediterranean evergreen woodlands.

1. Introduction

The forest ecosystems around the Mediterranean basin have long been shaped by human activities, which influenced their distribution, structure and species composition (Blondel and Aronson, 1999; Quézel and Barbero, 1990). After a reduction of the Mediterranean forests cover to half of their potential area during the 19th century (Quézel,

1976), the deep socio-economic changes that occurred in the northern Mediterranean during the 20th century (e.g. the rural depopulation, the shift toward fossil fuels, the agriculture mechanisation and the Common Agricultural Policy) triggered an extensive spontaneous afforestation of abandoned fields (Mouillot et al., 2005; Poyatos et al., 2003; San Roman Sanz et al., 2013; Serra et al., 2008) as well as changes in forest structures (Poyatos et al., 2003; Quézel and Barbero, 1990). Holm oak

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(*Quercus ilex* L.) forests cover more than 6 Mha in the Mediterranean Basin, mostly in its western part (Ducrey, 1992) and about 350,000 ha in southern France where they were traditionally coppiced on short rotations (from 7 to 30 years; Ducrey, 1988) for charcoal or tannins production (Terradas, 1999). These coppices have been generally abandoned and under-logged since the second half of the 20th century, which resulted in alterations of the forests structure mainly due to aging (Barbero et al., 1990) and increased the forests sensitivity to perturbations such as pests, fire and drought (Ducrey, 1992; Rodríguez-Calcerrada et al., 2011).

General Circulation Models forecast a global increase in temperatures and local shifts in precipitation patterns (IPCC, 2014) and, although regional projections in climate change are still uncertain, it is likely that the Mediterranean region will be particularly exposed to increased temperatures and decreased precipitations (Giorgi and Lionello, 2008). The Mediterranean basin climate is characterized by mild wet winters and hot and dry summers that induce strong water limitations on the vegetation. Mediterranean forests will therefore probably undergo substantially stronger water limitations by the end of the 21st century (García-Ruiz et al., 2011; Ruffault et al., 2013a), which has already been observed in the south of France during the four last decades (Ruffault et al., 2013b) and raises the question of holm oak forests vulnerability in the future.

In this context, thinning has been considered as a way to address the structural aging (Ducrey, 1988) and, more recently, to mitigate the impact of climate change on holm oak forests (Rodríguez-Calcerrada et al., 2011). Thinning has a positive effect on growth and vigour of seasonally dry forests by decreasing the stand density and leaf area, and therefore releasing the competition for water amongst trees (Bréda et al., 1995; Keyser and Brown, 2014; Moreno and Cubera, 2008; Rodríguez-Calcerrada et al., 2011; Sohn et al., 2016). The subsequent increased water availability to the remaining trees is expected to improve their water status and hence their carbon assimilation (Limousin et al., 2010). Furthermore, a decreased seasonal water stress allows trees to sustain cell turgor and therefore to maintain the meristematic and cambial activity (Faticchi et al., 2014). Whether tree growth is limited by carbon assimilation (i.e. source limitation) or cambial activity (i.e. sink limitation) is still unclear and likely depends on the locally most limiting resource (Guillemot et al., 2015), but in either case growth should be favoured by thinning. In strongly water-constrained ecosystems such as Mediterranean forests, sink activity appears to be more limiting than carbon supply and to be the main driver of tree growth (Lempereur et al., 2015). Stem growth in holm oak forests has been reported to depend mainly on climatic variables, and especially on winter temperatures and on summer precipitations and temperatures (Corcuera et al., 2004; Gutiérrez et al., 2011). Lempereur et al. (2015) further proposed that holm oak growth could be predicted by the duration of spring growth, which onset depends on winter temperatures and which cessation is controlled by a water potential threshold. Here we hypothesize that thinning improves tree growth by decreasing water competition and consequently delaying the drought-induced summer growth cessation.

To test this hypothesis, we applied a daily water balance model to simulate the date of drought-induced growth cessation and predict tree growth in a *Quercus ilex* forest in which several thinning intensity treatments were conducted and followed over a 30-year period. The specific objectives of our study are to (i) quantify experimentally the long-term effect of thinning on tree growth and wood production in a Mediterranean *Q. ilex* coppice and (ii) verify the growth duration hypothesis proposed by Lempereur et al. (2015) in stands with a wide range of tree densities, using a modelling experiment.

2. Material and methods

2.1. Site description

The study site is located 35 km northwest of Montpellier, Southern France, in the state forest of Puéchabon (43°44′29″N, 3°35′45″E, 270 m a.s.l.). This forest has been managed as a coppice for centuries with a clear-cut frequency of approximately 25 years, but its exploitation stopped in the first half of the 20th century. Depending on the plots, the last clear cut took place in 1928 or 1942 and no fire or management occurred since then.

Q. ilex is the dominant species and forms a dense canopy at an average height of 5.5 m. The average stand density was 4700 stems ha⁻¹ in 2014 and the average diameter at breast height (DBH, measured at 1.30 m) was 8.4 cm. The main understory species are *Buxus sempervirens*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Pistacia terebinthus*, and *Phyllirea latifolia* and form together a sparse shrubby layer with less than 25% of coverage.

The shallow bedrock has a Jurassic limestone origin and the volumetric fraction of rocks in the soil is 75% in the top 0–50 cm and 90% below, making a limited soil reserve of extractable water around 140 mm. The stone-free fine fraction of the top-soil (within 0–50 cm) is a homogeneous silty clay loam (USDA texture triangle; 38.8% clay, 35.2% silt and 26% sand). Most of the root biomass is located in the top horizon, however *Q. ilex* roots have been observed to extract water up to a depth of 4.50 m.

The climate is Mediterranean with a mean annual rainfall of 924 mm over the period 1984–2014. Approximately 80% of the annual precipitation falls between September and April, and the summer months are characterized by an important water deficit. The mean annual temperature over the same period is 13.3 °C, the coldest month being January (5.5 °C) and the hottest month July (22.9 °C). A meteorological station located on-site since 1984 provides daily recordings of precipitation and minimum and maximum air temperature.

2.2. Thinning experiment

The thinning experiment started in 1986 and is composed of 15 plots of 1000 m² each, divided into 3 blocks. The last clear-cut occurred in 1942 for the blocks 1 and 2, and in 1928 for the block 3. Selective thinning from below (*sensu* Assman, 1970), which consists in removing the smallest stems to the benefit of the biggest ones, was applied in March 1986 when stems were 44 years old in the blocks 1 and 2 and 59 years old in the block 3. Five thinning intensities were applied where approximately 0%, 25%, 45%, 60% and 80% of the basal area was removed, hereafter named Control, T25%, T45%, T60% and T80%, respectively. Each treatment level was applied to a 1000 m² plot and replicated in each of the three blocks. The number of stems that were removed varies between 55%, for T25% and 90% for T80%.

The Diameter at Breast Height (DBH) of each *Q. ilex* stem was measured during two full inventories in 1986, before and after thinning. The Control and T80% plots of the block 1 were fully inventoried again in 2015. In each of the 15 plots, the DBH of a sub-sample of trees (45 stems in the thinned plots and 60 stems in the control plots) was measured annually from 1986 to 1991 and then again in 2013 and in 2015. DBH was consistently measured in winter during dry conditions using a diameter tape, at a location on the stem identified by a painted mark in order to minimize the error between repeated measures. In the thinned plots, the sampled stems were selected to be representative of the diameter distribution within each plot, whereas in the control plots more of the larger stems were selected in order to include stems of similar diameter than in the thinned plots. The characteristics of this sampling are summarized in Table S 1.

2.3. Data processing and analyses

The effect of thinning on tree growth was analysed based on the stem Basal Area Increment (BAI) as a measure of growth. BAI was calculated from DBH variations assuming a circular stem section, as the change in basal area ($BA = DBH^2 \times \pi/4$) between successive stem measurements.

Statistical analyses were conducted within R (R Core Team, Vienna, Austria), using linear models with the individual stems as the experimental unit and blocks and treatments as independent explanatory variables. Before the beginning of the experiment, the different plots within each of the 3 blocks had a comparable diameter distribution (Ducrey et al., 1987). However, the thinning from below introduced a strong heterogeneity in the diameter distributions among the plots. In order to deal with the induced differences in diameter among blocks and treatments, the analyses all included the stems initial diameter as a covariate. The resulting ANCOVA models (e.g. Fig. 4) were used to estimate the stem growth for a given common diameter. Pairwise differences in size-corrected BAI means between blocks and treatments were then assessed by post hoc analyses, using Holm's (1979) correction procedure for multiple comparisons.

As yearly growth measurements were available for the period 1986–1990 only, the effect of time on BAI was tested for each treatment with student's one sample t-tests on the average BAI for the periods 1991–2012 and 2013–2014 compared with the annual BAI for the period 1986–1990.

The proportions $n_{\text{sample},i}/n_{\text{total},i}$, where $n_{\text{sample},i}$ and $n_{\text{total},i}$ are, respectively, the number of sampled stems and the total number of stems for a given class of diameter – i , were estimated for all the plots at the start of the experiment in 1986. These proportions were used to estimate the actual number ($n_{\text{total},i}$) of stems for each diameter class the following years.

The individual stem biomass (in g) was then estimated using an allometric equation based on the stem DBH (in cm), that was calibrated for the site (Rambal et al., 2004):

$$\text{Biomass} = 191.2 \cdot \text{DBH}^{2.171} \quad (1)$$

The total exploitable wood biomass has then been calculated for each plot by summing the wood biomass of all the living stems with a DBH larger than 3 cm. This minimum size criterion excludes the understory and resprouts from the exploitable biomass. In order to take into account the uncertainty around the estimates of $n_{\text{total},i}$ the years following thinning, we calculated the standard-error of the plot wood biomass by bootstrapping (each plot was resampled 1000 times by random sampling with replacement and plot biomass was re-estimated for each resampling). These biomass estimates were compared against data from the exhaustive inventories of 2015 in the control and T80% plots of block 1. Both datasets gave consistent estimates of exploitable wood biomass (Fig. 2).

2.4. Water balance model

Daily predawn leaf water potential (Ψ_{lpd} in MPa) values were simulated at the plot scale with the water balance module from the process-based vegetation model SIERRA (Mouillot et al., 2001). In this module, the soil is characterized by its depth (p in mm), estimated to be 4500 mm which is the maximal *Q. ilex* rooting depth observed at our site (Rambal et al., 2003), and by its stone fraction (k). The vertical fine root distribution was set to 70% in the upper 1000 mm and 30% in the rest of the profile below down to 4500 mm, in order to reflect the higher fine root density in the topsoil. Ψ_{lpd} is assumed to be equal to the soil water potential (Ψ_s in MPa; Hinckley et al., 1978) plus a disequilibrium offset Ψ_{po} . Ψ_s fluctuates with the relative soil water content (θ) following a Campbell-type retention equation (Campbell, 1985). The resulting equation for computing Ψ_{lpd} is:

$$\Psi_{\text{lpd}} = -a\theta^b + \Psi_{\text{po}} \quad (2)$$

Variations in θ result from the balance between the precipitation (P , mm) and the water outputs, divided by the soil effective depth:

$$\Delta\theta = \frac{P - (In + R + D + ET)}{p(1-k)} \quad (3)$$

where In (mm) is the quantity of water intercepted and evaporated by the canopy, R (mm) and D (mm) the water loss due to surface runoff and deep drainage and ET (mm) the system evapotranspiration. ET is a function of the potential evapotranspiration (PET in mm), estimated according to the Priestley-Taylor formula (Priestley and Taylor, 1972) modulated by the soil water potential Ψ_s (Mouillot et al., 2001) and the plot Leaf Area Index (LAI), following the Beer-Lambert light extinction law:

$$ET = PET \cdot (1 - e^{-0.5 \cdot \text{LAI}}) \cdot \left(1 - \frac{\Psi_s}{\Psi_{s\text{max}}}\right) \quad (4)$$

The simulations Ψ_{lpd} have been validated against field measurements of Ψ_{lpd} obtained with a pressure chamber (PMS Instruments, Corvallis, OR, USA) on 4 individual trees in the immediate vicinity of the block 1. Those measurements were performed about 10 times a year between April and October from 2003 to 2009 (Limousin et al., 2012). The relationship between simulated and measured Ψ_{lpd} had an $R^2 = 0.94$.

2.5. Leaf area Index computation

The LAI needed to simulate ET in Eq. (4) is the total plot LAI. Before thinning, the contribution of the understory to the plot LAI was assumed to be negligible. The Leaf Area (LA in m^2) supported by each stem before and just after thinning was estimated from their DBH (in cm), using the following allometric equation, which was calibrated on-site (Rambal et al., 2004):

$$LA = 9.1 \cdot 10^{-2} \cdot \text{DBH}^{1.875} \quad (5)$$

LAI values before and right after thinning were then obtained for each plot as the ratio between the total plot LA obtained from Eq. (5) and the plot area.

Thinning can substantially modify the relationship between LA and DBH (Brix and Mitchell, 1983) or between LA and the sapwood area (Aussenac and Granier, 1988; Pothier and Margolis, 1991) and is also susceptible to allow the growth of understory species (Ducrey and Boisserie, 1992). For these reasons and because no LAI measurement was available for the period of the experiment, Eq. (5) was not used to simulate the post-thinning LAI dynamic, which was computed instead based on two assumptions. First, following the eco-hydrological equilibrium hypothesis (Eagleson, 1982), which was verified in *Q. ilex* dominated ecosystems (Hoff and Rambal, 2003; Joffre et al., 1999), we assumed that the LAI of undisturbed stands remained constant over time while the LAI of thinned plots progressively recovered pre-thinning values. In order to verify this hypothesis additional measurements of LAI by optical means (LI-COR LAI 2200 Plant Canopy Analyzer, Li-Cor Inc., Lincoln, NE, USA) were realized in 9 out of the 15 experimental plots in spring 2015 (Fig. S 1). Second, the dynamic of LAI recovery after thinning was assumed to be linear. In our model, each plot's LAI therefore varied linearly between its post-thinning value in 1986 to its pre-thinning value in 2014.

Thereafter, the calculated LAI values were used as input to the water balance model to simulate daily values of Ψ_s over the period 1986–2014 in each of the 15 experimental plots.

2.6. Stem growth model

BAI was simulated according to two model formulations: without (null model) or with (WB model) the effect of the water balance on

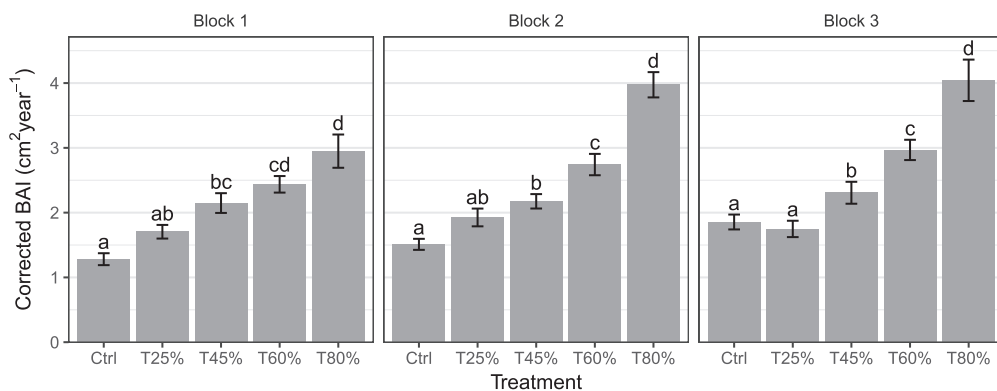


Fig. 1. Mean annual stem Basal Area Increment (BAI) over the period 1986–2015, corrected for the size effect within each block (mean ± SE; n = 41–66 trees plot⁻¹). Different letters denote different BAI values among treatments within each block (pairwise t-test at p < .05).

growth. The null model was intended to isolate the effect of thinning on diameter distribution. In the null model, BAI was computed as a function of the initial DBH (1985), which was calibrated over the period 1986–2014 in the control plots (BAI_{size} in cm²):

$$BAI_{size} = 0.28 \cdot DBH - 0.89 \quad (6)$$

To include the effect of water balance on growth, the WB model was based on the work of Lempereur et al. (2015), who showed that *Q. ilex* stem growth is linearly related to the duration of spring growth (Δt , day). The relationship between the *Q. ilex* stem growth and Δt (BAI _{Δt}) was calibrated on-site using ring-width chronologies from 12 stems. The stems were selected outside of the plots among the largest size classes of the stand (10 cm < DBH < 16 cm) and were cut down in 2008. Cross-sections were collected at stump height and the longest growth radius for each cross-section were selected and compared pairwise under binocular magnifier. Cross-correlation coefficients on annual tree-ring indices calculated among the twelve individual series were all higher than 0.6 (P-value < 0.05). The ring width at stump height and along the longest radius was then rescaled to the tree DBH at the time of the cut after correcting for the tapering and the bark thickness (see methodological details on ring-width measurements in Lempereur et al., 2017). The following equation was calibrated over the period 1984–2008 (Lempereur et al., 2017).

$$BAI_{\Delta t} = 0.134 \cdot \Delta t + 1.23 \quad (7)$$

where Δt is defined as the number of days between growth onset (t_0 , DOY), which is a function of the mean winter temperature (January to March), and growth cessation (t_1 , DOY), defined as the first day of the year when Ψ_{ipd} reaches a threshold of -1.1 MPa (Lempereur et al., 2017). t_1 was calculated for each year and each plot based on the simulated Ψ_{ipd} . In the WB model growth is then calculated as the product of BAI _{Δt} and the ratio between BAI_{size} at the plot average DBH and BAI_{size} at DBH = 8.8 cm (8.8 cm being the grand mean DBH in 1985 of all the trees that have been used to build the Eq. (7)).

Growth was simulated according to both model formulations for the periods 1986–1990, 1991–2012, 2013–2014 and 1986–2014.

3. Results

3.1. Experimental effect of thinning on basal area increment and wood production

Before thinning, the mean stem diameter in blocks 1, 2 and 3 was respectively 4.9 cm, 5.5 cm and 7.4 cm and their stem density was respectively 8800 stems ha⁻¹, 7700 stems ha⁻¹ and 6300 stems ha⁻¹, which was representative of the natural heterogeneity of the Puéchabon state forest. During the 30 years of the study, the control plots underwent a structural aging and, for instance, in the control plot of block 1 the basal area increased from 20 m² ha⁻¹ to 28 m² ha⁻¹ while the stem density decreased from 7600 stems ha⁻¹ to 4800 stems ha⁻¹.

Thinning had an overall positive effect on tree growth in the 3 blocks over the period 1986–2014, and the effect increased with thinning intensity (p < .0001 for blocs 1, 2 and 3; Fig. 1). The correction of BAI by DBH shows that the thinning effect on stem growth was not due merely to the selection of bigger trees. The average DBH-corrected BAI was not significantly different between the control plots and the T25% treatments but increased for stronger thinning intensities was the largest in the T80% plots (Fig. 1). Thus, we did not observe a saturation of the thinning effect on BAI even for very strong thinning intensities. Because stem diameter had a strong effect on BAI and was larger on average in the thinned plots, the thinning effect on growth was even more pronounced for uncorrected BAI values (i.e. the raw plot average BAI; Fig. S 2).

The initial exploitable wood biomass in the blocks 1, 2 and 3 was respectively 60 ± 1.6 Mg ha⁻¹, 78 ± 1.1 Mg ha⁻¹ and 105 ± 3.1 Mg ha⁻¹ (mean ± SE, n = 5). Thinning significantly reduced the standing wood biomass in all the thinned plots, in relation to the thinning intensity and biomass was reduced by up to 75% in the

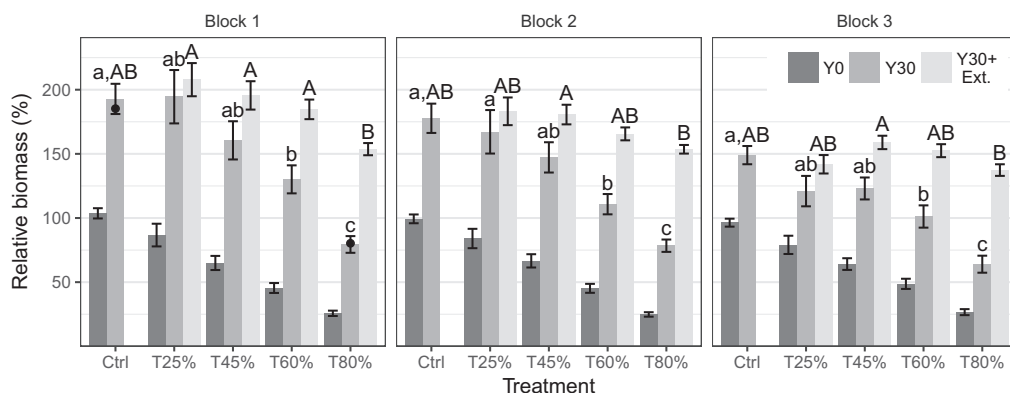


Fig. 2. Exploitable wood biomass per plot just after thinning (in 1986, Y0), 30 years after thinning (in 2015, Y30) and the sum of the standing biomass 30 years after thinning plus the biomass extracted during thinning (Y30 + Ext.), relative to the biomass before thinning (1985). Results are bootstrapped averages and standard errors. Significant differences (p < .05) in biomass between treatments and within each block are shown by lower case letters for Y30 and by upper case letters for Y30 + Ext. The two black dots show the biomass in the control and T80% plots of the block 1 as estimated using the exhaustive inventory done in 2015.

treatment T80% (Fig. 2). In 2015, 30 years after thinning (Y30) the biomass in the control plots had increased by 152–183%, whereas the biomass of the thinned plots was always lower or similar to the biomass in the control plots and tended to decrease with thinning intensity. When accounting for the wood biomass that was extracted during the thinning treatments, the total wood biomass of the thinned plots (i.e. extracted + standing) was always statistically equal to that of the control plots, and tended to exceed it for the low to medium thinning intensities (T25–45%).

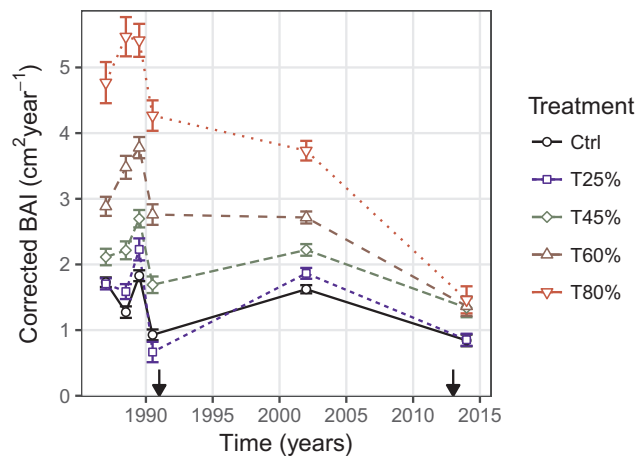


Fig. 3. Size-corrected annual stem Basal Area Increment (BAI) for each period between two consecutive measures. Error bars represent the standard error (n = 124–192). Arrows show the measure cessation and resuming dates.

3.2. Temporal trend of the thinning effect on BAI

Along the 30 years of the study BAI slightly decreased in the control ($0.65 \text{ cm}^2 \text{ year}^{-1}$ between the periods 1986–1990 and 2013–2014, $p < .05$; Table 1). Except for the treatment T25% for which it was not significant, the decrease of growth over time was more pronounced in the thinned plots (BAI difference between 1986–1990 and 2013–2014 = $0.83 \text{ cm}^2 \text{ year}^{-1}$, $p < .05$ for T45%; $1.79 \text{ cm}^2 \text{ year}^{-1}$, $p < .01$ for T60%, and of $3.47 \text{ cm}^2 \text{ year}^{-1}$, $p < .001$) and stronger in heavily thinned treatments. The effect of thinning on growth (i.e. the growth difference between treatments and control) only slightly decreased for T45% between 1986–1990 and 2013–2014 ($0.17 \text{ cm}^2 \text{ year}^{-1}$, $p < 0.1$), but it was significantly reduced for T60% ($1.14 \text{ cm}^2 \text{ year}^{-1}$, $p < .005$) and T80% ($2.82 \text{ cm}^2 \text{ year}^{-1}$, $p < .0001$). As a result, 28 years after thinning, BAI was similar among the treatments T45%, T60% and T80% ($p = 0.90$) but it was still significantly larger than in the control and T25% treatments ($p < .01$, $p < .01$ and $p < .001$ for T45%, T60% and T80%, respectively).

Table 1

Annual stem Basal Area Increment (BAI; $\text{cm}^2 \text{ year}^{-1}$) estimated at the overall mean DBH for each time period between consecutive measurements. Results are means \pm SE. Characters represent significant differences between treatments for each period ($p < .05$). For each treatment, periods for which growth significantly differs from that of the period 1986–1990 are denoted with asterisks ($p < .05$: *, $p < .01$: **, $p < .001$: ***).

Treatment	Control	T25%	T45%	T60%	T80%
1986–1990	1.5 ± 0.06^a	1.58 ± 0.08^a	2.17 ± 0.11^b	3.16 ± 0.12^c	4.94 ± 0.23^d
1991–2012	1.62 ± 0.06^a	1.86 ± 0.08^{ab}	2.22 ± 0.09^b	2.72 ± 0.09^c	$3.73 \pm 0.15^{d*}$
2013–2014	$0.84 \pm 0.09^{a*}$	0.85 ± 0.09^a	$1.34 \pm 0.14^{b*}$	$1.36 \pm 0.15^{b**}$	$1.46 \pm 0.21^{b***}$

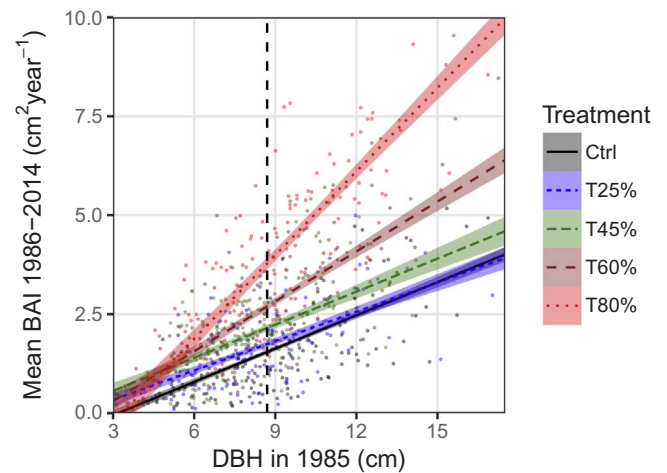


Fig. 4. Relationship between mean annual stem Basal Area Increment (BAI) over the period 1986–2014 and initial stem DBH in 1985. The regression lines represent the ANCOVA model including the effect of DBH, treatment and their interaction (all the effects are significant: $p < .0001$; $R^2 = 0.72$). Shaded areas show the standard error and the vertical dashed line, the mean DBH in 1985 (8.8 cm).

3.3. Thinning effect on the size-growth relationship

The positive effect of thinning on BAI was dependent on stem size ($p < .0001$) and the relationship between initial DBH and mean annual BAI over the period 1986–2014 differed significantly among thinning intensities ($p < .0001$; Fig. 4). Thinning intensity had distinct effects on the slope and the intercept of this relationship. The slope of the size-growth relationship was similar among control, T25% and T45% treatments but increased significantly for the strong thinning intensities T60% and T80% (Table 2). The x-axis intercept, tended to decrease for thinning of low and mild intensity, the lowest value being reached for T45%, and increased back to the value of the control for the strongest thinning intensities.

3.4. Modelling the effect of thinning on growth through the date of growth cessation

We tested the hypothesis that a delayed drought-induced growth cessation could explain the effect of thinning on stem growth. Using the water balance model, we simulated t_1 dependency upon LAI (Fig. 5). In spite of an important inter-annual variability due to climatic variations, we predicted later t_1 for lower LAI. For LAI values below 1.4, the summer drought-induced cessation does not occur every year and t_1 is then bounded to 300 (late October), which is the average DOY corresponding to the end of the autumn growth period (Lempereur et al. 2015). The number of years for which a drought-induced growth cessation is simulated decreases with LAI for LAI < 1.4 and growth duration is never limited by drought for LAI < 0.7.

Table 2

Parameters (mean ± SE; n = 124–192) of the regression lines between the BAI and the DBH, for each treatment. Letters denote significant differences at p < .05. DBH threshold is the intercept with the x-axis.

Treatment	Control	T25%	T45%	T60%	T80%
Slope (cm ² year ⁻¹ cm ⁻¹)	0.280 ± 0.026 ^a	0.246 ± 0.036 ^a	0.278 ± 0.042 ^a	0.420 ± 0.035 ^b	0.704 ± 0.033 ^c
DBH threshold (cm)	3.2 ± 0.4 ^a	1.8 ± 0.8 ^b	1.0 ± 0.7 ^c	2.3 ± 0.5 ^d	3.3 ± 0.3 ^a

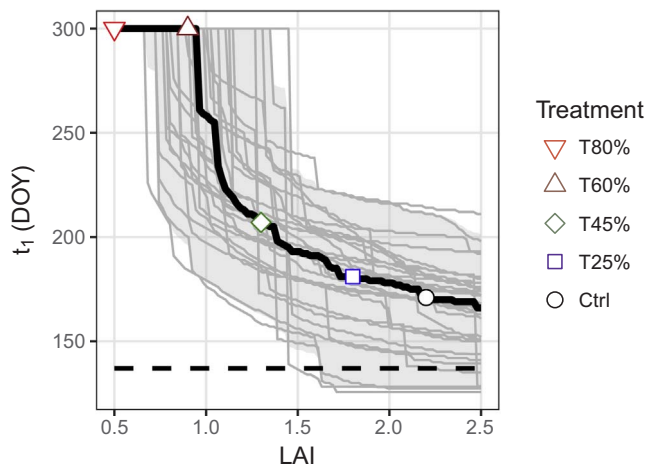


Fig. 5. Simulated date of drought-induced growth cessation (t_1 , the day of year when simulated predawn leaf water potential reaches a threshold of -1.1 MPa, bounded to DOY 300 - late October) as a function of LAI. The grey solid lines represent the yearly values of t_1 over the period 1984–2014, the black solid line is the median and the shaded area represents the 95% interval. The points represent the median t_1 corresponding to the average post-thinning LAI in each treatment. The dashed black line represents the average date of growth onset (t_0) on the same period.

In our simulations, LAI was minimum, and therefore t_1 maximum, the years following thinning. LAI was then progressively increased to pre-thinning values over the following years. Accounting for the effect of LAI on the date of growth cessation made the WB model more accurate than the null model for predicting growth. On average, the null model predicted a BAI of 1.60 ± 0.35 cm² year⁻¹ for the control plots over the period 1986–2014 (Fig. 6). The null model predicted a slight growth increase with thinning intensity (1986–2014, T80%: BAI = 1.86 ± 0.43 cm² year⁻¹) as the treatment induced a shift in the DBH mean and distribution of the plots. Over 1986–2014, the null model therefore explained 34% of the inter-plot BAI variations

(Table 3). Its performance was higher however at the end of the study (2013–2014: $R^2 = 0.45$) than at the beginning (1986–1990: $R^2 = 0.27$).

In simulations using the WB model, the predicted spring growth duration varied greatly, depending on the treatment and year. It was shortest for the control treatment ($\Delta t = 33$ days on average) and longest for T85% ($\Delta t = 80$ days). All treatments combined Δt was longer at the beginning of the study ($\Delta t = 95$ days during years 1986–1990) than at the end ($\Delta t = 26$ days during years 2013–2014). These variations in Δt led the WB model to predict larger growth at the beginning (BAI = 2.25 ± 0.86 cm² year⁻¹ during years 1986–1990) than at the end of the study (BAI = 1.51 ± 0.31 cm² year⁻¹ during years 2013–2014). The WB model also predicted a larger growth for thinned plots (e.g. T80% on the period 1986–2014: BAI = 3.66 ± 0.39 cm² year⁻¹) than for control plots (BAI = 1.66 ± 0.30 cm² year⁻¹). The WB model could thus explain 85% of the inter-plot BAI variation over the period 1986–2014, which was 2.5 times higher than the null model. Contrary to the null model, the WB model performed best at the beginning of the study, explaining 95% of the inter-plot variations over the period 1986–1990. The WB model performance decreased through time, and while it was still high over the period 1991–2012 ($R^2 = 0.79$), it was comparable to the null model performance over the last period of the study ($R^2 = 0.44$).

Although the WB model performed better than the null model, both models exhibited significant departure from the 1:1 line, when regressed against measured growth, except for the period 2013–2014. While the growth simulations in the control and light thinning treatments (T25% and T45%) were relatively close to the measurements, the growth of plots with a stronger thinning intensity (T60% and T80%) was consistently underestimated, except on the period 2013–2014.

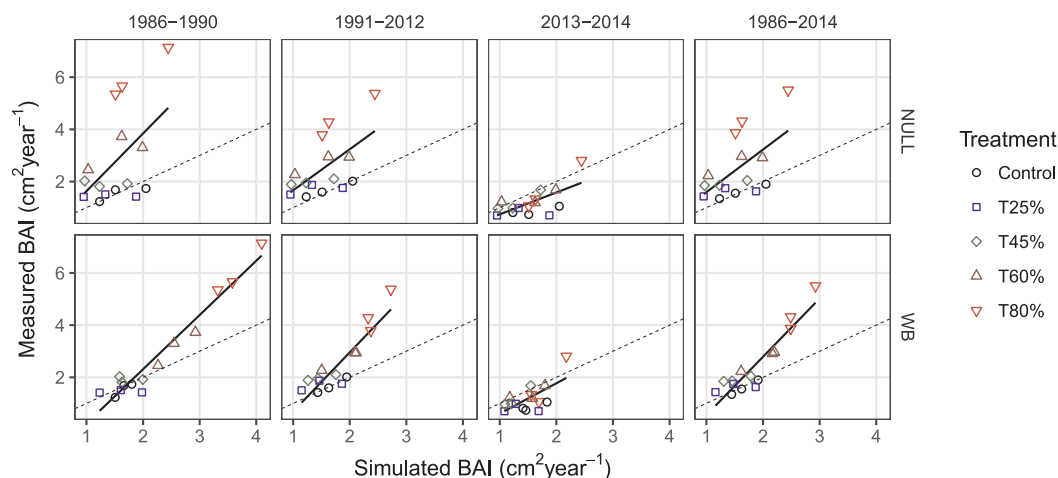


Fig. 6. Relation between the measured and simulated average annual Basal Area Increment (BAI). Simulations were done accounting for the effect of LAI on the water balance (WB model) or not (null model), for the 3 periods 1986–1990, 1991–2012 and 2013–2014 and for the overall period of the study (1986–2014). Black lines are regression lines and the dashed lines represent the 1:1 line.

Table 3

R² and slope of the regression lines between measured and simulated BAI when taking into account (WB model) or not (null model) the effect of Δt on stem growth for the 3 periods 1986–1990, 1991–2012 and 2013–2014 and for the overall period of the study (1986–2014). The best of the two models for each period and for each metric of model performance is pointed out in bold.

Period	Null model					WB model				
	Slope	R ²	AIC	RMSE Ctrl-T45%	RMSE T60-80%	Slope	R ²	AIC	RMSE Ctrl-T45%	RMSE T60-80%
1986–1990	2.2	0.27	157	0.48	3.19	2.1	0.95	143	0.27	1.78
1991–2012	1.6	0.35	154	0.49	2.04	2.3	0.79	140	0.34	1.57
2013–2014	0.8	0.45	153	0.61	0.35	1.2	0.44	145	0.55	0.40
1986–2014	1.6	0.34	155	0.44	2.09	2.2	0.85	138	0.28	1.49

4. Discussion

4.1. Thinning improves stem growth through a delayed drought-induced growth cessation

Stem growth in the control plots was within the range of values commonly observed for *Q. ilex* stands of similar age and structure (e.g. Camarero et al., 2016). Thinning substantially increased the growth of *Q. ilex* stems in the three blocks of our study (Fig. 1), consistently with previous results reporting radial growth improvement by thinning in Mediterranean forests (Cañellas et al., 2004; Mayor and Rodà, 1993) and other forested biomes (Aussenac and Granier, 1988; Bréda et al., 1995; Keyser and Brown, 2014; Mäkinen and Isomäki, 2004; Sohn et al., 2016).

The LAI reduction due to thinning is expected to result in reduced stand evapo-transpiration and soil water depletion, allowing for better stomatal conductance, carbon assimilation, or prolonged non water-limited growth periods (Bréda et al., 1995; Gebhardt et al., 2014). Accordingly, the date of spring growth cessation t_1 was simulated to occur later as the stand LAI decreased. Taking into account the effect of the daily plant water status on t_1 in the WB model allowed to explain 85% (95% for the period 1986–1990) of the growth differences among plots compared to 34% (27% for the period 1986–1990) when this effect was not included (Table 3). The increased growth duration resulting from a lower LAI in thinned plots therefore explained most of the thinning effect on stem growth. This supports our initial hypothesis that the effect of thinning on stem growth is mostly due to a lower water stress during summer (Aussenac and Granier, 1988; Bréda and Granier, 1996; Giuggiola et al., 2016; Moreno and Cubera, 2008; Rodríguez-Calcerrada et al., 2011), and in particular to a delayed drought-induced cessation of stem growth during summer, and hence an extended growth period duration (Brzostek et al., 2014; Lempereur et al., 2015). Wood formation is often paused in summer under Mediterranean climate (Camarero et al., 2010; Gutiérrez et al., 2011; Pacheco et al., 2017), presumably as a result of the inhibition of cell enlargement by low water potentials (Cosgrove, 1993a; Lockhart, 1965). The water potential threshold used to calculate the date of drought-induced growth cessation thus certainly corresponds to the limit below which cell turgor becomes too low to sustain cell enlargement in the forming xylem (Cosgrove, 1993b; Fatichi et al., 2014; Körner, 2015; Salomón et al., 2017).

Although the WB model explained most of the effect of thinning on stem growth, it clearly underestimated growth for strong thinning intensities (Fig. 6; T60–80%). In Mediterranean forests such as our study site, water availability is considered as the most limiting resource for tree growth (Moreno and Cubera, 2008; Rodríguez-Calcerrada et al., 2011) and is therefore expected to outweigh other factors in explaining the effect of thinning (Giuggiola et al., 2016). However factors not accounted for in our model, such as light (Elkin et al., 2015; Goudiaby et al., 2011) or nutrients availability (Leuzinger and Hättenschwiler, 2013), are also improved by thinning and could contribute to the thinning effect on stem growth in stands of lower densities.

Alternatively, such a bias in the simulations could be the

consequence of inadequate assumptions on the LAI recovery. Based on the eco-hydrological equilibrium hypothesis (Eagleson, 1982), we first assumed that the plot's LAI should eventually recover pre-thinning values. This assumption is corroborated by previous studies that verified the eco-hydrological equilibrium hypothesis in *Q. ilex* dominated ecosystems (Hoff and Rambal, 2003; Joffre et al., 1999) and by LAI measurement realized 30 years after thinning, which exhibited little differences among treatments (Fig. S 1). Second, the assumption of a linear LAI recovery seems conservative in regard to other studies that describe a rapid recovery after thinning, usually in a few years (Le Dantec et al., 2000; McJannet and Vertessy, 2001). However, underestimating the LAI recovery rate would likely have resulted in an overestimation of the stem growth during the second period of the study (1991–2012) compared to the first period (1986–1990), whereas the contrary was observed instead (Table 3). The LAI recovery might therefore be slower at our site where *Q. ilex* grows remarkably slowly, compared to more productive stands.

More likely, the simulation bias suggests that the increase in water availability after thinning did not only result in improved growth duration but also increased stem growth rate. By decreasing the stand evaporative surface, thinning diminishes transpiration at the stand scale (Jimenez et al., 2008; McJannet and Vertessy, 2001) and thus delays the summer edaphic drought and growth cessation. However, the reduced stand density also implies that the remaining stems have a larger share of the water resource, which increases transpiration at the tree level (Jimenez et al., 2008; Morikawa et al., 1986). Consequently, thinning likely improves growth through both increased growth duration and growth rate (Aussenac and Granier, 1988; Bréda et al., 1995). A higher water use per individual tree may favour the growth rate either through larger carbon assimilation (Flexas and Medrano, 2002) (i.e. release of the source limitation) or further release of the sink limitation on growth (Fatichi et al., 2014) (e.g. increase in the cambial cell expansion rate). Whether the growth rate is source- or sink-limited has deep consequences on the modelling of the processes controlling growth. Understanding the drivers of stem growth rate in addition to the drivers of stem growth duration, and especially the respective roles of source and sink limitations in determining trees growth rate therefore appears necessary here in order to model stem growth in strongly thinned stands.

4.2. Moderate thinning as a multi-purpose management practice

Increasing forest resistance and resilience to extreme events, and in particular to drought conditions, is an important objective of silviculture in the Mediterranean area, where the combination of structural aging (Barbero et al., 1990), increased temperatures and decreased precipitations (Giorgi and Lionello, 2008) will likely put the forests at risk in the future (Allen et al., 2015; McDowell and Allen, 2015). Drought-induced dieback has already been observed in *Quercus ilex* coppices of Southern Europe during most severe episodes, and this phenomenon seems exacerbated by slow growth (Camarero et al., 2016; Gentilesca et al., 2017). Thinning could therefore mitigate the effects of climate change on Mediterranean forests by reducing water stress

(Rodríguez-Calcerrada et al., 2011), and increasing individual stem growth, which is an indicator of tree vigour (Waring et al., 1980). In dense and unmanaged *Quercus ilex* coppices such as in our site, self-thinning remains substantial even more than 60 years after a clear-cut (around 1.4% year⁻¹, data not shown). By removing the weakest stems that are the most susceptible to die (Camarero et al., 2016), thinning accelerates the natural reduction of the stand density and reduces very significantly the mortality rate (Rodríguez-Calcerrada et al., 2011). However, in spite of its important positive effect on stem growth, thinning also resulted in a decrease of the standing wood biomass at the plot scale relative to the control. Even 30 years after thinning, the reduction was still substantial for strong thinning intensities (T60–80%; Fig. 2). This result is in line with the expected effect of thinning on stand biomass as reviewed by Zeide (2001) that increased growth of the remaining stems rarely compensates for the biomass and the growth potential of the removed stems. The overall wood production of the thinned plots (i.e. standing + extracted) was nonetheless statistically equal to the control for all thinning intensities (Fig. 2). This suggests that on overall the effect of thinning is neutral regarding wood production of holm oak coppices, and potentially also carbon sequestration. Thinning could thus be preferred over clear-cutting for harvesting wood energy in a context where climate change fosters the need for alternatives to fossil fuels (Canadell et al., 2007; Edenhofer et al., 2012) and the use of wood biomass as a source of renewable energy (FAO, 2016). Additionally, thinning is potentially beneficial in terms of ecosystem function and services such as reducing the risk of fire hazard (Crecente-Campo et al., 2009; Graham et al., 1999; Moritz et al., 2014) or increasing the ground water supply (Ameztegui et al., 2017; del Campo et al., 2014), and have a lower impact than clear-cutting on soil erosion and water quality (McClurkin et al., 1987) or biodiversity (Torrás and Saura, 2008).

The outcomes of thinning depend, however, on the thinning intensity and the site conditions (Gracia and Retana, 1996; Jacobson et al., 2000; Misson et al., 2003a, Misson et al., 2003b). The optimal thinning intensity to target is thus likely to vary locally according to soil and climate (Ameztegui et al., 2017; Cao et al., 2006). At our study site, the sum of standing and extracted wood biomass was highest for moderate thinning intensities (T25%–T45%), although not significantly higher than in the control (Fig. 2). Moderate thinning also exhibited a more stable effect on growth through the 30 years of the study. In 2013–2014 the growth in T60% and T80% was similar to that of T45%, which was still higher than that of the control and T25% (Fig. 3), suggesting that moderate thinning could optimize the coppice productivity over the long-term. In addition, the development of the understory observed by Ducrey and Boisserie (1992) at the study site in 1989, increased with the thinning intensity due to the resprouts of *Q. ilex* and shrubs. In 2015, the understory was still more abundant in the strongly thinned plots (T60–80%) than in the low and moderately thinned plots (T25–45%; authors' personal observation), thus increasing the fire hazard because of the accumulation of fine fuel. Taken together, these results point out to moderate thinning as the best management practice at our study site.

4.3. Managing stand density to optimize the competition for water

Stand response to thinning also depends on the relation of competition between the remaining stems (Gillespie and Hocker, 1986). In our study, stems of all size-classes benefited more evenly from the reduced competition for low to medium thinning intensities (T25–45%) than for heavy thinning (Fig. 4). The intercept with the x-axis of the relationship between BAI and DBH can be interpreted as the minimum DBH above which growth occurs, whereas its slope represents the growth efficiency (Le Moguédec and Dhôte, 2012) or the degree of size-asymmetry of growth (i.e. the ability of large stems to grow faster than smaller ones; Guillemot et al., 2014). Consistently with previous studies showing that the size-asymmetry of competition is positively correlated with site

fertility (Forrester et al., 2013; Guillemot et al., 2014; Pretzsch and Biber, 2010), we observed that the strongest thinning intensities (T60–80%) resulted in an increase of the slope of the BAI-DBH relationship (Table 2). In the strongly thinned plots, the larger stems therefore benefited more from the improved resource availability induced by thinning, presumably because they have a higher growth potential (Stephenson et al., 2014) and a higher capacity of exploration through root production (Lopez et al., 2003; Parsons et al., 1994) and crown development (Muth and Bazzaz, 2003; Pretzsch and Dieler, 2012). For moderate thinning intensities (T25%–T45%), on the contrary, the growth increase resulted from a lower intercept rather than from a steeper slope, indicating that stems of all sizes grew faster as in response to reduced competition (Table 2). These results suggest that an optimal stand density exists that maximizes both the number of stems per unit area and the growth of these stems, while further reducing stand density below this optimum increases the size asymmetry in competition for water (Schwinning and Weiner, 1998).

The simulations of t_1 as a function of LAI showed that at high LAI values drought stress might occur too soon to allow any stem growth in dry years. On the opposite, a drought stress severe enough to impair stem growth does not occur in wet years below a given value of LAI (Fig. 5). The effect of thinning on reducing the water stress thus levels off at low residual densities, and the excess water might be lost in drainage or runoff, or result in more asymmetric competition as a result of the growth of the largest stems and the understory. Based on these results, we argue that the optimal LAI should maximize the duration of the growth period without cancelling completely the summer drought in wetter years. The optimal LAI can be identified using our water balance model and depends on the different factors influencing the stand water balance, such as the soil water holding capacity, the evaporative demand and the seasonal and inter-annual variability of precipitation. Following this hypothesis, the optimal thinning intensity at our site is realized for a LAI around 1.4, which corresponds approximately to the treatment T45%. This seems supported by our results whether we consider the wood biomass production, the sustainability of the thinning effect, the stem-to-stem competition, or the understory regrowth.

5. Conclusion

We observed that thinning strongly improved *Q. ilex* stem growth at our study site as a consequence of a delayed drought-induced growth cessation in summer. The resulting increase in growth duration explained most of the effect of thinning on stem growth, which highlights the relevance of integrating sink-limitation processes to simulate growth in water limited environments. Because our water balance model and phenological approach underestimated the effect of thinning on stem growth, we suggest, however, that the effect of thinning on tree growth rate should also be taken into account.

Moderate thinning that delays the drought onset without completely lifting the growth limitation by summer drought was observed to be the best thinning intensity in terms of wood production, sustainability of the effect, stem-to-stem competition and understory abundance. Considering the many positive effects of thinning on ecosystem functions and services, we argue that it is a suitable management practice to adapt Mediterranean *Q. ilex* stands to the current climatic and socio-economic challenges. Our water balance model approach seems adequate to assess the optimum thinning intensity as a function of local climatic and edaphic conditions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.11.030>.

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