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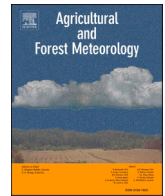
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Thinning enhances hydraulic safety but not growth resistance to drought in Atlas cedar on the long-term

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ABSTRACT

Reducing forest stand density through thinning has the potential to improve tree vigor and mitigate hydraulic risk as it reduces competition for water, thereby improving soil water availability at the tree level. However, these positive effects might be compensated over time by the growth of the remaining trees and understory, an aspect that remains understudied. We investigated the long-term effects of thinning on vegetation regrowth, growth resistance to drought and hydraulic risk in a 1968 *Cedrus atlantica* plantation in southeastern France where contrasting thinning intensities were applied in 1992, resulting in stand densities of 1200 (unthinned control), 800, 600 and 400 trees.ha⁻¹. Field measurements were conducted in 2017, 25 years after thinning, during the most severe drought since the trial's establishment. To explore underlying mechanisms, they were complemented by a modeling test using SurEau within the cohort-based model MEDFATE.

Our results show that 25 years after thinning, despite similar stand leaf area index across all thinning treatments, trees in thinned stands exhibited significantly higher growth and reduced hydraulic risk (i.e., higher water potential, wider hydraulic safety margins, lower native embolism) than in the unthinned control. Model simulations suggest that this long-term reduction of hydraulic risk by thinning may result from niche partitioning between the overstory and the understory, either spatially (due to differences in rooting depth) or temporally (due to differences in ecophysiological properties). Interestingly, growth resistance to drought did not differ significantly among thinning treatments. Our results emphasize the potential long-lasting role of thinning in reducing hydraulic risk despite vegetation regrowth. Moreover, this study shows that ecophysiological indicators provide a more accurate understanding of tree drought responses during a specific drought event than the commonly used growth-based indicators.

1. Introduction

Forests are facing more frequent, long and intense droughts due to climate change, leading to an increase in drought-induced mortality events all around the world (Hammond et al., 2022; Senf et al., 2020)

and affecting crucial ecosystems functions such as carbon uptake or wood production (IPBES, 2019; Van der Woude et al., 2023). In this context, high expectations are placed on management strategies to foster forest adaptation to drought. Among them, thinning is one of the most robust and popular, often combined with understory management

Abbreviation: BAI, Basal Area Increment; CBH, Circumference at Breast Height; DBH, Diameter at Breast Height; HSM, Hydraulic Safety Margin; LAI, Leaf Area Index; PAR, Photosynthetically Active Radiation; PLC, Percent Loss of Conductivity; RW, Ring width; VPD, Vapor Pressure Deficit.

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(Vilà-Cabrera et al., 2018). By reducing stand leaf area, thinning decreases stand-level rainfall interception and transpiration, thereby releasing the competition for water and enhancing tree growth and vigor (Aussenac and Granier, 1988; Bréda et al., 1995; Cabon et al., 2018; Sohn et al., 2016). An increase in wind exposure in thinned stands can further promote growth (Russel et al., 2018; Niez et al., 2019).

Thinning effects on drought response have largely been assessed using radial growth-based indicators, showing reduced growth sensitivity to drought (i.e., a weaker drought-growth relationship; Castagneri et al., 2022) and improved resistance to drought *sensu* Lloret (Castagneri et al., 2022; Sohn et al., 2016). However, two important shortcomings remain. First, more direct ecophysiological indicators of water stress such as water potential, hydraulic safety margins or native embolism, have been rarely employed, despite their importance as indicators of tree mortality risk (Choat et al., 2018; Sanchez-Martinez et al., 2023). The few studies measuring tree water potential consistently reported a lower drought-induced stress in thinned stands, evidenced by less negative water potential than unthinned controls within the one to four years following thinning (Bréda et al., 1995; Moreno and Cubera, 2008; Rodríguez-Calcerrada et al., 2011; Simonin et al., 2006; Stoneman et al., 1996; Donner, 1984; McDowell et al., 2008; McDowell, 2006). Second, only a few studies have addressed long-term effects (>10–15 years). Using growth-based indicators, Manrique Alba et al. (2020) and Giugliola et al. (2016) found reduced growth sensitivity to drought even 20 and 45 years after thinning for xeric *Pinus halepensis* and *Pinus sylvestris* stands, respectively, whereas Thompson et al. (2018) reported no difference in growth resistance to drought 30 years after thinning for *Pseudotsuga menziesii*. To our knowledge, only Whitehead et al. (1984) measured the long-term effect of thinning on tree water relations, reporting slightly lower water stress in thinned *P. sylvestris* 14 years after thinning, when leaf area index (LAI) remained lower than in the control.

In the years following the thinning operation, the remaining tree crowns expand in the space newly available, their leaf area too, and consequently their transpiration increases, which might dampen the positive effect of thinning on stand water consumption (D'Amato et al., 2013; Sohn et al., 2013; Del Campo et al., 2019). At the same time, thinning also fosters root system expansion (both vertically and horizontally; Vargas et al., 2009; Olesinski et al., 2012; Lopez et al., 2003; Parsons et al., 1994; Nielson and Dencker, 1988; Kerhoulas et al., 2013; Moreno et al., 2005) which enhances the tree ability to access larger water resources. This effect is reinforced by the fact that thinning operations, conducted “from below”, typically favor dominant and vigorous trees that may already have more developed root systems than their removed competitors (Gavin et al., 2020); yet, a post-thinning reduction in average fine root depth has also been suggested by Giugliola et al. (2016), as the remaining trees have enhanced access to the shallower soil water. The increase in light and precipitation reaching the ground after canopy opening can trigger understory development, which competes for water and contributes to increased stand water demand (Balandier et al., 2022). As understory develops, competition may shift from intra- to inter-specific, potentially amplifying or mitigating the overstory water stress through several mechanisms.

First, in mixtures, species may rely on different soil layers for water uptake (spatial root niche partitioning; Laclau et al., 2013; Schume et al., 2004; Hackmann et al., 2025), and tree root production can be enhanced when mixed with an understory (Laclau et al., 2013). Furthermore, trees might benefit from hydraulic lift by a more deep-rooted understory, although empirical evidence remains limited (Moreira et al., 2003; Hawkins et al., 2009; Filella and Penuelas, 2003). Overall, belowground resource partitioning between overstory and understory remains poorly understood due to scarce data on rooting depth and distribution (Balandier et al., 2022). Second, species can also differ in their drought-coping strategies, depending on stomatal regulation and xylem vulnerability to embolism (Delzon, 2015; López et al., 2021). A water-spender understory might increase the overstory water stress during drought by maintaining transpiration after overstory stomatal

closure, depleting soil water (e.g., Mas et al., 2024; Moreno et al., 2023; Decarsin et al., 2024), whereas a water-saver understory may alleviate it through early stomatal closure (temporal resource partitioning; Moreno et al., 2023; Schnabel et al., 2024). Third, as the canopy closes, the understory might benefit from favorable microclimatic conditions (lower radiation, vapor pressure deficit and wind speed) reducing its transpiration and soil water depletion (Prévosto et al., 2020; Balandier et al., 2022). Consequently, significant uncertainty remains regarding the long-term effects of thinning on tree response to drought, which has critical implications for forest management under climate change.

In this study, we aimed to address the following questions: (1) Does thinning still influence tree drought response in the long-term? (2) Does the observed response depend on the type of indicator used (growth-based vs ecophysiological indicators)? (3) What mechanisms could underlie the long-term effects of thinning on tree drought response?

To answer these questions, we assessed the long-term effects of thinning on tree drought response by combining field measurements of tree ring-widths and tree water relation with process-based simulations. We focused on a 1968 *Cedrus atlantica* (Manetti ex Endl.) Carrière experimental plantation in southern France. Twenty-five years after contrasting thinning intensities were applied, we evaluated tree drought response strategies during the extreme drought of 2017 by measuring growth-based and ecophysiological indicators. Process-based modelling of forest functioning is a valuable tool to explore underlying mechanisms explaining the observed drought stress patterns accounting for specificities in local soil structure, climate variability, and tree species ecophysiology. To complement field measurements, we used the process-based model MEDFATE coupled with the SurEau plant hydraulic module (De Cáceres et al., 2023; Ruffault et al., 2022) to explore whether differences in root exploration, stand structure, and tree ecophysiological trait acclimation could explain the differential drought stress between thinned and unthinned plots. This study was conducted on *Cedrus atlantica*, which is largely used in reforestation programs in the South of France as a drought-adapted species holding significant potential for wood production. Currently covering c.a. 20,000 ha in France, *C. atlantica* has recently gained interest among forest managers. It now ranks as the fourth most planted species in recent years according to annual statistics provided by the French Ministry for Agriculture, Alimentation and Forest. However, signs of dieback have recently been observed in *C. atlantica* stands, including within its natural range (Navarro-Cerillo et al., 2019; Sarmoun et al., 2018), underscoring the need to evaluate adaptation strategies such as thinning to mitigate the negative effects of drought on those forests.

2. Material and methods

2.1. Study site and experimental design

The thinning experiment was established in a 1968-origin *C. atlantica* plantation located in the municipal forest of Valliguières, southeast France (lat 44.020° N; long 4.624° E; alt 250 m). It covers an area of 3.4 ha on a plateau with a slight topographic slope (<5 %) toward the south. The plot is located on karstified cretaceous limestone with urgonian facies. The soil can be assigned to both calcisol and rocky peyrosol typical of this geomorphological formation (Baize et al., 2009). Soil rock fraction content is high (75–90 %; table S1), with the presence of karst morphologies (i.e. empty or soil/clay filled cavities) and numerous cracks and diachases probably several meters deep which can be prospected by tree roots. The understory vegetation consists mainly of *Quercus ilex* L., with sparse *Buxus sempervirens* L., *Juniperus oxycedrus* L. and *Rhamnus alaternus* L..

The climate is Mediterranean with a mean annual temperature of 15.0 °C and mean annual precipitation of 768.5 mm (1991–2020), with high inter-annual variability (1264.0 mm in 1996; 350.1 mm in 2017; weather station of Chusclan; see Section 2.2). Those site conditions are among the toughest encountered for *C. atlantica* in the french

mediterranean region, its plantation being not recommended below 600–700 m elevation – and highly discouraged below 400 m (Courbet et al., 2012).

In winter 1968, after subsoiling to 0.5 m, 1-year old seedlings grown in containers were planted every 1.7 m in lines 4.6 m apart at an initial density of 1200 trees.ha⁻¹. At the end of 1992 (age 25), eight plots of c.a. 0.2 ha each were established. Two plots were kept unthinned (control plots; hereafter referred to as treatment T1200 or control) whereas selective thinning treatments from below with contrasting thinning intensities were applied on the other plots, each with two plot-level replicates. The thinning operation removed 31 %, 43 % and 57 % of the stand basal area, resulting in stand densities after thinning of 800, 600 and 400 trees.ha⁻¹, respectively (hereafter referred to as treatments T800, T600 and T400; Fig. S1). Each plot was surrounded by a buffer of two plantation lines wide (c.a. 10 m) subjected to the same treatment to avoid edge effects.

The status of every tree (alive or dead) was assessed every year in winter from 1991 to 2004, and then in 2008, 2015 and 2017, together with the circumference at breast height (CBH, at 1.3 m above ground) of each living tree.. Tree height and crown ratio (defined as the ratio of living crown length to total tree height) were measured on a CBH-stratified sample, representing approximately 20 % of trees in 1991 and 60 % in 2017. Tree height was measured by climbing, and crown base height (i.e., the height from the ground to the lowest living branch) was measured using a graduated pole.

We carefully assessed the homogeneity of the soil environmental conditions among plots using (i) site index, an indicator of site productivity for even-age stands defined as the mean height of the dominant trees (i.e., of the 100 trees of largest diameter per hectare; Bastien and Gauberville, 2011); (ii) dominant diameter at breast height (DBH); (iii) mean DBH; and (iv) soil electrical conductivity, measured by electromagnetic induction to inform about soil depth variability across the experimental site (Carrière et al., 2021). For each thinning treatment, the plot that most closely matched the soil environmental conditions of the control plot, was selected from the two available to carry out the field measurements (see table S2).

2.2. Climatic conditions and drought characterization

Climatic variables (daily precipitation, air temperature, relative humidity, solar radiation and wind speed at 10 m) were extracted from the weather station of Chusclan located at 14.5 km NE from the study site (lat 44.135° N; long 4.708° E; alt 30 m). However, since records were only available starting from 2001 for some climatic variables, we extracted them from the closest grid point of the French SAFRAN atmospheric reanalysis system for the complete 1968–2020 period (8 × 8 km grid; Vidal et al., 2010). A multivariate bias correction method preserving the climatic variables' correlation structure was then employed to adjust the SAFRAN reanalysis data to the weather station data (Cannon, 2018). For each month, we calculated the climatic water balance defined as Precipitation minus Potential EvapoTranspiration (computed with the Penman-Monteith equation; Penman and Keen, 1948; Zotarelli et al., 2013).

Note that 2017 was by far the driest year at the study site since the plantation in 1968, showing the lowest annual precipitation and climatic water balance (Fig. S2).

2.3. Tree growth and growth resistance to drought

2.3.1. Individual tree growth

In spring 2018, 11 to 15 trees per thinning intensity were selected to accurately represent the treatment. The selection was based on two criteria: (i) spatial distribution, ensuring the trees were evenly distributed within the treatment area and avoiding border lines to prevent edge effects, and (ii) size, based on a CBH-stratified inventory. The selected trees were cut and ring-widths (RW) were measured on stem cross-

sections at 1.3 m on 8 radii per disk with the WinDENDRO software (Regent Instruments Inc.). Crossdating was carefully checked using the dplR package (Bunn et al., 2021) from the R software version 4.4.2 (R Core Team, 2024). Tree RW series were obtained by averaging RW values from the 8 radii.

RW were then converted into Basal Area Increments (BAI), assuming a circular cross-section of the stem to account for the trend caused by the geometric constraint of adding a wood volume to a stem with an increasing radius. The average BAI over the 10 years preceding thinning (1982–1991, defined as the pre-thinning period due to limited data availability before 1982) was used to compute BAI indices normalized to pre-thinning growth for each tree.

2.3.2. Growth resistance to the 2017 drought

As a growth-based indicator of tree response to the 2017 drought, we computed the resistance index developed by Lloret et al. (2011) which quantifies the tree growth during the dry year relative to pre-drought growth levels. Recovery and resilience indices could not be computed, as stem cross-sections were cut in the year immediately following the drought. Growth resistance *sensu* Lloret was calculated for each tree as:

$$\text{Growth resistance} = \text{BAI}_{2017} / \text{BAI}_{\text{prec}(L)}$$

Where BAI₂₀₁₇ is the BAI of the year 2017, and BAI_{prec(L)} the averaged BAI on the L-years period preceding 2017. We tested pre-drought periods (L) ranging from 1 to 4 years and calculated resistance using detrended ring-width indices instead of BAI, which led to similar results (RW were detrended into Ring Width Indices using a cubic spline with a 50 % frequency cutoff at a 27-years moving window, corresponding to 2/3 of the mean series length; Klesse, 2021, 2025; Table S3; see Veuillen et al., 2023). Therefore, we present results for L = 2 only.

2.3.3. stand-level growth

Exhaustive CBH measurements were used to calculate stand-level basal area growth, defined for each treatment as the sum of all individual living tree Basal Area Increments between two consecutive CBH measurement dates. Since CBH measurements started in winter 1991, we could not calculate stand-level growth prior to thinning.

2.4. Stand leaf area index

Stand LAI was assessed using 18 to 21 hemispheric photographs per treatment. Pictures were taken every 5 to 10 m between two plantation lines per thinning treatment at sunset in October 2017. We used a Nikon D3200 camera with a sigma 4.5 mm EX DC HSM fisheye lens mounted on a tripod at 1.3 m above ground. The photographs were recorded in RAW format (exposure adjusted manually for the sky) and developed on a computer using DCRAW (Coffin, 2008) with no gamma correction, and converted to black and white, retaining only the blue channel in order to better distinguish the sky from the vegetation. For each picture, the sky was separated from the vegetation by double thresholding using the method of Leblanc et al. (2005). For each thresholded image, a plant area index was then calculated using Miller's formula (Miller, 1967) and used as a proxy for stand LAI (defined as the total one-side projected leaf area per ground area; m².m⁻²).

2.5. understory development

The understory was described in autumn 2017 by recording the species identity and DBH of all individuals with a DBH greater than 2 mm on half of the area of each selected plot. In addition, to account for smaller individuals, understory cover was visually estimated within two 9m-radius circular sub-plots per plot, stratified in two vertical layers (below and above 1 m, expressed as a percentage of ground area). Note that the understory exceeding 1.3 m high is included in the stand LAI. The cover of the herbaceous layer was also visually assessed within these sub-plots.

2.6. Tree hydraulic traits

2.6.1. Parameters of the pressure-volume curves

In autumn 2017, pressure-volume curves were established on 10–15 cm long leafy shoots collected from the upper canopy of twelve trees, six in each of the two most contrasting thinning treatments (T1200 and T400). Pressure-volume curves were obtained using a PMS pressure chamber (PMS 1000; PMS instruments) following the methodology described in Limousin et al. (2022). Five ecophysiological traits related to plant water content in relationship with plant water potential were derived from these curves (osmotic potential at full turgor, turgor loss point, relative water content at turgor loss point, bulk modulus of tissue elasticity and apoplastic water fraction; Tyree and Hammel, 1972).

2.6.2. Vulnerability curves to cavitation

In autumn 2017, 40 cm long branches, collected from the upper canopy of ten of the twelve trees sampled for pressure-volume curves (five in T1200 and only four in T400 as the fifth had to be discarded because of measurement issues), were used to draw the vulnerability curves to cavitation. Measurements were performed in the PHENOBOIS platform (PIAF, INRAE, Clermont-Ferrand) following the methodology described in Cochard (2002) and Cochard et al. (2005). The curves were used to evaluate the Ψ_{50} values (defined as the water potential at which 50 % of hydraulic conductivity is lost) and the slope of the conductance - water potential relationship at Ψ_{50} . Ψ_{50} values were not biased by exposure to the 2017 drought, as native embolism levels were low (see section 3.3).

2.6.3. Residual leaf conductance

We sampled 40–50 cm long branches on eight trees of the control treatment and measured the residual leaf conductance G_{res} using the droughtbox device (Billon et al., 2020) following the methodology described in (Burllett et al., 2025). As the droughtbox tool was not yet available in 2017, the trees were sampled a few years after, in 2024. We sampled only the control, because management operations have been undertaken since 2018 in the other treatments.

After completing the drought-box procedure, leaves were separated from shoots, and the dry masses of leaves and wood were measured for each sample. Wood area was calculated assuming the branch was cone-shaped, based on branch length and basal diameter measurements. 30 needles per sample were scanned and then projected leaf area was calculated with the ImageJ software (Schneider, 2012). Leaf Mass per Area (LMA) was calculated as leaf dry mass divided by leaf area for these subsamples. Each sample's projected leaf area was calculated by dividing the total leaf dry mass by the LMA. Finally, the residual leaf conductance (G_{res}) was calculated considering the sample area as its developed leaf area, approximated here as twice the projected leaf area, to which was added the wood area. This method might slightly underestimate the developed leaf area, since *C. atlantica* leaves are not exactly flat (see Jasińska et al., 2013).

2.7. Tree physiological response to drought

The predawn and midday leaf water potentials (Ψ_{pd} and Ψ_{md}) were measured on 48 trees (12 per thinning treatment; including the trees sampled for hydraulic traits) at four dates during the 2017 summer. Samples were collected during the two hours before sunrise and between 2 and 4 PM, for predawn and midday water potentials, respectively. For midday water potentials, samples were collected from well-exposed sunlit branches. Samples were immediately concealed in waterproof plastic bags in an icebox. Water potential measurements were performed at the study site, within max. 2 hours after the sampling, with a PMS pressure chamber.

The sampled trees were selected according to a CBH-stratified inventory to best represent tree CBH distribution within each thinning treatment. The trees selected for water potential measurements were not

the same as the ones selected for ring-width measurements.

We used the tree hydraulic safety margin (HSM) and native embolism (Percent Loss of Conductivity; PLC) as ecophysiological indicators of the water stress experienced by the trees during the 2017 drought.

Tree Hydraulic Safety Margin (HSM) was defined as the difference between the minimum water potential experienced by the tree during summer 2017 (i.e., at the third sampling date; Fig. S3) and Ψ_{50} (Choat et al., 2012; Sanchez-Martinez et al., 2023). Although midday water potential are usually used to compute HSM according to its definition (HSM_{md}), here we decided to also compute HSM_{pd} using predawn water potential, which is more reliable as it is less dependant on (i) the height and exposition of the sampled leaves and (ii) fluctuating meteorological conditions around midday (see Decarsin et al., 2024).

Native embolism, defined as the percent of embolized conductive xylem, was measured on samples collected from the upper canopy of the same ten trees used for establishing vulnerability curves by X-ray microtomography at the PHENOBOIS platform (PIAF, INRAE, Clermont-Ferrand) following the methodology described in Cochard et al. (2015).

Field measurements are summarised in Table 1.

2.8. Statistical analysis

In order to assess the thinning treatment effect on annual growth, growth resistance to the 2017 drought, LAI and HSM, after ensuring that the assumptions were satisfied, we performed simple one-way analysis of variance (ANOVA) followed by Tukey's post-hoc tests. Unpaired Wilcoxon rank-sum tests were performed for understory cover, Ψ_{50} , parameters of the pressure-volume curve and PLC due to the limited number of samples (Table 1). All analyses were performed using the R software (R Core Team, 2024).

2.9. Hypothesis testing using the MEDFATE-SurEau modelling framework

We relied on different modelling tests to explore hypotheses likely to explain the long-term effects of thinning, linked to (1) spatial niche partitioning of the root system between the overstory and the understory, (2) temporal niche partitioning and (3) understory contribution to the total LAI. For this purpose, the behavior of the two most contrasting thinning treatments (T1200 and T400) was simulated during the 2017 drought using the soil-plant-atmosphere MEDFATE-SurEau, a recent version of the MEDFATE model incorporating the plant hydraulic scheme of SurEau (De Cáceres et al., 2023; Ruffault et al., 2022; see supplementary method 1 for model description), implemented in the R

Table 1

Summary table of field measurements and corresponding sample sizes by thinning treatment, conducted in summer–autumn 2017 and spring 2018, except for G_{res} , which was measured in 2024. Forest inventory measurements conducted before 2017 are not included. Because pressure–volume curves, vulnerability curves, native embolism, and G_{res} measurements are very demanding, they were performed only on the two most contrasting treatments (only on the control for G_{res} ; see Section 2.6.3).

thinning treatment	T1200 (control)	T800	T600	T400
circumference	all trees (250)	all trees (151)	all trees (111)	all trees (154)
height, crown ratio	102 trees	91 trees	75 trees	113 trees
tree ring-widths	15 trees	11 trees	12 trees	15 trees
Leaf area index (LAI)	21 pictures	21 pictures	20 pictures	18 pictures
understory cover	4 plots	2 plots	2 plots	4 plots
pressure–volume curves	6 trees	–	–	6 trees
vulnerability curves	5 trees	–	–	4 trees
residual leaf conductance (G_{res})	8 trees	–	–	–
tree water potential (Ψ)	12 trees	12 trees	12 trees	12 trees
native embolism (PLC)	5 trees	–	–	5 trees

software. We simulated forest hydraulic functioning during the year 2017 under different assumptions (see below) and compared qualitatively the differences between the two treatments in terms of hydraulic risk obtained with model simulations and measured data.

The model requires (i) daily climate data (which are internally disaggregated into hourly values), (ii) stand characteristics (leaf and root vertical distribution among cohorts), (iii) ecophysiological traits linked to stomatal regulation of transpiration and vulnerability to drought-induced embolism and (iv) soil characteristics (soil layer widths, textures and rock fraction contents) which are described in [Section 2.9.1](#). We implemented two forest stands representing the two most contrasting thinning treatments (T1200 and T400).

- The first stand (control; T1200) was set to be composed of only one cohort of *C. Atlantica* trees.
- The second stand (thinned treatment; T400) was set to be composed of a cohort of *C. Atlantica* trees (overstory) and a cohort of *Q. ilex* understory, which represented more than 90 % of the understory basal area according to field measurements (Table S4).

2.9.1. Input data

(1) Daily climate data

We used the 2017 daily precipitation, air minimum and maximum temperatures, air minimum and maximum relative humidities, wind speed, and solar radiation from the weather station of Chusclan.

(2) Stand characteristics

For each of the two implemented stands, the cohort characteristics (mean diameter, height, and crown ratio for the trees; mean height and cover for the understory) were implemented from field measurements (Table S5), as well as the stand total LAI ($3.19 \text{ m}^2 \cdot \text{m}^{-2}$; median of the LAI measured in control and T400; see [Section 3.1](#)).

(3) Ecophysiological traits

The model relies on a set of species-specific ecophysiological traits linked to stomatal regulation of transpiration and vulnerability to drought induced embolism. For *C. atlantica*, we chose to use the median of the parameters measured in this study for parameters of the pressure-volume and vulnerability curves, based on the non-significant or marginally significant differences between the control and T400 (see [Section 3.2](#) and Table S6). *C. atlantica* G_{res} was also measured in this study; while values from the literature were used for the leaf nitrogen content N_{leaf} , the maximal stomatal conductance G_{swmax} , and properties of the Transition phase temperature of G_{res} : T_{phase} , Q_{10a} and Q_{10b} . Regarding *Q. ilex*, as no field measurements were conducted, we entirely relied on existing literature (Table S6).

(4) Soil characteristics

Soil layer widths, textures and rock fraction contents were estimated from soil pits, which revealed the existence of two different soil layers with a dominating clay-loam texture and high rock-fraction content (details in Table S1). However, the soil Total Available Water (i.e., the maximum amount of water trees have access to) calculated based on those soil properties measured on the field, when used in the model, was far too low to be compatible with *C. Atlantica* survival during the 2017 drought (results not shown). Therefore, we implemented the control (T1200) in the model and adjusted width and rock fraction content of the soil layers to align the predicted Ψ_{pd} and PLC values with the measured ones (calibration phase). Then, we implemented an additional 4th soil layer in order to test the hypotheses described below (see section

2.9.3; Table S7). Maximum depth of 5 m was set according to seasonal variations in electric resistivity measured on transects in each plot (data not shown).

2.9.2. Model application and hypothesis tests

To explore the potential effects of thinning on drought stress, we modified the parameters of the thinned treatment in order to test (1) three different scenarios of root distribution (spatial root niche partitioning between overstory and understory), (2) two scenarios of understory ecophysiology (temporal niche partitioning between overstory and understory) and (3) two scenarios of LAI partitioning between overstory and understory. Climate, soil, stand total LAI and *C. atlantica* ecophysiological parameters were kept constant between the different implementations of the thinned treatment, while root distribution, *Q. ilex* ecophysiological parameters and LAI partitioning between the two cohorts were modified according to the different tested hypotheses, which are detailed below.

We then used hydraulic risk indicators predicted by the model (PLC and HSM) and compared the simulations results, HSM being calculated using the predicted Ψ_{pd} on the same day it was measured in the field.

(1) Variability in rooting vertical profile (spatial root niche partitioning)

We tested three possibilities: no spatial root niche partitioning, deeper-rooted understory, and deeper-rooted overstory (see supplementary method 2).

Without spatial root niche partitioning, overstory and understory share the same fine root vertical distribution, and thus the same water volume ("normal" root distribution; Table S8). The results then depend on the understory ecophysiological traits: a more water-spender understory might accelerate soil water depletion, thus increasing overstory hydraulic risk compared to the control treatment; whereas a more water-saver understory should reduce it (see [section 2.9.2 \(2\)](#); Gebauer et al., 2012; Goisser et al., 2016; Grossiord et al., 2014; Moreno et al., 2024).

Under the deeper-rooted understory hypothesis, *Q. ilex* is assumed to access deeper water resources than *C. atlantica*. This is supported by its likely resprouting origin from old stumps predating the plantation, as was observed in another *C. atlantica* plantation experiment, established after clear-cutting of a mixed *P. halepensis* and *Q. ilex* natural stand (Belvaux and Tron, 1996). Additionally, *Quercus* species can develop deep root systems ($>4.5\text{--}6 \text{ m}$ measured for *Q. ilex*; Jackson et al., 1999; Cabon et al., 2018; Moreno et al., 2005; Nijland et al., 2010). Under this hypothesis, we expect a reduced competition for water in the shallow soil layers, and thus a lower hydraulic risk for the *C. atlantica* overstory.

Under the deeper-rooted overstory hypothesis, thinning enhances overstory root development in deeper soil layers, thereby constraining understory root development. As a result, a reduced overstory hydraulic risk is expected in the thinned compared to the control stand, depending on the understory ecophysiological traits.

(2) Variability in understory stomatal regulation traits (temporal niche partitioning)

Because *Q. ilex* shows large intraspecific variability in stomatal regulation according to the existing literature (supplementary method 3), we tested the sensitivity of the previous scenarios to understory stomatal behaviour. Simulations were run using the two most contrasting sets of *Q. ilex* traits from the literature, hereafter referred to as drought-avoidant and drought-tolerant understory (Blackman et al., 2023 and Limousin et al., 2022, respectively). Note that the most drought-avoidant *Q. ilex* exhibits ecophysiological parameters close to those of *C. atlantica* (Table S6). We therefore expect competition with a drought-avoidant understory to alleviate water stress for *C. atlantica*, while competition with a drought-tolerant understory, which depletes water resources more quickly, should exacerbate it.

(3) Variability in the understory contribution to the total stand LAI

In the modelling framework used here, LAI must be discretized among cohorts. Because current methods of LAI estimation from hemispherical photographs do not allow to quantify species-specific LAI, we tested two scenarios in which the understory represented either 10 % or 30 % of total stand LAI, resulting in different levels of transmittance beneath the overstory (Fig. S4&5). The herbaceous layer was neglected, even though its development differs between the two stands (see Table S4) to limit sources of variability among simulations. Corresponding stand characteristics and LAI vertical distribution are provided in Table S5 and Fig. S4, respectively. Increasing the understory contribution to the stand LAI is expected to reduce *C. atlantica* water stress if the understory is drought-avoidant, but to increase it if the understory is drought-tolerant.

3. Results

3.1. Tree growth and stand structure

Individual tree Basal Area Increment (BAI) was higher following thinning than in the pre-thinning period, the significance of this difference increasing with thinning intensity (Fig. S6). BAI in T400 was significantly higher than in the control during the pre-thinning period; but it was not the case for T600 and T800 (Fig. 1a). In the 25 years following the thinning operation, the greater the intensity of the thinning treatment, the higher the annual BAI (significant difference except

for a few years in T800; Fig. 1a). BAI was more than two times larger in T400 than in the control, and even more than three times larger from 2010 on (Fig. 1a).

Stand-level growth was higher in the control than in the thinning treatments in the first years after thinning. However, this difference gradually decreased over time, reversing in 2016–2017 (Fig. S7). This pattern was the result of the gradual increase in the difference in individual tree BAI among treatments (Fig. S6), as stand density remained stable from 1991 to 2017 with low mortality rates across all treatments (3.8, 4.4, 5.1 and 3.7 % in the control, T800, T600 and T400 treatments, respectively; no notable mortality events). In 2017, stand basal area was 43.4, 39.4, 32.7 and 34.8 m².ha⁻¹ in the control, T800, T600 and T400 treatments, respectively.

In 2017 the mean stand LAI was of 3.19 ± 0.33 m².m⁻² with no significant difference among treatments ($p = 0.77$; Fig. 1b; Table S9).

The understory primarily consisted of *Q. ilex* in all treatments. Understory was sparse in the control and in T800 (mean cover of 13.8 and 13.5 % and basal area of 0.022 and 0.011 m².ha⁻¹, respectively) while it was significantly more developed in T600 and T400 (mean cover of 47.5 and 47.5 % and basal area of 0.139 and 0.045 m²/ha, respectively; Fig. 1c; Table S4). The herbaceous layer, mainly composed of the graminoid *Brachypodium retusum* (Pers.) P.Beauv., was less developed in the control (mean cover of 16.3 %) than in the thinning treatments (>40 %; Table S4).

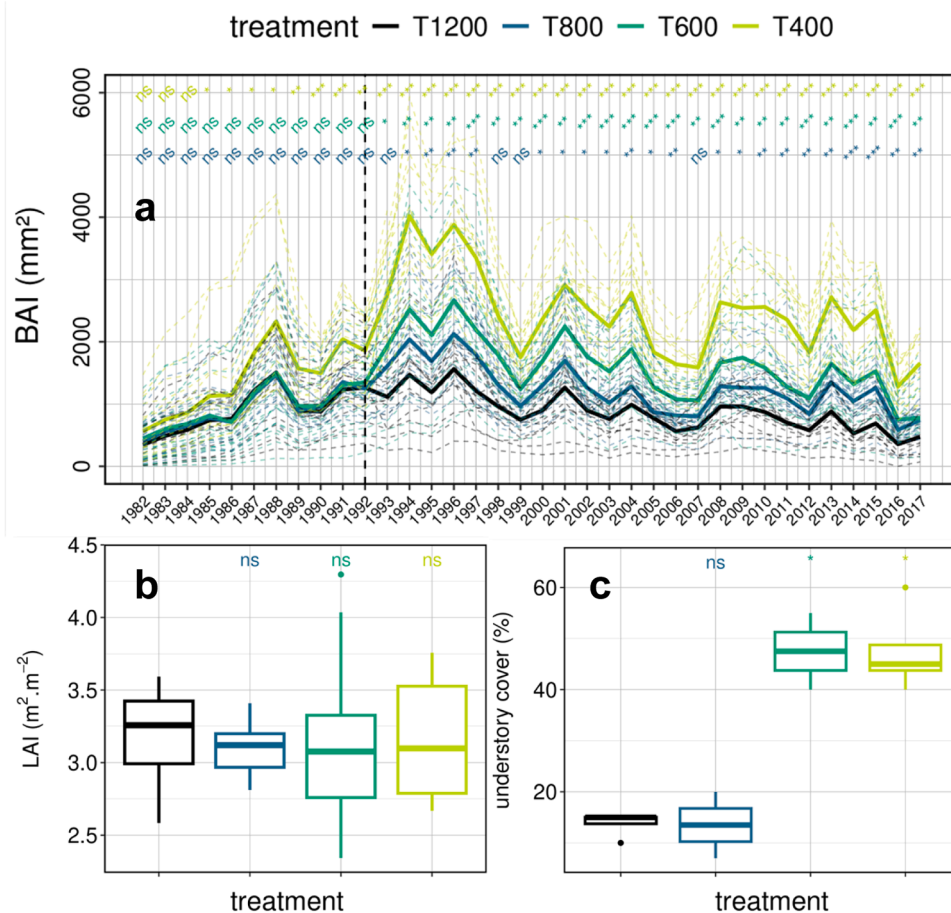


Fig. 1. Comparison of tree growth and stand structure among thinning treatments.

(a) Individual tree (dashed lines) and treatment chronologies (solid lines) of Basal Area Increment (mm²); (b) Leaf area index (LAI; m².m⁻²) per thinning treatment; (c) Total understory cover (%) per thinning treatment. For each thinning treatment, the significance of the difference with the control is indicated (ns; *: $p > 0.01$ & $p \leq 0.05$, **: $p > 0.001$ & $p \leq 0.01$, ***: $p \leq 0.001$).

3.2. Tree hydraulic traits

There were no significant difference in measured *C. atlantica* Ψ_{tlp} , RWC_{tlp} , Ψ_{50} and slope at Ψ_{50} between the control and T400 according to Wilcoxon tests, with a median Ψ_{tlp} of -2.99 MPa, RWC_{tlp} of 74 %, Ψ_{50} of -5.30 MPa and slope at Ψ_{50} of 41.0 %MPa $^{-1}$ (Fig. 2; Table 2). Consequently, we used the median Ψ_{50} to compute Hydraulic Safety Margins (see Section 3.3). On the contrary, π_{100} was significantly higher and ϵ_0 significantly lower in T400 than in the control; but the significance of the difference was not strong (pvalue of 0.04 and 0.02, respectively; Fig. 2; Table 2). The residual leaf conductance (G_{res}) was of 1.107 mmol.m $^{-2}$.s $^{-1}$ (min. 0.92, max 1.35 mmol.m $^{-2}$.s $^{-1}$; G_{res} measured only in the control; see Section 2.6.3).

3.3. Tree response to the 2017 drought

Growth resistance *sensu* Lloret, defined as tree basal area increment (BAI) during the 2017 dry year relative to mean BAI during the preceding years, was not significantly affected by thinning (Fig. 3a; Table S3).

Both predawn and midday water potentials showed some significant differences among treatments at different dates during the 2017 drought, indicating that water stress decreased with increasing thinning intensity (Fig. S3, Table S10). This translated into increased Hydraulic Safety Margins (HSM_{pd}) with thinning intensity, HSM_{pd} being significantly higher in T400 and T600 (2.6 ± 0.3 MPa and 2.3 ± 0.2 MPa, respectively) but not significantly in T800 (2.2 ± 0.1 MPa) compared to the control (mean of 2.0 ± 0.3 MPa; Fig. 3b; Table 3). HSM_{md} ranked similarly to HSM_{pd} among treatments (Fig. S8).

PLC in T400 was of 1.2 ± 1.9 %, showing low variability among trees, while it was higher and more variable in the control (7.2 ± 10.2 %; Table 3a; Fig. 3c); although not significantly different ($p = 0.14$). Since there was no significant difference in Ψ_{50} between the two most contrasting treatments, this difference in HSM and PLC was due to the

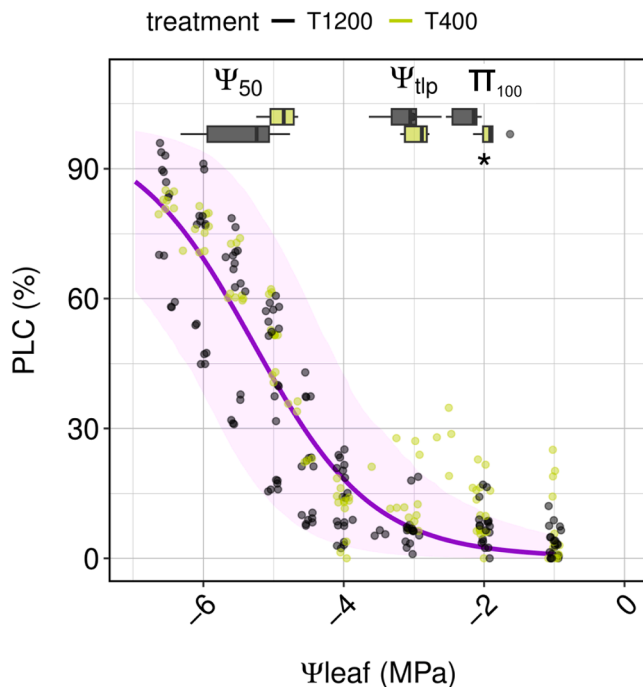


Fig. 2. Vulnerability curve to cavitation.

Percent Loss of Conductivity (PLC, %) as a function of leaf water potential for trees of the control (5 trees) and T400. Points depict the individual measurements, and the purple line and area the fitted sigmoid function and associated 95% confidence interval. The distributions of the Ψ_{50} , Ψ_{tlp} and π_{100} values per treatment are also represented. Symbols as in Table 2.

Table 2

Tree hydraulic traits for the 2 most contrasting treatments (T1200 and T400): osmotic potential at full turgor (π_{100}) and at turgor loss point (Ψ_{tlp}), relative water content (sympastic water) at turgor loss point (RWC_{tlp}), bulk modulus of tissue elasticity (ϵ_0), apoplastic water fraction (AWF) at full turgor, water potential at 50 % loss of conductivity (Ψ_{50}), slope of the loss of conductivity at Ψ_{50} , and residual leaf conductance (G_{res}). The values presented here are the medians per treatment along with the pvalue of the wilcoxon rank-sum unpaired tests testing for difference between the 2 treatments. Significance levels: ns: no significant difference with control, ***: pvalue < 0.001 , **: pvalue < 0.01 , *: pvalue < 0.05 .

Parameter	control (T1200)	T400	pvalue
π_{100} (MPa)	-2.15	-1.91	0.04 *
Ψ_{tlp} (MPa)	-3.05	-2.89	0.38 (ns)
RWC_{tlp} (%)	77	72	0.17 (ns)
ϵ_0 (MPa)	8.93	5.67	0.02 *
AWF (%)	0.15	0.15	0.81 (ns)
Ψ_{50} (MPa)	-5.67	-5.22	0.2 (ns)
slope at Ψ_{50} (%MPa)	39.2	41.0	0.4 (ns)
G_{res} (mmol.m $^{-2}$.s $^{-1}$)	1.107	NA	NA

differences in tree water potential among thinning treatments (Fig. S3, Table S10; Table 3b).

3.4. Results of the simulations of stand functioning

3.4.1. Model calibration

The predicted Ψ_{pd} aligned well with the measured Ψ_{pd} dynamics in the control treatment, even though predicted Ψ_{pd} decline was slightly too slow to match the field measurements dynamic between the first and last measurement dates (Fig. S9). At the end of the drought season, the predicted PLC was 8.8 %, which is consistent with the measured PLC in the control treatment.

3.4.2. Model predictions under the different tested hypotheses

Model predictions showed that thinning reduced overstory hydraulic risk (i.e., higher HSM and lower PLC; Fig. 4) under all tested hypotheses, except when the overstory shared water resources with a drought-tolerant understory (i.e., same root distribution). Overall, thinning effects were relatively small, with predicted differences between the control and the thinned treatment of less than 0.3 MPa in HSM and 6 % in PLC.

Regardless of understory ecophysiological properties or LAI contribution, the scenarios involving a deeper-rooted overstory — enabling access to a soil layer not depleted by the understory — consistently resulted in the greatest positive predicted effect of thinning on HSM, followed by the deep-rooted understory scenarios and finally the scenarios of same root distribution. However, considering PLC, the deep-rooted understory scenario slightly outperformed the deep-rooted overstory when the understory accounted for 30 % of total LAI.

Predicted thinning effects were consistently more beneficial when considering a drought-avoidant understory rather than a drought-tolerant understory. The positive effects of a more drought-avoidant understory increased with its LAI contribution; while it was the opposite for a drought-tolerant understory. The impact of the understory LAI contribution on the results was more pronounced when the understory strongly competed with the overstory for water (i.e. when the two cohorts shared the same root distribution, or when the understory had a deeper root system).

4. Discussion

Using a thinning experiment in a *C. atlantica* plantation, we explored whether the effects of thinning on different drought stress indicators (growth-based or ecophysiological indicators) were still visible 25 years after thinning. We found that total stand LAI had converged across all treatments, due to understory development and overstory canopy

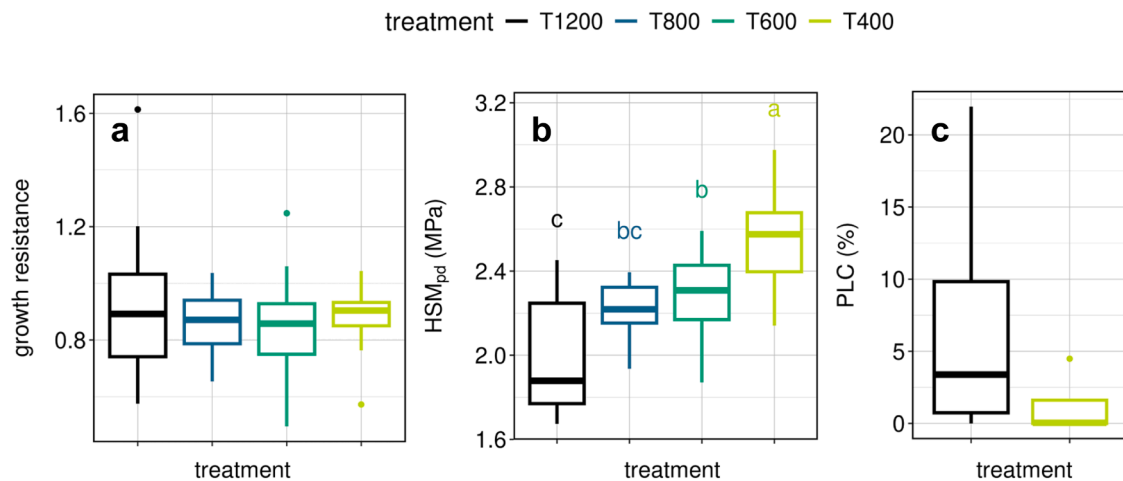


Fig. 3. Tree response to the 2017 drought.

(a) *C. atlantica* growth resistance to the 2017 drought *sensu* Lloret considering a pre-drought period of 2 years (resistance = $BAI_{2017}/BAI_{prec(2)}$); (b) Hydraulic Safety Margin (HSM_{pd} ; MPa); and (c) Native embolism (Percent Loss of Conductivity; PLC; %).

Table 3a

Mean $\pm$ standard error of Hydraulic Safety Margin (HSM_{pd} ; MPa) and Percent Loss of Conductivity (PLC; %) for each of the thinning treatments.

Treatment	T1200	T800	T600	T400
HSM_{pd} (MPa)	2.0 ± 0.3	2.2 ± 0.1	2.3 ± 0.2	2.6 ± 0.3
PLC (%)	7.2 ± 10.2	–	–	1.2 ± 1.9

Table 3b

Results of the Tukey-HSD post-hoc tests for the Hydraulic Safety Margin (HSM_{pd}). Shown values are for the difference between treatments (diff), lower (lwr) and upper (upr) confidence intervals at the 0.05 threshold, adjusted p-values and associated significance (sign.).

compared treatments	diff	lwr	upr	adjusted pvalue	sign.
T400-T1200	0569	0323	0815	0	***
T400-T600	0253	0006	0499	0042	*
T400-T800	0325	0079	0571	0005	**
T600-T1200	0316	0,07	0562	0007	**
T600-T800	0072	–0174	0319	0861	ns
T800-T1200	0244	–0002	0,49	0053	ns

closure in the thinned stands. Unexpectedly, although trees in the thinned stands exhibited similar growth resistance to drought *sensu* Lloret compared to the control, they still experienced lower hydraulic risk, as indicated by higher HSM and lower native PLC. We therefore face a paradox in that despite similar water demand (similar LAI), thinning still reduces tree water stress. In the following, based on our observations and simulations, we discuss the possible mechanisms that could explain this paradox, as well as the relevance of different drought stress indicators.

4.1. Effect of thinning on tree growth

We found that *C. atlantica* radial growth was still better in thinned treatments than in the control 25 years after thinning. Thinning from below thus enhanced tree radial growth in the long-term, despite vegetation regrowth (Fig. 1; Fig. S6). This could be due to the release of intra-specific competition for resources, the selection of dominant trees, and/or the increase of wind exposure (Niez et al., 2019). Manrique Alba et al. (2021, 2020) also reported better growth of *Pinus nigra* and *Pinus halepensis* 13–14 and 20 years after thinning, respectively. Gavinet et al. (2020) and Thompson et al. (2018) found the same results for *Quercus ilex* and *Pseudotsuga menziesii* 15 and 20–35 years after thinning,

respectively. However, because stand leaf area index (LAI) was not reported in those studies, it remains unclear whether stand-level water demand had already reached levels comparable to the control in the thinned stand, as observed in our study.

4.2. Tree hydraulic traits

The hydraulic traits measured for *C. atlantica* at our study site were in agreement with previously reported values for this species (Blackman et al., 2023; Cochard et al., 2006; Ladjal, 2001; Froux et al., 2002). Traits measured in the field did not differ significantly between the control and T400, except for marginal differences in some cases (Table 2). Those differences should be viewed cautiously, given the limited sample size for hydraulic traits (Table 1). Nonetheless, the observed trends suggest a potential, albeit subtle, adjustment of hydraulic traits under higher water stress in the control. This adjustment would be indicated by slightly more negative values of π_{100} , Ψ_{tlp} and Ψ_{50} ; along with higher values of ε_0 and RWC_{tlp} in the control compared to the most intensively thinned treatment (T400). An adjustment of hydraulic traits to drought has recently been reported by Moreno et al. (2024), who found a significant drought-induced acclimation of Ψ_0 , Ψ_{tlp} and Ψ_{50} in *Quercus ilex*; although no such response was observed for *P. halepensis* or *Quercus pubescens*. However, at our study site, native embolism was higher in the control compared to T400 (Fig. 3c). Consequently, even though a slight acclimation to drought may have occurred in the control treatment, it was insufficient to offset the adverse effects of competition on water stress; besides, it does not explain the observed paradox of similar stand LAI but reduced hydraulic risk in thinned stands compared to the control. Alternatively, the slight differences in *C. atlantica* hydraulic traits between treatments could reflect the impact of the extreme 2017 drought, as measurements were conducted the following autumn. Indeed, even if native embolism was overall relatively low at the study site, it is possible that the most vulnerable tracheids embolized during the drought, leaving only the more resistant ones to be measured (Fig. 3c).

4.3. Growth-based versus ecophysiological indicators of drought stress

We did not find any significant effect of thinning on growth resistance to the 2017 drought *sensu* Lloret. This result aligns with the only other study, to our knowledge, that examined long-term effects of thinning on growth resistance to drought: Thompson et al. (2018) similarly found no effect of thinning on *Pseudotsuga menziesii* growth resistance to drought 20 and 35 years post-thinning at two out of three

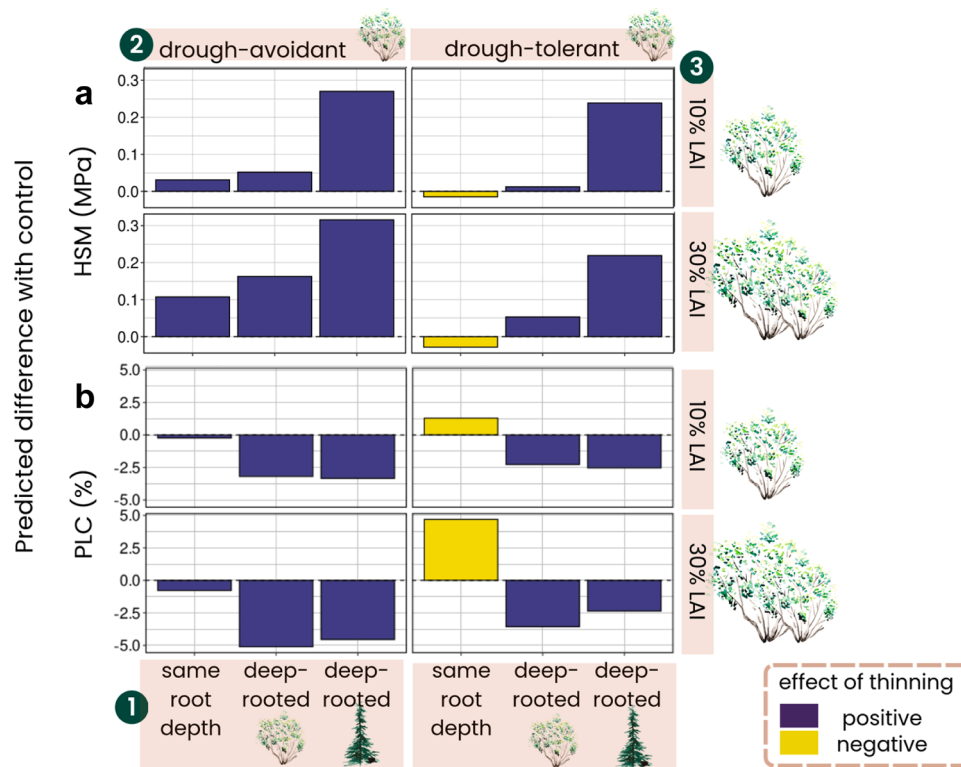


Fig. 4. Results of the simulations of stand functioning.

Predicted differences in *C. atlantica* hydraulic safety margin (HSM, upper panels) and percent loss of conductivity (PLC, lower panels) between the control and the T400 thinning treatments during the 2017 dry year under the different tested hypotheses: (1) Spatial root niche partitioning (same root distribution between trees and understory, deeper-rooted understory, or deeper-rooted overstory); (2) Temporal niche partitioning (drought-avoidant or drought-tolerant understory); (3) Understory LAI contribution, with the understory representing 10 or 30% of the total LAI.

study sites (with higher resistance observed in the stand with reduced competition at the third site). However, we found that thinning reduced drought stress 25 years after thinning, when using ecophysiological indicators of drought stress (HSM, native PLC).

This discrepancy between growth-based and ecophysiological drought stress indicators may be due to the timing of the 2017 drought relative to *C. atlantica* cambial activity phenology. Specifically, (i) *C. atlantica* radial growth is closely linked to late winter–early spring precipitation in its native range (Navarro-Cerrillo et al., 2019; Esper et al., 2006; Linares et al., 2013); and (ii) the 2017 drought occurred late in the growing season, likely exerting only limited effects on growth (Limousin et al., 2012; Ruehr and Nadal-Sala, 2025). This suggests that most of radial growth was completed when the drought occurred, explaining both the absence of a significant growth reduction in 2017 (Fig. 1) and the lack of a treatment effect on growth resistance to drought, despite 2017 being the driest year since the experiment began (Fig. S2). Dendrometers were installed at the study site in March 2025 to gain more information on *C. atlantica* cambial phenology and corroborate these results.

In contrast, ecophysiological indicators effectively captured the dynamic of the water stress experienced by trees during drought (Fig. 3; Fig. S3). These findings highlight the complementarity of ecophysiological and growth-based indicators, emphasizing the added value of direct ecophysiological indicators in providing a more complete understanding of tree drought responses during a given drought, beyond what is revealed by the commonly used growth-based indicators. However, their use on the long-term is more demanding as they do not offer the retrospective insights provided by radial growth records. Our study also emphasizes the importance of considering drought timing, not only its intensity, when studying tree response to drought using growth-based indicators (Aldea et al., 2022; Limousin et al., 2012).

4.4. Mechanisms likely explaining the long-term reduction of hydraulic failure risk by thinning despite vegetation regrowth

4.4.1. Changes in leaf area vertical and specific distribution

Our results showed that thinning reduced the trees hydraulic risk despite similar total stand LAI. In this section, we explored whether this may be partly explained by changes in LAI spatial distribution—namely, (i) altered stand vertical structure and (ii) redistribution of foliage across species with differing ecophysiological traits—without changes in rooting depth.

Modelled transmittance of Photosynthetically Active Radiation (PAR) under the overstory canopy was 21 % in the control and 24–32 % in the thinned stand depending of the understory distribution (Fig. S5). These values are higher than field measurements reported in other coniferous studies, where transmittance ranged from 8 % in control to 27 % in thinned *P. halepensis* stands (Prévosto et al., 2018) and from 5–15 to 10–25 % in stands with a basal area of 45 m².ha⁻¹ to 35 m².ha⁻¹ (*Larix decidua*, *Picea abies*, *Pseudotsuga menziesii* and *Pinus sylvestris*; no data on LAI values; Sonohat et al., 2004). The higher simulated transmittance compared to field values reported in the literature likely led to an overestimation of understory transpiration, and thus an underestimation of the beneficial effect of substituting overstory with understory LAI in mitigating the overstory hydraulic risk. This overestimation might result from (i) the fact that the woody compartments (trunks, branches) are not accounted for in PAR extinction calculations and/or (ii) the use of a default spherical leaf angle distribution for both canopy layers due to the lack of species-specific data.

To parameterize the drought-tolerant and water-spender *Q. ilex* understory, we used values measured at the experimental site of Puchéabon where the minimum Ψ_{pd} reached -5 MPa during the 2017 extreme drought - the lowest ever recorded there, causing leaf browning

and shedding (Limousin et al., 2022; Martin-StPaul et al., 2020). No such symptoms were observed at our site in 2017, suggesting that *Q. ilex* understory experienced less severe water stress. This may reflect lower drought intensity, more favorable microclimatic conditions reducing transpiration, or differences in *Q. ilex* ecophysiological properties between the two study sites. Although our modelling approach cannot confirm the actual *Q. ilex* ecophysiological properties at the study site it underlines the importance of the ecophysiological traits of the competing species (here *Q. ilex* understory) in explaining the drought stress of the target species (here *C. atlantica*; De Cáceres et al., 2021; Moreno et al., 2023), and argues for the inclusion of the understory in future field measurements.

Our simulations suggest that the understory development, depending on its ecophysiological properties and LAI, may partly explain the observed paradox but are not sufficient to explain the observed reduction in hydraulic risk by thinning, supporting the hypothesis of changes in rooting depth among treatments.

4.4.2. Root niche partitioning between the overstory and the understory

Trees selected by thinning from below in the more intense treatment were already larger and more vigorous than control trees before thinning (Fig. 1a; Fig. S6), which suggests that they already had developed more extensive root systems (see also Gavinet et al., 2020). This, along with the fact that thinning can foster root system expansion, supports the hypothesis of deeper-rooted *C. atlantica* in thinned stands. Deeper roots would provide enhanced water access at the onset of the drought, delaying water stress. This is confirmed in the deeper-rooted overstory simulations, which predict the strongest positive effects of thinning on cedar HSM.

Interestingly, the model also predicts lower hydraulic risk when the understory is deep-rooted. The differences between the two scenarios when considering HSM or PLC likely reflect the slower depletion of deeper soil layers by the understory than by the overstory, due to its smaller LAI and water demand, resulting in a slightly higher hydration of the upper soil layers through passive hydraulic lift, thus marginally lowering tree embolism risk. Both species may also develop deeper roots in mixed stands (see Bello et al., 2019), a hypothesis that could be tested by conducting isotopic analyses of xylem and soil water at different depths (e.g., Carrière et al., 2020; Bello et al., 2019). Root system expansion might also occur horizontally in low density stands (Moreno et al., 2005). Testing this would require a spatially explicit model of belowground competition for water among root systems of neighboring trees (e.g., Manoli et al., 2014; Simioni et al., 2016), which would also be useful to represent hydraulic isolation processes during drought progression which may temper the negative impact of a more drought-tolerant understory.

4.5. Limitations of the modelling approach

4.5.1. underestimation of microclimatic effects

The current version of MEDFATE accounts for the vertical extinction of radiation and wind, which affects the leaf energy balance of the understory, but does not model vertical profiles in relative humidity, air temperature and the resulting air Vapor Pressure Deficit (VPD). However, their vertical variations within a forest stand can be substantial and could decrease the atmospheric water demand, and thus the transpiration of the understory. For example in a *P. halepensis* stand located 70 km southeast of the study site with a similar LAI ($2.9 \text{ m}^2 \cdot \text{m}^{-2}$), Prévosto et al. (2020) measured a VPD at 30 cm above ground level of 0.8 to 1 kPa lower under the canopy cover than in the open. Moreover, the higher structural diversity found in mixed stands enhances the forest temperature buffering effect relative to pure stands (Schnabel et al., 2024). The implementation of vertical VPD profile to better account for microclimatic effects according to stand structure (such as implemented in the MuSiCa model, Ogée et al., 2003) is one of the priorities for the improvement of MEDFATE in the near future.

4.5.2. non-consideration of thinning effects on local water balance

Models such as the one we used perform water balance calculations at the stand scale. In our simulations, we accounted for the fact that the crown rainfall interception capacity of needleleaves is higher than that of broadleaves, due to the fascicled needle arrangement (Barbier et al., 2009; Keim et al., 2006). Consequently, at similar LAI, the part of water intercepted by the canopy (that does not enter the soil water balance) is larger in the unthinned pure *C. atlantica* stand than in the mixed *C. atlantica*-*Q. ilex* thinned stand, leading to a more negative water balance at the stand scale. We also accounted for the fact that broadleaves have higher reflectance, thus lower water demand than needle-leaves.

However, the local water balance can also be affected by thinning, as a consequence of changes in stand structure. Due to their larger size in the thinned stand compared to the control, *C. atlantica* trees may individually benefit from higher stemflow during rainfall events (i.e., water running down the trunk funnelled to the base of the tree; André et al., 2008; Chen et al., 2019), thus very locally improving the soil water balance. In the thinned stand, this hydrological process may affect the spatial distribution of soil moisture at the expense of the understory. This effect might be substantial since stemflow can represent between 1 and 14 % of incoming rainfall depending on species, stand and rainfall event characteristics (Levia et Germer, 2015).

4.6. Considerations for forest management

A removal of 43 to 57 % of stand basal area (corresponding to T600 and T400, respectively) led to significant growth increases in the 25 years following the thinning and reduced hydraulic failure risk during the 2017 extreme drought 25 years after the thinning, while a removal of c.a. 30 % of the stand basal area (T800) was not sufficient to induce significant changes (Fig. 1&3). A removal of 40–60 % of basal area could thus be recommended from our results to alleviate tree water stress in the long-term for *C. atlantica* and species with similar ecophysiological behaviour in drought exposed forests, which is slightly more than recommended in previous studies (e.g., Balandier et al., 2022). This might depend on the capacity of the tree crown and root biomass to expand and fill the available space after thinning, which is species- and site-dependant (Sohn et al., 2016); as well as on the ecophysiological difference between overstory and understory species, as highlighted here. Moreover, this also depends on the stand LAI. Balandier et al. (2022) reported that the total forest evapotranspiration can be minimised for an overstory LAI close to 3, which corresponds to the range of LAI reported in our study. However at lower LAI values, the understory development might be enhanced. In the case of a more drought-tolerant understory, cautious opening of the overstory canopy in order to not foster too much understory development and/or removal of the understory (mechanical, or by prescribed burning) can be considered in order to improve stand water balance and increase forest resistance to disturbances (e.g., drought and wildfires; Vilà-Vilardell et al., 2023). However, we must underline here the clear lack of data on the understory, and on the plausible detrimental consequences of understory removal on microclimate and biodiversity (Prévosto et al., 2018; Balandier et al., 2022). The presence of understory might influence fire behavior due to greater fuel quantity and vertical and horizontal continuity of the vegetation (Keeley et al., 2011). Nevertheless, the understory layer can also significantly improve the thinned stand microclimate (Prévosto et al., 2020) and soil communities (Birjol et al., 2024). Furthermore, excessive thinning can lead to increased wind exposure and an elevated risk of breakage until the trees reach a sufficient diameter to ensure their mechanical safety.

4.7. Conclusions and perspectives

Based on a thinning experiment in a *C. atlantica* plantation, we showed that 25 years after thinning, trees in the thinned stands still

experienced lower hydraulic risk - as indicated by higher HSM and lower native PLC - than in the unthinned control. This highlights the possible long-lasting effectiveness of thinning for reducing hydraulic risk, despite vegetation regrowth. While the modelling approach allowed us to explore potential underlying mechanisms, definitive conclusions would necessitate complementary field investigation. In particular, it would require a more thorough investigation of the effect of thinning on root development, which could be achieved by conducting isotopic analysis of xylem and soil water at different depths or root system excavation. Our study also highlights the importance of taking into account competition with the understory.

Interestingly, our results also indicate that ecophysiological indicators can offer a more accurate understanding of tree responses to a specific drought event than the commonly used growth-based indicators, especially when the drought extends beyond the annual cambial activity period.

CRedit authorship contribution statement

Léa Veuillen: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Guillaume Simioni:** Writing – review & editing, Supervision, Resources, Project administration, Project administration, Investigation, Funding acquisition. **Miquel De Cáceres:** Writing – review & editing, Software, Methodology, Investigation, Conceptualization. **Eric Badel:** Writing – review & editing, Methodology, Investigation. **Simon D. Carrière:** Writing – review & editing, Methodology, Investigation. **Hervé Cochard:** Writing – review & editing, Resources, Investigation. **François Courbet:** Project administration, Funding acquisition, Conceptualization. **Claude Dousan:** Investigation, Conceptualization. **Arsène Druel:** Writing – review & editing, Methodology, Investigation. **Jean Ladier:** Project administration, Investigation. **Bernard Prévosto:** Writing – review & editing. **Kevyn Raynal:** Writing – review & editing, Investigation. **Nicolas Martin-StPaul:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2026.111019](https://doi.org/10.1016/j.agrformet.2026.111019).

Data availability

Data will be made available on request.

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