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ORIGINAL PAPER

The effects of thinning intensity and tree size on the growth response to annual climate in *Cedrus atlantica*: a linear mixed modeling approach

Joannès Guillemot · Etienne K. Klein · Hendrik Davi · François Courbet

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Abstract

• ***Key message*** **With a retrospective growth analysis over 20 years, we showed that silviculture (in particular thinning) of *Cedrus atlantica* (Manetti) could to some extent mitigate the effects of drought episodes. Severe reductions of density resulted in faster recovery of radial growth after severe drought episodes.**

• ***Context*** Climate change is expected to increase the frequency and the intensity of drought in southern Europe. Silviculture could help in mitigating the effects of water deficit on forests.

• ***Aim*** The aim of this study is to assess the effect of thinning intensity on the climate-growth relationship of different crown classes in *Cedrus atlantica* (Manetti).

• ***Material and methods*** A 20-year annual survey was conducted on plots managed under contrasted thinning regimes in a site of the southern French Alps. Using a linear mixed modeling approach, we evaluated the modulation of the growth response to annual climate by thinning (climate×thinning interaction effect) during the experiment. The effect of thinning on the growth sensitivity to annual climate and the effect of thinning on the growth response to pointer years were also quantified.

• ***Results*** The highest intensity of thinning significantly changed the climate-growth relationship of the two most dominant crown classes. Heavy thinning reduced the impact of negative pointer years during a period of 4–5 years and improved the post-drought recovery for a decade. Heavily thinned plots and dominant crown classes had significantly higher relative growth sensitivities to annual climate over the studied period.

• ***Conclusions*** Forest management has the potential to reduce the effect of water deficit on the growth of Atlas cedar stands. We provide keystones for future silvicultural guidelines, in the context of a larger introduction of *C. atlantica* in the French territory.

Keywords Forest management · Crown classes · Stand density · Water deficit · Resilience · Competition · Dendrochronology

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Contribution of the co-authors J.G. conducted the analyses and wrote the paper, F.C. designed the experiment and supervised the work, E.K.K. provided support in statistical analyses, H.D. provided support in discussing ecophysiological aspects; all authors corrected the manuscript.

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1 Introduction

Climate change is expected to affect greatly the functioning of European forest ecosystems, especially through a greater frequency and intensity of drought. In the Mediterranean area,

drought is already the principal factor limiting tree growth and survival (Andreu et al. 2007). Understanding how water deficits affect Mediterranean forests is therefore important for predicting the consequences of increased drought in this region as well as the future consequences of climate change for northern zones. Indeed, 60 to 80 % of the French metropolitan territory may experience a Mediterranean type climate by the end of the twenty-first century (Roman-Amat 2007). The acclimation of existing forest stands to increasing drought relies on different physiological adjustments, among which leaf area reduction seems of particular importance over the long term (Martin-StPaul et al. 2013), and may be related to changes in stem density (Barbeta et al. 2013). Thinning operation, which modulates stem density and stand vertical structure, can thus accelerate this stand acclimation and has been reported to improve tree resistance to drought stress (Misson et al. 2003) and post-drought resilience (Martín-Benito et al. 2008; Sohn et al. 2013). Silviculture is therefore discussed as an important option to mitigate the negative impact of water deficit on forest (Guillemot et al. 2014).

The annual tree growth is considered as an efficient proxy for tree vitality (Dobbertin 2005) and appears to be modulated by the combined effects of annual climate and competition intensity. These dependencies have often been studied separately. The effect of the annual climate on tree radial growth has been widely investigated to gain insight into the autecology of tree species (e.g., Lebourgeois et al. 2005) or the drivers of forest dieback (Williams et al. 2013). This approach generally neglects the effects of competition on tree growth. Contrastingly, empirical tree growth models aim to predict the long-term growth response to thinning, i.e., to competition modulation. In this second approach, the annual effect of climate on growth is either neglected in a multi-year modeling step or controlled by adding explicit climate variables to the models (Le Goff and Ottorini 1993; Mehtätalo et al. 2014).

Few studies have explicitly investigated the short (annual) and long (decadal) term effects of the interaction between competition and annual climate conditions on tree growth. The effect of competition intensity on the climate-growth relationship was often based on experiments that did not reproduce actual silvicultural guidelines: studies were conducted in stands that had not been thinned for decades (Gea-Izquierdo et al. 2009; Martínez-Vilalta et al. 2012), in stands thinned once (Misson et al. 2003) and in stands lightly thinned (Piutti and Cescatti 1997; Timbal 2002; Kohler et al. 2010; but see Olivar et al. 2013 and Sohn et al. 2013). As a consequence, several important aspects of management impact on forest functioning were overlooked: (i) the short- and medium-term effects of thinning, (ii) the cumulative effect of successive thinning and (iii) the prospective analysis of the effect of thinning intensities beyond the current guidelines. Moreover, most of the previous studies focused on the growth response of dominant trees, which is not always representative of the functioning of the entire stand (De Luis et al. 2009; Mérian and Lebourgeois 2011). Conversely, annual size surveys allow the competition intensity to be quantified yearly, along with the assessment of the effect of social position on the tree growth responses.

The effect of thinning on the climate-growth relationship of trees has primarily been assessed using growth series standardized with mathematical functions fitted to data (e.g., Misson et al. 2003). This empirical detrending separates competition from annual climate effects, based on the expected frequency variations they induced on growth (year period for annual climate and decade period for competition). The sharp growth responses to thinning are then likely overlooked because the variation frequencies induced by the different factors (annual climate and thinning) overlap. Contrastingly, detrending based on individual growth models allows a competition-based standardization that accounts efficiently for the growth response to thinning (Piutti and Cescatti 1997). However, this latter approach often ignores the departure from the assumption of independent error terms induced by the multilevel (plot, tree, year) organization of tree-ring data, thus preventing valid statistical tests (Fortin et al. 2007). As a result, Miina (2000) suggested the use of linear mixed models (LMMs) for tree-ring standardization. In this approach, the fixed part of the model incorporates the individual growth responses, whereas the random effects represent the hierarchical structure of the data. LMMs have recently been used to standardize tree-ring series (e.g., Martínez-Vilalta et al. 2012), but rarely to explicitly quantify the effect of thinning on the climate-growth relationship (Olivar et al. 2013).

In this paper, we present the results of a case study that was conducted to determine the short- and long-terms effects of thinning on the climate-growth relationship of trees from different crown classes. An experiment was conducted during 20 years, based on extensive surveys of plots under contrasted thinning treatments. Linear mixed models were used to disentangle the growth signals in the context of abrupt thinning-induced changes in the competition intensity. This study was conducted in an important Mediterranean species, *Cedrus atlantica* (Manetti). More than 20,000 ha are predominantly planted with *C. atlantica* in France (Courbet et al. 2007). In the context of climate change, a larger introduction of *C. atlantica* is now recommended by the French national guidelines (Roman-Amat 2007) but decline and mortality events have been recently reported in its native area (Allen et al. 2010; Linares et al. 2011), urging for deeper insight in Atlas cedar drought tolerance. We therefore aimed to answer the following questions: (1) Does a reduction in stand competition induced by thinning affect the climate-growth relationship of Atlas cedar? (2) How long after thinning do its effects persist? (3) Does social position affect the growth responses of Atlas cedar trees to annual climate?

2 Materials and methods

2.1 Study site

The study site was selected to be homogeneous in terms of physical environment (slope, elevation, exposure, soil depth) and stand characteristics. The Mediterranean area displays a strong local heterogeneity of climate and soil (Ruffault et al. 2013) and the site was consequently limited to a small (1.5 ha) area. It was located on Mont Ventoux in the southern French Alps. This region has a Mediterranean mountain climate. The site (44° 07′ 05″ N, 5° 20′ 38″ E, 1170 m a.s.l.) is located at an altitude between two nearby stations of the national meteorological network (44° 09′ 00″ N, 5° 19′ 06″ E, 1455 m a.s.l. and 44° 05′ 18″ N, 5° 25′ 00″ E, 792 m a.s.l.). The values of the climatic variables at the study site were estimated from the datasets of these stations. The monthly average temperatures were calculated assuming a decrease in temperature proportional to altitude. The monthly average rainfall was calculated as the mean between the two stations. The mean annual rainfall over the 1989–2010 period was 1076 mm, which is a high value for the Mediterranean climate context, but is the average within the natural range of this species (Benabid 1994). The Gaussen diagram shows one growth-limiting month during the summer (Fig. 1). The soil is a calcaric Leptosol, with a substantial gravel component resulting from the limestone substrate. As a result, the soil is permeable and has low water holding capacity (30 mm to a depth of 25 cm of soil, the calcareous substrate prevents accurate estimation for the entire extent of the prospected soil).

2.2 Experimental design

The experiment was initiated in 1989 in a homogeneous and even-aged 25-year-old plantation, with an initial density of 2500 trees ha^{-1}. The stand was divided into four contiguous plots ranging from 1200 to 1400 m^2, each plot surrounded by a buffer zone (with a minimum thickness of 10 m) to avoid edge effects. Every winter from 1989 to 2010, the stem circumference over bark (CBH) of every tree was measured to the nearest millimeter at breast height (1.3 m), which had been previously marked with paint. We derived the annual basal area increments (BAIs) from the circumference measurements, assuming a circular cross-section of the trees. In 1989, each tree was definitively assigned to one of 5 crown classes—dominant, co-dominant, intermediate, overtopped, and suppressed—based on its size, social rank, and distance to trees from the same crown class. Stem densities and average CBHs within each crown class were similar between plots whereas average CBHs generally differed significantly among the crown classes of each plot (Table 1). To ensure robust tests on the tree growth response dependencies, our analyses included a substantial number of trees per plot. Overall, 1391 trees have been measured and managed annually (Table 1).

The control plot (plot 4) was never thinned during the experiment, whereas plots 1 to 3 were managed with contrasted thinning intensities (Fig. 2). The first thinning consisted of removing one, two, or three crown classes in plot 3 (the most lightly thinned), 2 (the moderately thinned plot) or 1 (the most heavily thinned), respectively, starting with the most overtopped class. The second thinning consisted of removing the remaining most overtopped class in each managed plot (Table 2). Thinning treatment is defined as the number of crown classes remaining in the plot after thinning. The managed plots experienced therefore two different thinning treatments during the studied period, whereas the control plot only experienced the "5 crown classes" treatment (Table 2).

2.3 Environmental homogeneity of the experiment

Our experimental design did not include plot-level replications. For this reason, we carefully checked the homogeneity of the growth conditions among plots before the initiation of the experiment, using phytocentric methods (Skovsgaard and Vanclay 2008), in order to minimize the plot effects on growth not driven by the thinning treatment. The homogeneity of the physical environment was assessed in 1989, comparing: (i) site indexes, i.e., the top height values at an age of reference (Skovsgaard and Vanclay 2008). (ii) mean CBHs of the different crown classes, with one-way ANOVAs. Because no cutting occurred in the stand before 1991, these later tests compared the actual production of the 4 plots, from seedling plantation until the initiation of the experiment.

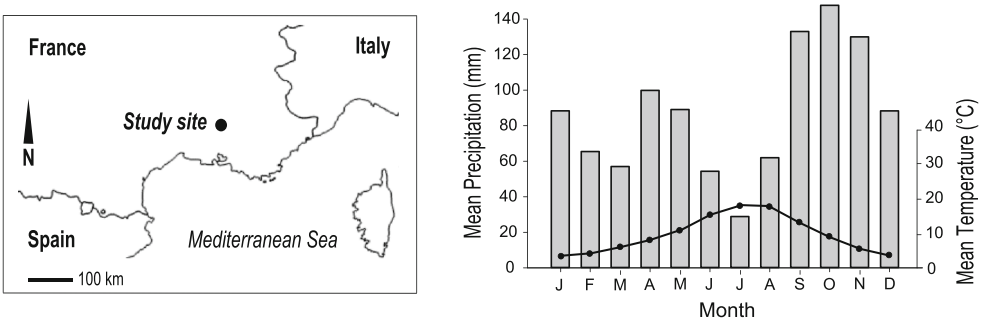


Fig. 1 *Left* Geographical location of the study site. *Right* Gaussen diagram (*line* mean monthly temperatures, *bars* cumulative monthly precipitations). Data are averaged over the last 30 years. Months with a mean rainfall less than twice the mean temperature are considered limiting for vegetal development

Table 1 Average circumferences over bark (CBH) of the crown classes and site indexes, measured in 1989. ANOVA analysis revealed no significant differences in the average CBH of a given crown class between plots or in the total stand average CBH between plots. Within plots, crown classes generally differed in mean circumferences, except for values with the same letter (pairwise *t* tests at the 5 % probability level). Site index is the top height at the age of 25 years. Values in parenthesis are the number of trees

		Plot 1	Plot 2	Plot 3	Plot 4
Mean CBH (cm)	Dominant class	474.5 (33)	472.9 (35)	470 (32)	494.7 (29)
	Co-dominant class	446.5 (36)	409.5[a] (38)	420.7 (34)	426.1 (35)
	Intermediate class	398.2 (88)	400.6[a] (91)	396.3 (79)	402.5 (76)
	Overtopped class	368.5 (94)	352.1 (105)	356.6[b] (87)	350.8 (83)
	Suppressed class	356.4 (109)	344.3 (111)	358.1[b] (100)	327.9 (96)
	TOTAL	377.2 (360)	358.5 (380)	369.3 (332)	354.5 (319)
Site index (m)		9.8	9.9	9.7	9.9

2.4 Statistical analyses

2.4.1 Tree growth modeling

We used a linear mixed model (Littell et al. 2006) to detrend the growth signal, i.e., to separate the relative effects of the tree and plot-level variables on tree growth and isolate the inter-annual variability component from the raw growth signal. The fixed effects were selected from a large collection of dendrometric variables, which included tree-level and stand-level measurements as well as relative indexes measuring tree situation compared with stand characteristics (the variables not retained in the final model are listed in Table S1 of the supplementary material). Fixed-effect variables were log-transformed or included with quadratic effects after visual assessment of bivariate plots. The model selection was based on the protocol described in Zuur et al. (2009). We started with a model including all the considered fixed-effect variables along with their second order interactions, in order to find the optimal structure of the random component. In this step, the correlation among annual observations made on a given tree was accounting for by testing different autoregressive moving average (ARMA) models as the covariance structure for the error terms. Additionally, the heteroscedasticity of the data was considered by assuming the residual variance to be proportional to different power function of the predicted BAIs. In a second step, the optimal fixed structure was selected and the importance of random effects on covariate slopes was tested. The model selection was based on the Akaike's Information Criterion (AIC) and likelihood ratio tests were performed to check for significant model improvements.

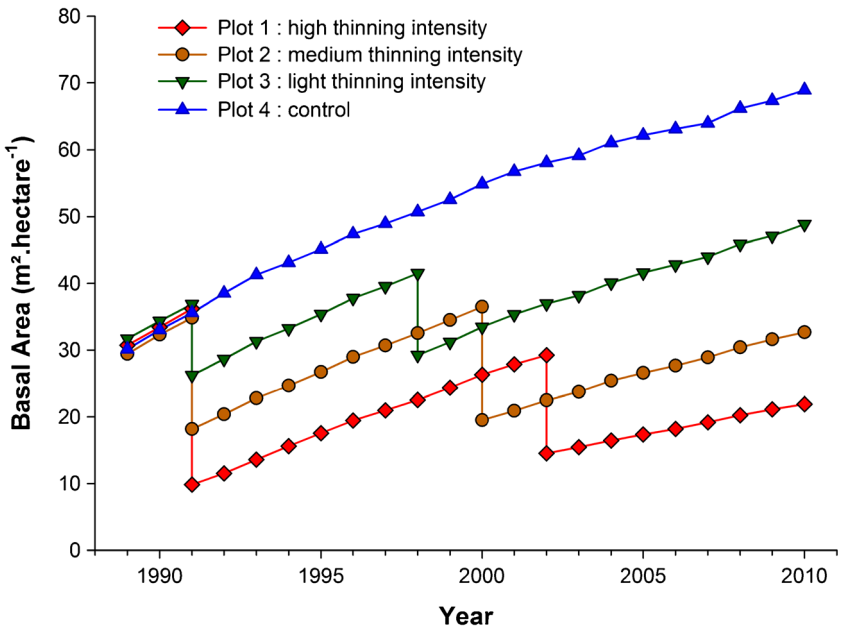


Fig. 2 Temporal changes in the stand basal area of the study plots

Table 2 Description of the thinning operations. Thinning intensity is given as a percentage of the stand basal area removed compared to the control plot. Thinning treatment corresponds to the number of crown class(es) remaining on the plot after thinning

	Plot 1		Plot 2		Plot 3		Plot 4
Management	High thinning intensity		Medium thinning intensity		Light thinning intensity		Control
Year of thinning	1991	2002	1991	2000	1991	1998	1991
Number of stems after thinning (N ha^{-1})	550	250	1200	550	1800	1200	2500
Thinning treatment	2	1	3	2	4	3	5
Basal area after and [before] thinning (m^2 ha^{-1})	9.6 [33.4]	14.5 [27.8]	18.2 [34.3]	19.5 [33.5]	26.2 [34.3]	29.2 [39.5]	33.1 [33.1]
Thinning intensity (%)	72	75	49	64	27	39	0
Crown class(es) remaining on the parcel	*Dom, Co-dom*	*Dom*	*Dom, Co-dom, Inter*	*Dom, Co-dom*	*Dom, Co-dom, Inter, Over*	*Dom, Co-dom, Inter*	*Dom, Co-dom, Inter, Over, Sup*

Dom Dominant, *Co-dom* Co-dominant, *Inter* Intermediate, *Over* Overtopped, *Sup* Suppressed

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The dependent variable was the basal area increment $BAI_{y,i,c,k}$ (mm^2 $year^{-1}$) of year y, measured on tree i from a crown class c in a plot k. The retained final model is written in Eq. 1.

$$\begin{aligned} BAI_{y,i,c,k} = {} & p0 + h1_c + \left(h2_c + C_y\right) \times SBA_{y,k} + p1 \\ & \times Tthin_{y,k} + p2 \times Tthin^2_{y,k} + h3_c \times Dratio_{y,i} + p3 \\ & \times Dratio^2_{y,i} + h4_c \times BAL_{y,i} + A_i + B_y + E_{y,i,c,k} \end{aligned} \quad (1)$$

where $p0$ is the overall intercept, $h1$ to $h4$ are parameters associated with the crown class effect on BAIs and $p1$ to $p3$ are parameters adjusting the covariates with a fixed effect.

The terms included were as follows:

- *Crown class* (a fixed effect);
- *Stand basal area (log-transformed)* (SBA, ln(m^2 ha^{-1}), a covariate with a fixed effect);
- *Basal area of the largest trees* (BAL, mm^2, a covariate with a fixed effect), average basal area of the five largest trees in the plot;
- *Ratio between diameter of the subject tree and the mean quadratic diameter* (*D*ratio, unitless, a covariate with a fixed effect) included with a quadratic effect;
- *Number of years since the last thinning* (*T*hin, year, a covariate with a fixed effect) included with a quadratic effect;
- *Tree effect on the intercept* (A, mm^2 $year^{-1}$, a random effect, $Var(A_i)=\sigma^2_A$), the between-tree variance of the overall intercept;
- *Year effect on the intercept* (B, mm^2 $year^{-1}$, a random effect $Var(B_y)=\sigma^2_B$), the between-year variance of the overall intercept;
- *Year effect on the SBA slope* (C, mm^2 m^2 ha^{-1} $year^{-1}$, a covariate with a random effect, $Var(C_y)=\sigma^2_C$), the between-year variance of the SBA slope.

$Var(E_{y,i,c,k})=\sigma^2_E$ is the residual variance within tree and year. A, B, C, and E are assumed to follow normal distributions with zero means. We retained a first-order autoregressive model (AR(1) equivalent to ARMA(1,0), Fallour-Rubio et al. 2009) as the covariance structure for the error terms and the residual variance was assumed proportional to the predicted BAIs (power exponent=1). The modeling was performed with the MIXED procedure of SAS software and the parameters were estimated with the REML method (Littell et al. 2006), except when simplifying the fixed part of the model when ML was used (Zuur et al. 2009). The Kenward-Roger correction was used to compute the degrees of freedom (Kenward and Roger 2009) required to test for the significance of fixed effects.

2.4.2 Growth response to annual climate

In Eq. 1, the inter-annual growth variability is isolated from the raw BAI signal and characterized by a year effect on the overall average BAI (B) and a year effect on the SBA slope (C). Assuming that the inter-annual growth variability is driven by annual climate, the yearly estimates of B and C thus allowed quantifying the effect of a SBA decrease on the growth responses to the different annual climatic conditions. We compared the predicted growth response to annual climate for different competition intensities (SBA=55, 40, 30, 20, 15, and 10 m^2 ha^{-1}). Average comparisons were conducted separately for the years displaying strong (named positive years) and low (named negative years) growth: a year was considered positive if its predicted growth response to climate at SBA=55 m^2 ha^{-1} (average of the control plot) was higher than the average, negative otherwise.

Additionally, a pointer year analysis was conducted on the fixed-effect model residuals. Pointer years were identified when the average of the BAIs from the control plot was negative and if at least 75 % of the trees had a BAI reduced by 10 % or more compared with the previous year (Lebourgeois et al. 2005). Plot responses were compared through the average of the fixed-effect residual values of each pointer year, the mean fixed-effect residual values of the subsequent year and the mean fixed-effect residual values over the five subsequent years. As an attempt to assess how annual climate drove growth reductions at this site, climatic variables were used as regressors to predict the fixed-effect residual values (for the years 1990 to 2010, n=21) of the control plot in a multiple linear regression model. The climatic covariates included precipitation; mean, maximum and minimum temperature; and the De Martonne aridity index; these variables were expressed as monthly and annual averages, and as seasonal means over the growth period (March to July) and the autumn months (October to December). For a given year y, the climatic variables of the years y and $y-1$ were considered.

The standard deviation (SD) and the Gini coefficient (GC) of the raw recorded growth series were calculated to compare the growth sensitivity to annual climate among plots and crown classes. SD is an absolute measurement of the growth sensitivity, whereas GC is a relative index, quantifying the sensitivity scaled by mean and sample size (Biondi and Qeadan 2008). SD and GC were calculated for each tree and averaged in a second step. For managed plots, SD and GC were calculated over sub-periods excluding year of thinning, the resulting values being averaged with a weight for the duration of the sub-period.

3 Results

3.1 Homogeneity of growth conditions among plots

The site indexes of the four plots had similar values (Table 1), indicating similar site productivity and thus a homogeneous

environment among plots. Accordingly, the mean CBH of the 5 crown classes—measured before the initiation of the experiment—did not differ significantly among plots (Table 1). We therefore considered only thinning-induced effects at the plot level in the growth model.

3.2 Tree growth drivers and variance partitioning

Several tree- and stand-level variables entered the final model to take into account the changes in tree growth conditions during the experiment (Table 3). Stand basal area, quantifying the competition intensity, was negatively associated to annual growth. *D*ratio a measure of the competitive ranking of a tree within a plot, and *T*thin entered the model with quadratic effects. The higher growth capacity of bigger trees compare to small ones was accounted for by the positive coefficient of BAL: for a given SBA, trees from a plot with lower stem density and higher stem sizes had higher predicted BAIs. SBA, *D*ratio and BAL had significant interactions with the crown class factor, indicating that the association between competition-related variables and the annual growth varied with the social position of the trees. The correlation between the variables entered in the final model was low (Table S2) and the variance inflation factors calculated on centered data was less than 3.5 for each predictor (Table 3), ensuring a tolerable multicollinearity among the variables (Belsley et al. 2005). The between-tree (σ_A) and between-year (σ_B) variances explained approximately 23 and 48 % of the intercept variance, respectively. The final model residuals showed no departure from the assumption of normally distributed error with homogenous variance (result not shown). The graphical agreement between the means of the annual observations and the fixed-effect model predictions is displayed in Fig. 3.

Table 3 Summary of the fitted linear mixed model of BAI. VIF is the variance inflation factor, calculated on centered data. The symbols in the sign column indicate the sign of the estimate value(s) for the corresponding variable. All estimate values are available in Table S3

	VIF	*F* value	*P* value	Sign
Crown class		615.6	<0.001	
SBA	1.4	259.7	<0.001	–
*T*thin	3.2	22.8	<0.001	–
*T*thin^2	3.1	72.4	<0.001	–
*D*ratio	1.0	5158.2	<0.001	+
*D*ratio^2	1.1	544.6	<0.001	+
BAL	1.8	830.2	<0.001	+
Crown class×SBA		257.1	<0.001	
Crown class×*D*ratio		85.9	<0.001	
Crown class×BAL		120.9	<0.001	
σ_A=630 σ_B=903	σ_C=460 σ_E=689			
AIC=30791.34	log Lik.=−15367.82			

BAI basal area increment, *SBA* stand basal area (log-transformed, ln(m^2 ha^{-1})), *T*thin the number of years since the last thinning (year), *D*ratio the ratio between diameter of the subject tree and the mean quadratic diameter (unitless), *BAL* the basal area of the largest trees (mm^2). See further explanations in the main text

3.3 Predicted effect of thinning on the growth response to annual climate

A decrease in SBA enhanced the predicted growth response to annual climate in negative years, indicating that thinning dampened the negative impact on growth when the year was constraining (Fig. 4). This benefit of thinning was only significant for heavy thinning as the minimum SBA range for significant difference in growth response was 40 to 15 m^2 ha^{-1}. Consequently, a significant thinning-induced improvement of the growth response to climate was observed on plots where only the dominant and co-dominant crown classes remained in the stand (Table 2, Fig. 2). Contrastingly, the growth enhancement observed in positive years was reduced for low SBAs, but no significant effects were reported (Fig. 4).

3.4 Pointer year analysis

The best AIC climatic model with two covariates was as follows:

$$\text{Residuals} = -619.1 + 0.33\,R(-1) + 11.07\,\text{DMI},$$

with R(−1) representing the autumn rainfall of the previous year and DMI the De Martonne index averaged over the growth period (March to July).

Rainfall and water balance (approximated by the De Martonne index) had a positive effect on growth. The model explained an important part of the inter-annual variability of the LMM residuals (R^2=0.68, RMSE=94.6, F=32.5, P value <0.001), with a predominant importance of the growth period DMI (partial R^2=0.55). Growth reductions in negative pointer years, identified as 1994, 1997, 2002, and 2005, were well predicted by the climatic model (Fig. 5).

The growth of the dominant crown classes was proportionally less affected by drought in plots where a thinning had recently decreased the stem number below 550 trees per hectare (i.e., in 1994 and 2002, in plots 1 and 2; respectively, Figs. 2 and 6; complete results in Table S4). Additionally, the heaviest thinning improved post-drought resilience of the stand during a decade (growth was proportionally higher in 1995 and over the periods 1995–1999 and 1998–2002 in plot 1). The benefits of thinning were maintained by successive operations as shown by the significantly higher growth of plot 1 in 1994 and 2003. The same pattern was found

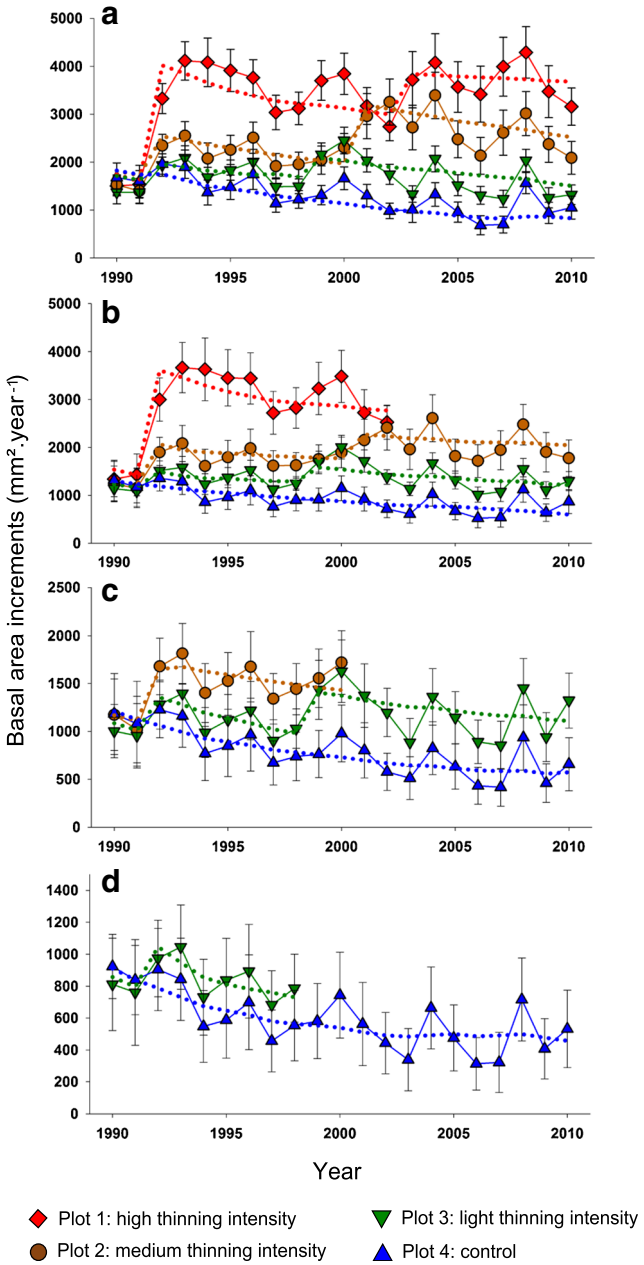


Fig. 3 Evolution of the observed averaged basal area increments (BAIs, *solid lines*) and averaged fixed-effect predictions from the linear mixed model (*dotted lines*), for the dominant class (**a**), co-dominant class (**b**), intermediate class (**c**), and the overtopped class (**d**). *Error bars* are standard deviations of the observed BAIs. For a better readability, error bars of the predictions are not represented

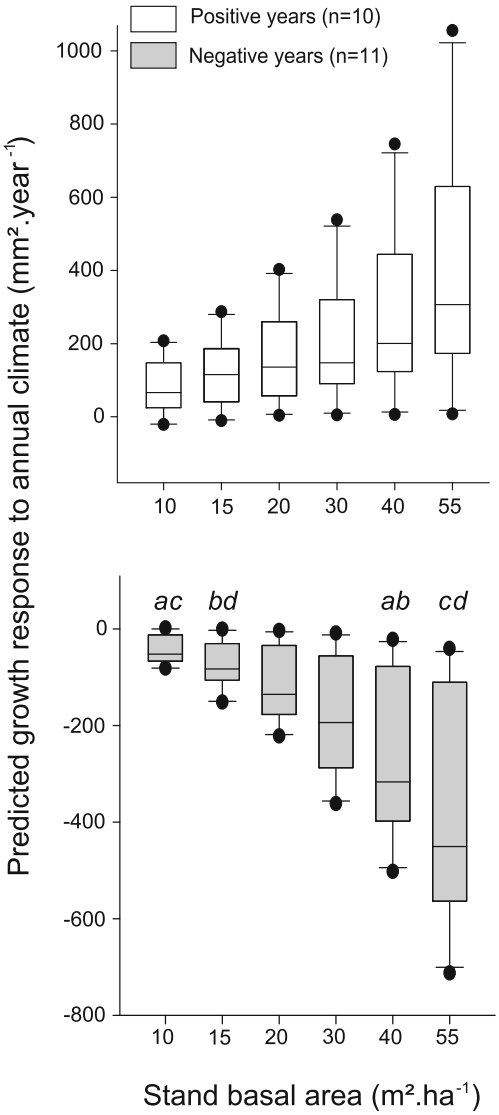


Fig. 4 Predicted growth response to annual climate (from 1990 to 2010) under contrasted stand basal areas. Predictions are obtained from *B* and *C* estimates in Eq. 1. For a given year *i*: Prediction$_i$=B_i+C_i×ln(SBA), where SBA is stand basal area. Positive and negative years correspond to years with high growth and low growth, respectively (see main text). Similar *letters* indicate a significant difference at the 5 % probability level in a Wilcoxon-Mann-Whitney test. No significant differences were reported for positive years

in the dominant and co-dominant crown classes (Table S4).

3.5 Growth sensitivity to annual climate

The SD and GC values were positively associated with thinning intensity in every crown class (Table 4). SD and GC increased significantly for thinning intensities that yielded a SBA lower than 19.5 m^2 ha^{-1} (or a stand density below 1200 trees ha^{-1}), i.e., below the value attained in plot 3 (Table 2). Moreover, inter-annual growth sensitivity was significantly higher for the dominant classes, regardless of the thinning treatment.

4 Discussion

We used a tree growth model to achieve an efficient competition-based detrending of annual growth series in the context of thinning-induced sharp competition changes. The

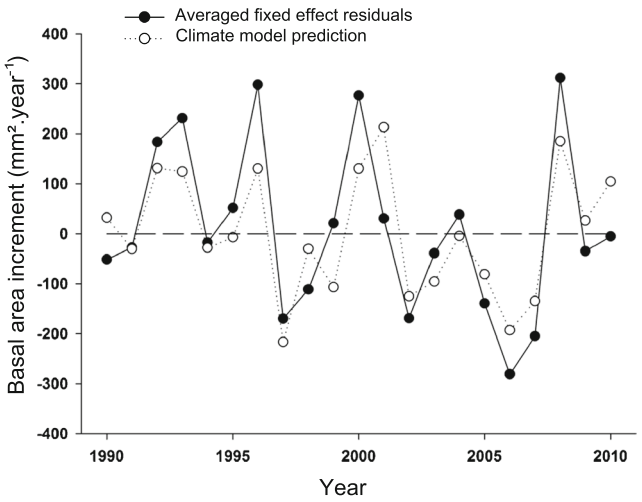


Fig. 5 Comparison of the averaged linear mixed model fixed-effect residuals of the control plot and the climatic model predictions

fixed part of the linear mixed model performed satisfactorily against observed BAIs in all crown classes and thinning treatments (Fig. 3), despite occasional discrepancies (e.g., in average, the model underestimated the growth of the dominant crown class in the control plot). Unbiased fixed-effect predictions were required to isolate the climate-driven component of the growth time series from the effects of tree age and thinning. Without additional ecophysiological measurements, the interpretation of the retained fixed effects is not straightforward because the dendrometric variables used in the LMM are proxies accounting for complex functional responses (Brooks and Mitchell 2011; Sohn et al. 2013). In particular, the predicted transient growth increase induced by thinning likely accounts for an improvement of the resource availability (Nambiar and Sands 1993; Bréda et al. 1995), for the enhancement of the remaining tree crown areas (Pretzsch 2014) and/or for the possible mobilization of stored non-structural carbohydrates in support of growth. The LMM provided a sound framework to disentangle management effects from the climate-driven signal and to quantify the interaction between thinning and climate on growth. LMMs have thus the potential to complement classical dendrochronological analyses as they can be used to separate signal components whose periods are not fully included in the growth series: competition effects were evaluated in this study using a dataset spanning two decades i.e., less than the signal period induced by thinning (Misson et al. 2003).

4.1 Crown class modulation of the climate-growth relationship

Summer drought has been widely reported as the most important factor limiting tree growth and productivity in the Mediterranean area. In line with these results, the aridity during the growth period was the principal factor controlling the annual variability of growth at our site, with a secondary carry-over effect of the previous year rainfall (Fig. 5). The increase in the absolute annual sensitivity of growth (quantified by the standard deviation) when average tree growth increases is a long known result in forest sciences (Cook 1985) and has been taken into account in the statistical modeling. Conversely, the reported increase in the relative annual sensitivity of growth (quantified by the Gini coefficient) of the two dominant crown classes highlights a different functional response to climate of dominant trees, regardless of the thinning treatment. The literature reports contradictory results regarding the crown class modulation of the tree growth responses to annual climate: certain studies report suppressed trees to be more sensitive to rainfall variability (De Luis et al. 2009; Olivar et al. 2013), whereas others report a greater sensitivity of the dominant trees, in line with our results (Martín-Benito et al. 2008; Mérian and Lebourgeois 2011). Performing a multispecies analysis along a wide climatic gradient, Mérian and Lebourgeois (2011) reported that larger trees of shade-tolerant species, such as *C. atlantica*, were significantly more sensitive to summer drought than smaller trees. This difference increased with increasing site xericity. The buffer effect on environmental conditions provided by dominant tree canopy (Aussenac 2000) could be more important at water-limited sites, thereby explaining that the suppressed trees at our study site are less sensitive to the inter-annual water balance variability. In another view, the lower growth sensitivity of suppressed trees is due to a loss of plastic capacity in those trees strongly constrained by competition (Linares et al. 2010). A third plausible explanation of the greater sensitivity of large trees to climatic stress is their higher water needs and the higher risk of cavitation that they face due to their longer xylem path (Bigler and Veblen 2009). We reported a significant increase in sensitivity between the co-dominant and the dominant classes, regardless of the thinning treatment. Moreover, the sensitivity of a dominant crown class increased with thinning intensity. As microclimate buffering and competition constraints are expected to be rather similar between the two most dominant classes, we assumed that the crown-class modulation of the growth response to annual climate was driven primarily by size-related constraints on tree functioning in this context (D'Amato et al. 2013).

4.2 Effect of thinning on the climate-growth relationship

Thinning was found to significantly modulate the growth response to annual climate of the dominant and co-dominant crown classes of cedar stands. Using a contrasted approach, Gea-Izquierdo et al. (2009) and Piutti and Cescatti (1997) also

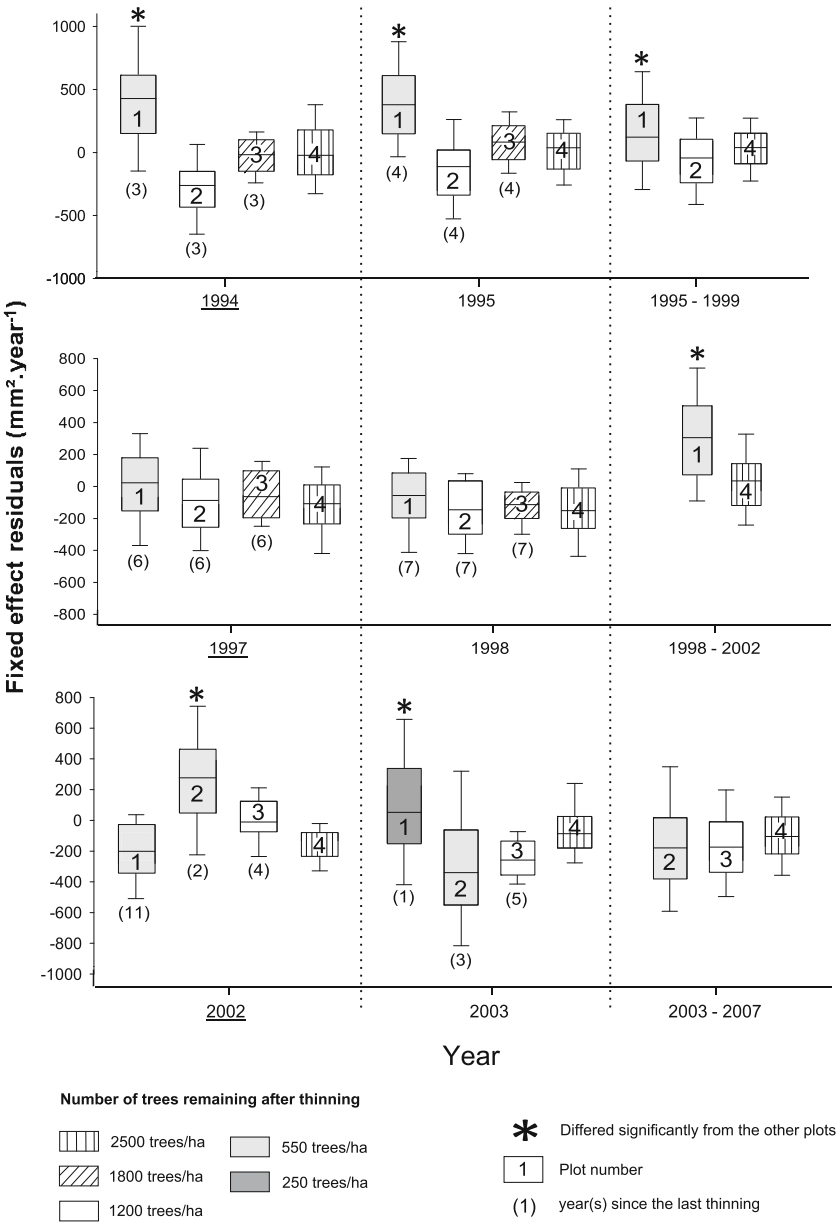


Fig. 6 Growth responses to three pointer years (1994, 1997, 2002, from *top to bottom*) in the dominant crown class. Pointer years (*underlined*) correspond to abrupt negative changes in the growth patterns. Results are presented for pointer year (*left panel*), 1 year after pointer year (*middle panel*) and post-pointer year period (*right panel*), when no thinning occurred. The *boxed numbers* refer to the corresponding plot. Plots with a "*" differed significantly from the others (at the 5 % probability level in a pairwise Tukey test). *Bottom numbers* (*X*) means "X years since the last thinning"

highlighted differences in the correlation between climate variables and annual growth among trees experiencing different competition intensities. Both studies reported a greater effect of water deficit (low precipitation and high temperatures) in denser stands. In line with these results, heavy thinning reduced the negative effect of drought years on dominant tree growth in our experiment. Note that only a heavy stand basal area reduction (40 to 15 m^2), which is beyond the current prescription (Courbet et al. 2007), significantly altered the climate-growth relationship. This suggests that light thinning does not affect the functional response of trees facing constraining years in dry sites, where inter-tree competition for water is strong (Olivar et al. 2013). Accordingly, the growth of heavily thinned stands (to less than 550 trees per hectare) was less affected by negative pointer years during the 4–5 years following thinning in both absolute (Fig. 6) and relative terms. This result agrees with Misson et al. (2003) and Sohn et al. (2013), who found a smaller relative growth reduction induced by severe drought in recently thinned stands. Conversely, Timbal (2002) reported a greater drought-induced reduction in the absolute growth of heavily thinned stands. Kohler et al. (2010) and McDowell et al. (2006) also reported this higher absolute decrease but additionally emphasized the occurrence of a lower relative decline, in line with our results. The contradictory literature results regarding the effect of thinning on the drought-induced absolute growth decline are most likely due to variation in the thinning and drought intensities imposed in the different studies. The ecological traits of the different studied species could also explain these conflicting results. Indeed, different strategies in the adaptation of the water conductivity system to

Table 4 Growth sensitivity to annual climate. Within a given crown class, values with different Latin letters differed significantly (at the 5 % probability level in a pairwise Tukey test). Within a given plot, values with different Greek letters differed significantly (at the 5 % probability level in a type I test)

		Plot 1	Plot 2	Plot 3	Plot 4
Dominant class	SD	723.3^{a}	$549.4^{b}{}_{\alpha}$	$387.0^{c}{}_{\alpha}$	$385.6^{c}{}_{\alpha}$
	GC	0.08^{a}	$0.06^{b}{}_{\alpha}$	$0.04^{c}{}_{\alpha}$	$0.04^{c}{}_{\alpha}$
Co-dominant class	SD		$450.4^{a}{}_{\beta}$	$307.3^{b}{}_{\beta}$	$289.2^{b}{}_{\beta}$
	GC		$0.05^{a}{}_{\beta}$	$0.03^{b}{}_{\beta}$	$0.03^{b}{}_{\beta}$
Intermediate class	SD			$294.9^{a}{}_{\beta}$	$264.5a^{a}{}_{\beta}$
	GC			$0.03^{a}{}_{\beta}$	$0.03^{a}{}_{\beta}$
Overtopped class	SD				194.4_{γ}
	GC				0.02_{γ}
Supressed class	SD				178.3_{γ}
	GC				0.03_{γ}

SD standard deviation, *GC* Gini coefficient

drought (Eilmann et al. 2009) or in the capture of resources (Cuny et al. 2012) are associated with distinct growth responses to environmental factors among species. Collectively, our results confirm that the increased water availability in recently heavily thinned stands of Atlas cedar allows trees to maintain higher growth during drought in our site. We additionally reported that high thinning intensity led to a greater post-pointer-year growth recovery of the dominant classes for a decade. This medium-term consequence of thinning has been reported in different species (Misson et al. 2003; Kohler et al. 2010; Sohn et al. 2013) and likely resulted from tree structural changes, such as increased foliage area and fine root biomass (Sohn et al. 2013). Benefits of thinning could be maintained by successive operations, as previously suggested by Le Goff and Ottorini (1993) and Timbal (2002) in *Fagus* and *Pinus*, respectively.

4.3 Management perspectives

Tree growth has often been shown to be a proxy for tree vitality, and numerous studies report that dying trees exhibit lower growth (Bigler and Bugmann 2004). Consequently, because thinning enhances the growth of remaining trees, it has been advocated to reduce drought effects and the mortality risk for different species and sites (e.g., Misson et al. 2003; Kohler et al. 2010). As an increasing drought frequency is projected by climate models, the reported ability of thinning to limit the negative impact on growth when the year is constraining confirms that silviculture could play a role in the adaptation of *C. atlantica* stands to climate change. Repeated heavy thinning has thus the potential to limit the risk related to drought by reducing both growth sensitivity to summer water deficit and the length of the forest rotation. However, except for a short post-thinning period, management increased the sensitivity of relative growth to annual climate variability. This result, which we interpreted as the effect of size-related constraints on cedar growth, agrees with a previous study reporting that *Pinus* with greater growth were proportionally more affected by drought (Martínez-Vilalta et al. 2012). The interpretation of this higher sensitivity from the viewpoint of the ability of cedar to cope with drought effects is not straightforward, and we still lack a conceptual framework linking the growth signal features to life traits (Cuny et al. 2012) and demography (Martínez-Vilalta et al. 2012). Indeed, previous studies produced seemingly contradictory results, reporting higher mortality rates for trees showing highly variable growth (Suarez and Ghermandi 2004) or a weaker correlation between the growth of the dying trees and the climate variables (Linares et al. 2010). As recent reports suggest a lower capacity of large trees to overcome severe drought (Bigler and Veblen 2009), the long-term effect on thinning on the ability of mature cedar stands to survive extreme water stress events need further investigations.

5 Conclusion

This research contributes to the analysis of the poorly studied interaction between stand structure and annual climate on tree growth. Our results suggest that heavy thinning mitigates the effect of drought on *C. atlantica* in a site of the southern French Alps. This site is characterized by a Mediterranean mountain climate with important annual rainfall and a low soil water holding capacity. In Europe, forest is often located on poor soils, where no profitable agriculture is possible (Chakir and Le Gallo 2013). Our study site is therefore representative of the growth conditions that will face the *C. atlantica* stands recently introduced in the northern Mediterranean zone and the temperate French territory in order to adapt forest to climate change. Our results regarding the stand density desirable to reduce the effect of drought on Atlas cedar functioning should now be integrated with the other relevant ecological factors impacted by thinning (e.g., regeneration and soil erosion) in order to design future management guidelines in these areas.

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