Variability of the climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients

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ABSTRACT

Tree ring widths provide very useful information to assess factors controlling tree radial growth and to estimate future growth trajectories under climate change. Radial growth variability has already been largely studied among tree populations that experience different environmental conditions and was most recently analyzed among individuals within populations.

In the present study we assessed, over the 1960–2011 period, the growth response of silver fir (*Abies alba* Mill.) individuals originating from ten populations located along two altitudinal gradients (1000–1600 m a.s.l.) in the south east of France. Tree ring increments were estimated from wood cores collected from 129 adult trees. Results showed that (i) 30% of the growth variance among individuals was explained by competition; (ii) the climates of both the current and previous years were correlated with growth. Most of the climatic variables affecting growth were consistent with those identified in previous studies and with the known physiology of the species: negative effects of summer drought of the current and past years as well as a positive effect of the spring temperature of the current year. However in our study, fir growth was also enhanced by previous year spring droughts. The growth responses to precipitation, temperature, and, relative humidity of the current and previous years varied between sites and/or altitudinal levels, reflecting population acclimation by plasticity or genetic adaptation to local conditions. By contrast, only summer rainfall induced variable responses between individual trees, result attributed to the edaphic micro local heterogeneity. The recent climate change did not significantly alter the fir growth response to climate.

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1. Introduction

The development of living organisms results from continuous interactions between individuals and their environment.

Over time, individuals change their behavior in response to climate variations and exhibit various phenotypes in different environments due to the phenotypic plasticity of their functional traits. In the northern hemisphere, the 1983–2012 period appears to be the warmest period of the last millennium and it can be hypothesized that the ongoing climate change (warming: ~0.85 °C from 1980 to 2012 and CO_2 rise: +40% since preindustrial times; IPCC, 2013) has already modified the relationships between climate and functional traits (Valencia et al., 2016).

Within species, populations living in different locations experience various environmental conditions that induce contrasting selection pressures which may lead to genetic differentiation or acclimation among populations. Different reaction norms (i.e. climate-functional trait relationship) may thus be expected among populations (e.g., Lebourgeois et al., 2010; Rolland et al., 1999). Additionally, variability of the reaction norm between individuals can also be expected either due to inter-individual genetic variability (e.g., Ettl and Peterson, 1995) or local plant interactions such as competition/facilitation (Callaway, 1998).

Quantifying the adaptive potential of populations to climate change implies to address the following issues: (i) to assess the response of traits to climate (ii) to assess whether this response vary between populations or between individuals, and (iii) to test whether this response is stable over time.

In trees, wood retains a 'memory' of the past and tree-ring width allows us to explore the effects of environmental variations, especially climate variables, on radial growth (Cook and Briffa, 1990; Fritts and Swetnam, 1989). Additionally, tree rings integrate multiple environmental and physiological signals (Cook, 1987) especially when working at the individual scale. Among them,

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the main biological effects are (i) tree age and size (Bontemps and Esper, 2011; Esper et al., 2003; Abdul-Hamid and Mencuccini 2008; radial growth is usually S shaped) and (ii) effect of the competition (Piutti and Cescatti, 1997).

Many studies have analyzed the relationship between climate and past growth to reconstruct climate (Esper et al., 2002), compare ecological niches (e.g., Lebourgeois, 2007), or evaluate the potential effects of climate change on trees (Rolland et al., 1998; Gea-Izquierdo et al., 2011). Some recent studies also considered the individualistic response of trees within population (Carrer, 2011; Galván et al., 2014; Rozas, 2015; Zhang et al., 2013). Less work has attempted to decipher how the climate growth relationships found at the population level can change along environmental gradients (but see Dittmar et al., 2003; Gea-Izquierdo et al., 2011 or Rolland et al., 1999; Rolland et al., 2000) or through time (for an individual or a population), especially when climate has drastically changed over long periods (e.g. Sarris et al., 2007). In this study, we evaluate the climate-growth response at both the population and tree levels to answer the following questions: (i) What are the climatic factors affecting the radial growth? (ii) Do climate-growth responses vary among altitudinal levels and/or among individuals? (iii) Have these climate-growth responses changed since the observed increase of temperature (i.e. mid-1980s for the studied sites)?

The climate-growth relationship was estimated for 5 climatic variables (temperature, relative humidity, precipitations, frost and drought) and 129 silver firs (*Abies alba* Mill.) distributed along two altitudinal gradients.

Silver fir is a shade-loving tree species (Michalet et al., 2008; Saccone et al., 2009) known to be drought sensitive (Aussenac, 2002; Lebourgeois et al., 2010). This species developed a drought avoidance strategy (Nourtier et al., 2014) making it vulnerable to carbon starvation and bark beetle attacks when recurrent droughts occur (Cailleret et al., 2014). Silver fir is thus an interesting model species for assessing the response of long-lived organisms to climate change, especially at the rear edge of its range.

2. Methods

2.1. Study sites

The study was conducted on two mountains representative of the inland region of Southeastern France: Mont Ventoux (Vtx), close to the Rhône Valley, and Issole (Iss), located 100 km to the east. At both locations, the sites were mostly deforested by over-exploitation and grazing pressures during the 19th century. In the late 19th, early 20th century, a decrease of the overgrazing associated with an active afforestation policy allowed the large-scale restoration of forest cover (Dreyfus, 2003). The planted stands (mainly using pines) were then naturally recolonized by post-pioneers (*Sorbus aria* L. and *Acer opalus* Mill.) and late-successional species (*Abies alba* Mill. and *Fagus sylvatica* L.). In the present study we registered 16 forest species in Vtx and 11 in Iss in the vicinity of the cored trees. The two mountains experience various soil conditions: bedrock is a calcareous karst in Vtx and, a calcareous clay in Iss. Soils are shallow (30–70 cm), and exhibit a high variability in depth and texture both among and within mountains. Soil water reserve is generally low (20–50 mm) and varies according to the proportion of coarse elements (30–80%) and depth of the bedrock (Cailleret et al., 2014). At similar altitude temperature is higher (+0.4 °C in average) and precipitations are lower (856 mm versus 1126 mm and 217 mm versus 243 for summer rainfall at 1250 m a.s.l) in Iss than in Vtx (Cailleret et al., 2014). Relative humidity is on average 75% on both

mountains. Temperature lapse rates 0.73 and 0.50 °C/100 m for Vtx and Iss, respectively.

Adult firs were sampled from the whole elevation range of the species (Table 1) on the north-facing slopes of the two mountains. Stands are quasi-exclusively composed of silver fir in Iss whereas stands are mixed in Vtx, with predominantly firs, beeches and pines. The tree height to diameter ratio was higher in Iss than in Vtx (Appendix G).

2.2. Wood core collection and tree-ring processing

In autumn 2011 and 2012, 129 trees were cored at tree dbh (diameter at breast height $\approx$1.30 m) on Iss (41 trees) and Vtx (88 trees) using a mechanical borer of 5.5 mm diameter oriented in the direction perpendicular to the slope. Cored trees from Iss were distributed over five elevation plots, whereas trees from Vtx were sampled along a continuous elevation transect and grouped into five altitudinal classes (Table 1). Hereafter, these ten elevation plots will be referred to as "stands". The location, dbh, and status (dominant, co-dominant or dominated) of each tree were registered. The cores were stored and dried for two to four months at room temperature until humidity stabilized. They were then sawed to obtain 2 mm thick boards.

Resins were extracted from the boards by immersion in pentane for one week. Then, the cores were dried again and X-rayed (Polge, 1970). Tree ring limits were identified from the scanned X-ray films using the Windendro® software (v. 2012a, Regent Instruments Inc.) allowing for automatic computation of ring width (**RW**). Seventy-five of the 129 studied trees had already been cored between 2006 and 2009 (Cailleret and Davi, 2011), and the two growth series were averaged.

Individual series were cross-dated using the R package *dplR* (R Core Team 2015; Bunn, 2010). When the cores did not reach the pith of the stem, the length of the missing segments and the number of missing rings were estimated either by the geometric method based on the curvature of the innermost rings (Esper et al., 2003) or by a model calibrated on our data set (see Appendix A). Finally, the annual basal area increments (**BAI**) were computed from RW assuming that the growth rings were circular.

2.3. Data adjustment for non-climatic effects

This step aimed to estimate the effects of (i) cambial age of the trees and (ii) competition on the ring widths in order to remove them for the ring series.

2.3.1. Cambial age effect

Cambial age effect was assessed from individual growth series using the mean regional age curve (**RC**) method (Esper et al., 2003) applied on the cumulative basal area increment (**BA**). The term "regional" refers to a geographical area with uniform climatic conditions. In our case, RC was estimated for (i) each mountain (global RC) and (ii) each stand within each mountain (stand RC) by fitting a Gompertz function to the BA by cambial age curve. Global RC and stand RC were then compared using Tukey's test to define the spatial scale at which the cambial age effect on growth should be considered. A radial growth index (CA_GI, for Growth Index adjusted for Cambial Age) was then calculated for each tree at each cambial age such as:

$$\text{CA\_GI}_{ij} = \left(\text{BA}_{ij}^{\text{obs}} - \text{BA}_{i(j-1)}^{\text{obs}} \right) \Big/ \left(\text{BA}_{ij}^{\text{RC}} - \text{BA}_{i(j-1)}^{\text{RC}} \right) \tag{1}$$

where $\text{BA}_{ij}^{\text{obs}} - \text{BA}_{i(j-1)}^{\text{obs}}$ is the basal area increment at the cambial age j and $\text{BA}_{ij}^{\text{RC}} - \text{BA}_{i(j-1)}^{\text{RC}}$ is the value computed from the RC fit for the regional scale (i.e., global or stand) i at cambial age j. GI values

Table 1
Main characteristics of the Mont Ventoux (Vtx) and Issole (Iss) stands where 129 studied silver firs were cored.

Stand	Elevation (m a.s.l., ± SD)	Coordinates (Lon, Lat)	Slope (°)	SWSC (mm)	N	Mean age of the cored trees (years)	Mean circ. (cm, ± SD)	Mean annual BAI (cm²)	Stand density[a] (trees/ha)	Fir proportion (% of trees)	Status (D/CoD/d)
Vtx1	1023 (±28)	5.235, 44.185	25	30.6	20	60	61 (±84)	80.9	1204	13	5/8/7
Vtx2	1138 (±31)	5.238, 44.183	22	20.0	15	58	75 (±83)	116.5	956	26	11/3/1
Vtx3	1248 (±28)	5.241, 44.180	22	20.0	23	60	84 (±97)	179.7	1047	30	10/10/3
Vtx4	1345 (±28)	5.243, 44.179	27	43.8	12	110	79 (±99)	92.6	1218	23	6/5/1
Vtx5	1462 (±45)	5.244, 44.177	28	24.5	18	108	79 (±105)	104.8	1433	11	9/4/5
Iss1	1129 (±0.5)	6.485, 44.026	38	41.7	7	167	114 (±47)	83.6	415	93	4/3/0
Iss2	1208 (±6)	6.485, 44.025	39	29.7	8	92	71 (±77)	75.2	691	92	4/4/0
Iss3	1268 (±8)	6.484, 44.023	23	27.5	9	84	78 (±75)	84.9	859	94	2/6/1
Iss4	1480 (±10)	6.465, 44.026	25	27.1	6	88	107 (±51)	114.5	503	83	3/3/0
Iss5	1565 (±0)	6.462, 44.024	35	50.3	11	77	108 (±58)	192.3	343	92	4/7/0

Lon: longitude, Lat: latitude, SWSC: soil water storage capacity computed according to soil texture method (Baize and Jabiol, 1995), N: number of cored trees, circ.: circumference measured in 2014, BAI: basal area increment, Status: D = dominant, CoD = codominant, d = dominated.

[a] Stand density was computed from the inventory of the trees neighboring the cored trees.

greater than 1 correspond to a basal area increment higher than the regional average increment.

2.3.2. Competition effect

The effect of the neighboring trees on the growth of the cored trees was fitted using a parametric competition index derived from the Hegyi index (Hegyi, 1974) adjusted by Canham et al. (2004). This model takes into account the tree neighbor features (dbh, species), their distance to the cored tree and their upstream vs downstream location (Appendix B).

The residuals of the model (i.e. tree growth index adjusted for age and competition) were used to evaluate the effect of climate variables on radial growth. For clarity, this will be referred to as "growth index" (and noted GI).

2.4. Effect of climate on the fir radial growth

This step aims to estimate (i) the climatic determinants of the fir radial growth both at population and individual levels and, (ii) the effect of the recent climate change on the fir growth response to climate. First, synthetic climatic variables were developed according to the correlations between fir individual radial growth and monthly climatic variables. Second, we tested the effect of every synthetic variable on (i) the average fir radial growth at the stand scale and, (ii) the individual radial growth.

2.4.1. Climatic data

The effects of the main climatic variables (air temperature, relative humidity, precipitation and number of freezing days) and of one bioclimatic variable (drought index) on GI were assessed over the 1960–2011 period. Daily temperatures (minimum, maximum and mean) were estimated from two long reference climate series provided by the French meteorological weather service (Météo-France): Barcelonnette (44°23′N; 6°40′E; 1155 m a.s.l., 43 km away from Iss) and Orange (44°09′N; 4°52′E; 57 m a.s.l, 30 km away from Vtx). These series were adjusted to the local conditions using local climatic data collected from 2007 to 2015 using Hobo micro data loggers located at each of the ten studied stands. To account for seasonal effects, series were divided into two subsets: (i) from

April to September and, (ii) from October to March. The linear regression models fitted for the 2009–2015 period (see Appendix C) were applied over the whole 1960–2011 period.

The number of freezing days (hereafter, "frost") was computed as the number of days per month with a minimum temperature below 0 °C.

Daily relative humidity and rainfall data were extracted from the SAFRAN analysis dataset (grid cells #8147 and #8340) provided by Météo-France (Vidal et al., 2010). Relative humidity data were adjusted to the local conditions of each stand using the methodology previously described for temperature. A unique series of precipitation data per mountain was used for all stands because of the inaccuracy of the rain data collected by the local rain gauges. Indeed, many precipitation data points are missing due to the under cover locations of the gauges that were often obstructed and, in winter, some of the collectors placed at highest elevations were saturated because of the snow.

Note that the SAFRAN data were used for relative humidity and rainfall because these data were not available from the reference climatic series. On the contrary, the reference climatic series data were preferred over the SAFRAN data for temperatures because of inconsistencies observed in the SAFRAN temperatures data (see Appendix D). All climatic data were computed on a monthly base.

For each stand, a bioclimatic self-calibrated Palmer drought severity index (Palmer, 1965; Wells et al., 2004) was also calculated at a monthly time step (hereafter noted DI). This index takes into account temperature, rainfall and soil water storage capacity. Negative drought index reflects dry conditions, while a positive index reflects rather wet conditions.

2.4.2. Identifying relationships between GI and seasonal climate at the individual and regional scales

A first step was to test the effect of each of the 84 climatic variables (7 variables × 12 months) from both the current and previous years (denoted n and n − 1 respectively) on each of the 129 individual radial growth index series using linear regressions (lm R function) of the form:

$$GI = \mu + b\,C \tag{2}$$

where C is the climatic variable. These regressions, referred to as "univariate regressions", were carried out based on raw data and on smoothed data. Analysis based on raw data will reveal the radial growth response to absolute climate variations, whereas analysis based on smoothed data will reveal the radial growth response to relative climatic variation.

Smoothing was performed by using a cubic spline function (*smooth.spline* in R) to remove the medium frequency signals (i.e., trends over about a 10 year period).

In a second step we merged some monthly variables to construct synthetic climatic variables based on step one results and without any *a priori* knowledge of the influence of climate on tree growth. The synthetic variables were defined using the three following criteria: (i) a variable corresponding to the average of several consecutive monthly climatic variables that induced the same type of growth response (positive or negative) for a majority of trees (Fig. 1) (ii) a variable containing at least a monthly climatic variable for which, at least in one stand, 30% of the individual growth-climate relationships are significant at a 5% threshold and (iii) a variable containing at least a monthly climatic variable for which, at least in one stand, 50% of the individuals follow the same growth trend.

2.4.3. Sensitivity of the growth response to climate change

Some studies have found changes in the climate-growth relationship due to climate change that are related to a decrease in water availability and an increase in temperature (Lempereur et al., 2016; Sarris et al., 2007). Thus, we also tested whether the climate-growth relationships computed before and after 1985 were significantly different. To test the assumption that ongoing climate change may already have changed the growth response to climate, a mixed effect corresponding to a before/after global warming factor (over the period of interest) was added to the previous univariate regressions (Eq. (2)). To be consistent with the observations made on the reference climate series (see Appendix E) while preserving statistical power in our analyses, the dataset was split into two equal parts: one containing data prior to 1985 (before global warming level of the mixed effect factor) and the other containing data from 1985 to 2011 (after global warming level of the mixed effect factor). The fixed versus mixed regression models were compared using the AIC criterion.

2.4.4. Global growth response to climate

A global growth response to climate was assessed by using a multi-variate linear mixed model (*lmer* function from the R package *lme4*). The synthetic climatic variables that have a significant global effect on radial growth for all stands and/or a variable effect between stands were selected by using the *step* function of the *lmerTest* package (R), applied to the complete model (Eq. (3)):

$$GI_{iys} = \mu + \sum_c a_c \times SC_c + \sum_{c,s} b_{cs} \times SC_c + \varepsilon_{iys} \quad (3)$$

where GI_{iys} is growth index of tree i of stand s on year y, $a_c \times SC_c$ is the fixed effect of the synthetic climatic variable c and $b_{cs} \times SC_c$ is the random effect of the synthetic climatic variable c according to the stand s.

The inter-individual variability of the effect of the synthetic climatic variables on radial growth was tested in the same way (Eq. (4)).

$$GI_{iys} = \mu + \sum_c a_c \times SC_c + \sum_{c,s,i} (b_{cs} + d_{csi}) \times SC_c + \varepsilon_{iys} \quad (4)$$

where $(b_{cs} + d_{csi}) \times SC_c$ is the random effect of the selected synthetic climatic variable c according to the stand s and the individual i. A first-order autoregressive model (AR1) was used, giving the temporal structure of the residuals.

Hereafter, these regressions will be referred to as "multivariate regressions". For the significant inter-individual random effects, the variability of the individual relationship slopes was compared between stands (*bartlett.test* R function).

3. Results

3.1. Stand growth according to cambial age and competition

The RC fitted for Iss3, Iss4, Iss5, Vtx1 and Vtx3 were significantly different from the global RC fitted for their respective mountains. In Vtx, the highest growth was observed at mid elevation (Vtx3), and lowest growth was observed at the lowest elevation (Vtx1; Fig. 2). The ratio of mean annual basal area increments between these two extremes averaged 2.2 (Table 1). In Iss, the lowest growth was observed at low and mid elevations and growth increased with altitude (Fig. 2). Indeed, the mean annual basal area increment was higher in Iss5 than in Iss1 to Iss3 by a factor of 2.4 and was higher in Iss5 than in Iss4 by a factor of 1.7 (Table 1).
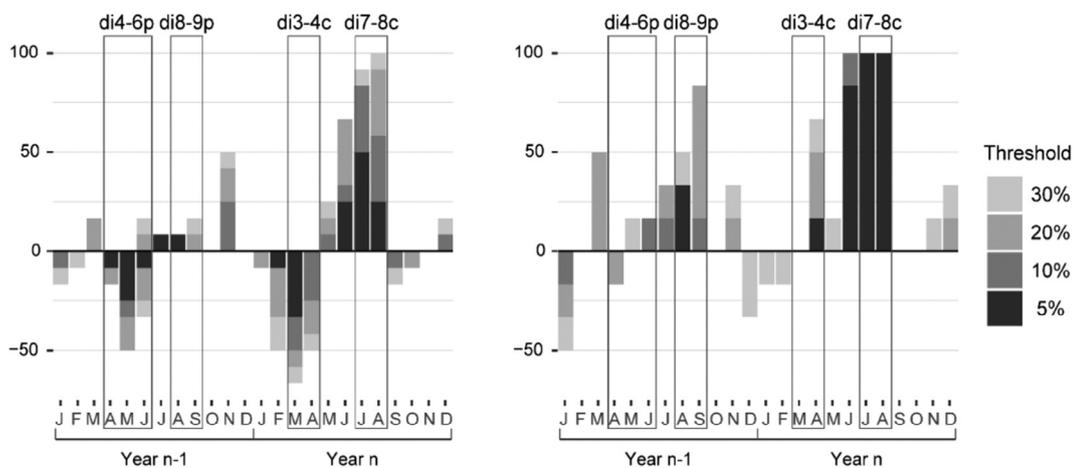

Fig. 1. Illustration of the identification of synthetic climatic variables for the drought index (DI) in Vtx4 (on the left) and Iss4 (on the right). Each vertical box corresponds to a synthetic variable. The code of each synthetic variable is noted above the box (see Table 2 for a code description). The y-axis corresponds to the percentage of individuals that responded positively or negatively to the monthly DI, at 5–30% significance thresholds (greyscale). These different thresholds allowed to detect the general trends.
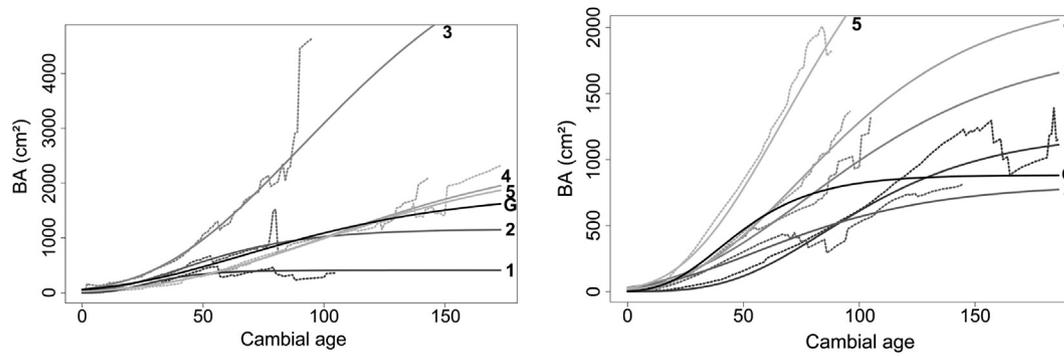
Fig. 2. Global and stand-specific Gompertz RC curves fitted for Vtx (left) and Iss (right). The solid lines are the RC curves. The dotted lines are the mean BA of the stand population. Each step in the dotted lines corresponds to the loss of an individual. Numbers 1–5 correspond to the stands for which the RC was fitted (1: low, 5: high) and G corresponds to the global RC curve. The mean BA of the overall population was not plotted.

Based on these results, the cambial age effect on growth was computed at the stand level.

Although different competition indexes were fitted for the two mountains, in both cases they explained a similar proportion of the GI variation (30%, see Appendix B).

3.2. Growth variation according to climatic conditions

3.2.1. Climatic variables correlated with tree radial growth (GI)

Based on the individual univariate regressions results, 15 synthetic climatic variables were selected (Table 2) for the multivariate regression. Most of these variables were related to the spring and summer periods, and half of them were from the n − 1 year. Individual growth relationships with all the temperatures (mean, maximum and minimum) were so similar that only the mean temperature was selected.

Among those 15 variables, 14 were retained in the multivariate regression models (Table 2; Fig. 3). As synthetic climatic variables were selected independently from one another, some significant correlations (Appendix F) were observed among groups of variables that correspond to different seasonal climate types (e.g.: frost days and low mean temperature (fd_1-4c, mt_2-4c); rainfall, relative humidity, low drought stress and moderate temperature (r_5-8c, rh_5-8c, di_7-8c and mt_6-8c). The multivariate model allows for the estimation of the effect on growth of each variable taking into account the effect of others. The results obtained from the raw data and from the smoothed data were so similar that only the results for smoothed data are presented hereafter.

During the winter-early spring period (from February to April) of the year n (year of the ring formation, *A. alba* radial growth was positively correlated with temperature (slope: s = 0.10) and negatively correlated with drought levels (s = 0.06) and with frost at high elevation (s = −0.04, Fig. 3).

In the summer of year n, less drought conditions estimated by the DI (that integrates rainfall and temperatures) had a very strong positive effect on radial growth, whatever the mountain or the altitudinal level (s = 0.31). On the same period, growth was related to rainfall, relative humidity and temperature, but reactions were contrasted among mountains or/and stands (Table 2; Fig. 3). Indeed, high relative humidity promoted growth in Vtx (s = 0.08 ± 0.04) while it decreased it in Iss (s = −0.09 ± 0.03). Heavy rainfalls favored growth in Iss (excepted in Iss3; s = 0.10 ± 0.12), as in the lowest stands in Vtx (Vtx1 and Vtx2; s = 0.10 ± 0.06). On the contrary, on the highest stands in Vtx (Vtx3 to Vtx5), rainfall was negatively related to growth (s = − 0.16 ± 0.12). High summer temperatures favored growth at the lower elevation of Vtx (Vtx1) while having a low but negative effect on growth at high elevation (Vtx5).

The climatic conditions of the previous year (n − 1) also had a significant impact on growth during year n (Table 2; Fig. 3). Thus,

Table 2
Synthetic climatic variables selected on the basis of the individual regressions of radial growth on monthly climatic variables.

Code[c]	Univariate regressions[a]		Multivariate regressions[b]		
	Positive response (%)	Negative response (%)	Global effect	Altitudinal Effect	Individual Effect
mt_2-4c	12.0	1.1	X		
mt_6-8c	0.7	9.5		X	
mt_5-6p	1.8	8.3	X	X	
mt_7-9p	1.0	8.8	X	X	
rh_3-4c	4.9	7.2			
rh_5-8c	15.2	0.8		X	
rh_1-3p	6.2	1.7		X	
rh_7-10p	9.7	0.9	X	X	
di_3-4c	4.9	6.0	X		
di_7-8c	21.8	0.0	X		
di_4-6p	2.1	5.1	X	X	
di_8-9p	10.3	0.3	X		
r_5-8c	14.7	0.7		X	X
r_6-8p	7.3	1.9		X	
fd_1-4c	1.3	9.7		X	

[a] Percentages of trees whose growth relationship was significantly correlated with the climatic variable at the 5% threshold.

[b] X: significant at the 5% threshold.

[c] mt = mean temperature, rh = relative humidity, di = drought index, r = rainfall and fd = number of freezing days. The numbers separated by dashes correspond to the month period; c = year of ring formation, p = year prior to ring formation (for example mt_2-4c correspond to the mean temperature from February to April of the year of ring formation).
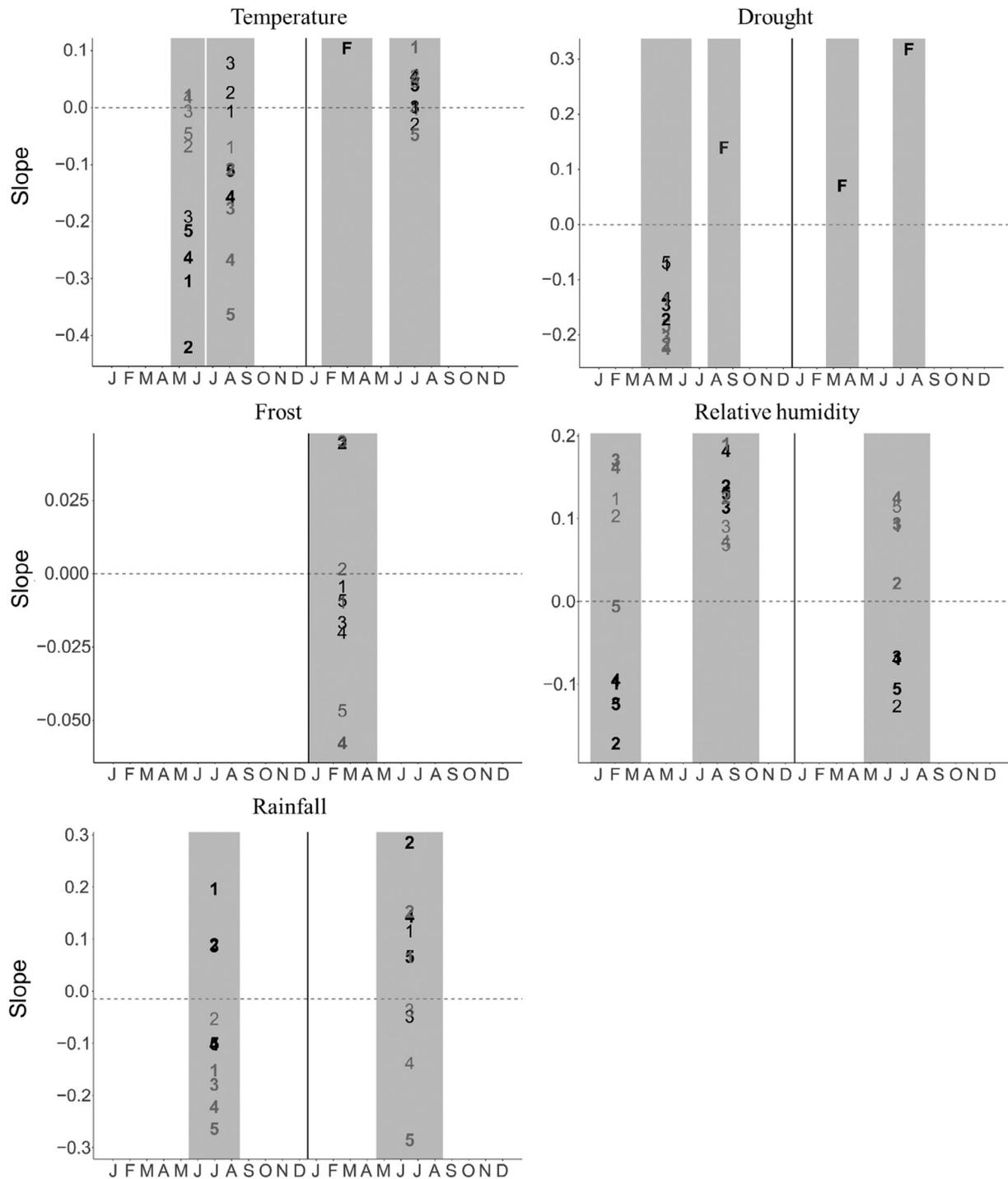
Fig. 3. Radial growth relationships of fir trees with 14 synthetic climatic variables. The regression coefficients that vary among stands are plotted for each stand (1–5) and mountain (Vtx in grey, Iss in black). Significant coefficients are in bold. Coefficients that are not significantly variable (i.e. fixed effects) are plotted as "F". The grey boxes delimit the months extend of each variable. Note that the negative drought index (DI) reflects dry conditions, while a positive index reflects rather wet conditions.

the relative humidity of the n − 1 winter (January to March) was negatively related to the growth of the trees from Iss and from the highest elevation of Vtx (s = −0.11 ± 0.05), whereas it was positively related to the growth of trees from the low and mid elevations of Vtx (s = 0.13 ± 0.03).

High temperatures during the previous spring reduced the growth in Iss (s = −0.29 ± 0.09) but slightly promoted the growth in Vtx1 (non-significant effect for Vtx2 to Vtx5). DI computed over the same period was negatively related to growth (s = −0.16 ± 0.05), i.e. the drier spring conditions were, the higher

the growth was the next year. It must be noted that DI over this period averages 0.9 in Iss and 1.6 in Vtx (less dry than in Iss), traducing the weak drought in spring on both sites except for very rare years where DI reached −2.4 in Iss and −1.1 in Vtx.

A moist n − 1 summer and early fall (i.e., high relative humidity) and a low water stress (high DI) favored tree radial growth (s = 0.12 ± 0.04 and 0.13 respectively; Fig. 3). At low elevations of Iss (Iss1 to Iss3), heavy rainfall was also favorable (s = 0.12 ± 0.06). On Vtx (all stands) and on the highest stands of Iss (Iss4 and Iss5), radial growth was favored by low rainfall

(s = −0.16 ± 0.07) and low temperature s = −0.19 ± 0.10). On Vtx, the positive relationship between growth and summer relative humidity decreased with increasing altitude and the negative relationship between growth and summer temperature increased with increasing altitude.

3.2.2. Inter-individual variability in the growth response to climate

The inter-individual variations in growth responses to climate variables were far fewer for smoothed data than for raw data (1 against 8; data not shown). Smoothing the data eliminated non-climatic factors that were not taken into account by the different data cleaning steps, such as residual effects of competition.

On smoothed data, the summer rainfall (June to August) of year n was the only variable having different effects on the individual tree growth. The inter-individual (i.e., intra-stand) variance of the growth response was equivalent for all of the stands (bartlett test p-value = 0.20) and was 20 time less than the corresponding inter-stand variance.

3.2.3. Evolution of the growth response to recent climate drift

The results from the individual univariate regressions on both raw and smoothed data did not provide evidence for an effect of the ongoing warming on the growth relationship.

Indeed, 99.3% and 99.9% of individual univariate regressions, respectively, on raw and smoothed data were significantly better (lower AIC) when considering a unique slope (i.e., regression coefficient) than when considering pre and post drift slopes.

4. Discussion

4.1. Effect of competition on fir growth

The large proportion of the silver fir radial growth variance attributed to competition is consistent with previous estimates. For example, Stadt et al. (2007) explained, according to the species, between 11% and 31% of the growth variance using a competition model containing only the neighbor dbh. Moreover, the best competition models developed by Canham et al. (2004) explained 33% and 59% of the growth variance of hemlock and red cedar, respectively.

4.2. Average climate-growth response

At the stand scale, climate significantly affected the tree radial growth, both during the year of ring formation (n) and previous year (n − 1).

Mild winter/early spring during year n favored tree growth. This result was obtained from observations collected in Ventoux and Issole from the whole fir altitudinal range (1000–1600 m a.s.l.), and it seems to be generalizable to a larger area. It is fully consistent with the results from previous studies based on pointer years and response function analyses conducted not only on the same species but also on Norway spruce and Scots pine (Lebourgeois, 2007; Lebourgeois et al., 2010; Rolland, 1993). In evergreen species such as fir, photosynthesis can occur in winter. Thus, high temperatures combined with good water availability play an important role in carbohydrate storage, and carbohydrates will be available for use during the next growing season (Lebourgeois, 2007). Warm late winter temperatures may also limit the risk of xylem embolism (Maherali et al., 2004), and they accelerate snow melt (particularly at high elevations) and therefore soil warming, which promotes mycorrhizal root growth (Lebourgeois et al., 2010; Rolland, 1993). Moreover, a warm early-spring activate cambium and buds earlier, resulting in the elongation of the following growing season for wood.

The unfavorable impact of frost in late winter/early spring may be attributed to the oceanic feature of fir. Frost causes damages to the developing buds and needles, which thus cannot be mobilized during the following growing season (Howe et al., 2003).

Summer rainfall, relative humidity and temperature of year n affected growth differently according to the mountain and/or stand. Summer high temperatures limited growth in the lowest stands of Issole and highest stands of Ventoux, but favored growth elsewhere. Different summer temperature effects on growth according to elevations have previously been found (Dittmar et al., 2003). This is not surprising because different elevations correspond to different positions within the species niche. Consequently, increasing temperature is expected to be favorable at higher elevation and unfavorable at the lowest elevation. The only unexpected result was the negative effect of temperature increase at the highest stand in Ventoux. One explanation for this could be the effect of temperature on the vegetation length. Higher temperature can cause a delayed end of vegetation season and an increased risk of frost damage during the fall.

In the same period (summer of year n), drought negatively impacted fir growth, regardless of stand, which is consistent with previous works showing that strong water deficits in August significantly reduce radial growth (Battipaglia et al., 2009; Cailleret and Davi, 2011; Lebourgeois, 2007; Rolland et al., 1999). This could be due to the "avoidance" strategy exhibited by firs, which is characterized by a rapid response to drought and particularly by stomatal closure that occurs quickly after the decrease in water availability (Guicherd, 1994).

It may be surprising that radial growth was sensitive to temperature of the late summer, when the growing season is supposed to be completed. However, previous studies have shown that, depending on the status and size of the trees, the length of the growing season can vary from three months for smaller trees to five months for the largest ones (Cuny et al., 2012; Rathgeber et al., 2011). For dominant and intermediate trees, the growing season usually begins earlier than for dominated trees, and it can continue until the end of September or early of October. In the present study, 86% of trees were dominant or intermediate, which could explain the significant responses to the climatic variables of late summer.

In this study, the climatic conditions of the previous year also had a strong impact on the growth of the current year. If the delayed effects of climate on growth are well known (Battipaglia et al., 2009; Desplanque et al., 1998; Lebourgeois, 2007; Lebourgeois et al., 2010; Rolland, 1993; Rolland et al., 1999), especially for firs, the period concerned is generally much smaller than the one identified in our study.

Firstly, as in previous studies, moist and cool conditions during the summer and early fall of year n − 1 promoted growth in year n, probably because these conditions increase wood growth and carbon reserves in year n-1.

One interesting and original result was the positive effect of a previous spring drought on silver fir growth. One hypothesis could be proposed to explain this result: during drought, growth and photosynthesis are decoupled, and growth stops before photosynthesis (Goulden et al., 1996; McDowell, 2011; Palacio et al., 2014), allowing for the synthesis and storage of carbohydrates. These carbohydrates could be used after mild drought to mitigate stresses or balance respiratory costs (Chapin et al., 1990), leading to an increase in post-drought growth. This assumption is also consistent with Peltier et al. (2016) results. To our knowledge none of the previous studies dedicated to silver fir (e.g., Battipaglia et al., 2009; Desplanque et al., 1998; Lebourgeois, 2007; Lebourgeois et al., 2010; Rolland, 1993; Rolland et al., 1999) highlighted this positive legacy effect of the previous spring drought on radial growth. The method used in this study, which allowed us to finely

eliminate the effects of age, population and competition on growth signals, probably helped to highlight climate signals that remain hidden when conventional dendroclimatic methods of detrending are used.

4.3. Variability of growth between populations, between individuals and over time

Silver fir mean cumulative growth varies greatly between stands. These differences can be due to either variations in fertility between stands, which are attributable to all biotic and abiotic environmental factors (soil, climate, stand characteristics), or to an interaction between age and time effects. Indeed, the younger trees have grown under more favorable conditions (higher temperature and atmospheric CO_2 concentration) than older ones, especially at higher elevations, where frost is a more limiting factor. This last effect acts differently in Issole and Ventoux because older trees are located at the lowest elevation in Issole and at the highest elevation in Ventoux. Despite this effect, in both sites the environmental conditions of low elevations are less favorable to growth. This result is consistent with previous studies (Cailleret and Davi, 2011) and demonstrates the large role of drought in determining fertility.

The method used in the present study has revealed, among other things, variable individual growth behavior within stands. The individual variability of the growth response to monthly climatic variables observed in univariate growth-climate regressions can be due to microsite variations (soil moisture, slope, insolation, etc.), individual genetic differences, or stochastic events that occur around the target tree. In the multivariate growth-climate regression, we did not observed significant variability among individuals except for the response to summer precipitation in year n. This variability was probably due to the high heterogeneity of water resources in the tested environments. Indeed, soils and subsoils are very heterogeneous at the local scale and individual responses can vary depending on the water reserve available for each tree (Nourtier et al., 2014). As drought conditions vary between trees, it is difficult to know whether these variations in growth response to precipitation between individuals are due only to the variations in soil conditions (i.e., a passive effect) or are, for example, due to a local acclimation following a change in carbon allocation to roots (i.e., an active effect).

The mountain-specific and stand-specific relationships can indicate the acclimation of trees to the climatic conditions, through genetic evolution or a plastic response (De Luis et al., 2013).

The first case could be due to genetic differentiation caused by local adaptation, whereas the latter could be a consequence of a plastic growth relationship along the altitudinal gradients. Roschanski et al. (2016) studied the molecular genetic variability of firs sampled from the same mountains, and observed low differentiation between the populations originating from the low and high elevations. This result supports the second hypothesis.

We also found that the silver fir relationship to inter-annual climatic variations did not significantly change over the decades. This last point is inconsistent with several dendrochronology studies (Briffa et al., 1998; Buntgen et al., 2008; Carrer et al., 2010; D'Arrigo et al., 2008; Esper et al., 2010) that highlighted changes in the sensitivity and/or changes in growth responses of trees to climate, which were associated with the significant warming of the climate that occurred during the last decades. Moreover, Gandolfo and Tessier (1994) show that the sensitivity of fir and spruce growth to inter-annual variations of climate has decreased since 1970.

We can hypothesize that, over the 1960–2011 period, the range of climate drift has not been strong enough to change the climate to growth relationships. However, it is expected that, over the next few decades, temperatures will continue to increase rapidly, and the frequency and duration of droughts will increase. The seasonality of precipitation will also change (IPCC, 2013). Based on our results, we can therefore assume that silver fir will suffer from an increase in droughts in the spring and summer (of the current and previous year) which is the first unfavorable factor reducing growth. Similarly, the impact of the temperature increase could be strongly negative, particularly in warm sites, such as Issole, where it already limits growth.

5. Conclusion

Our dendro-ecological approach gives evidence for strong relationships of silver fir radial growth to climatic variables of the current and previous year. This result is fully consistent with the known physiology of the species. It depicts the seasonal evolution of the relationships between climatic variables and growth and underlines its plasticity over the landscape of the local environmental conditions of the silver fir range.

Responses to drought and frost are consistent across mountains and altitudinal levels and thus reflect the temperament of the species: fir growth is sensitive to late frosts and drought occurring in the current year and in the previous summer, but is enhanced by drought during the previous spring. In contrast, responses to precipitation, temperature, and, relative humidity vary between sites and/or altitudinal levels, reflecting specific behaviors. Our experiment does not allow us to determine the origin, either genetic or plastic, of the growth response variability, although the hypothesis of a plastic response is supported by the low genetic differentiation between mountains and between stands, which was reported in previous works. To disentangle the genetic and plastic components of silver fir growth plasticity, we recently established a reciprocal transplant experiment on the same mountains (Latreille and Pichot, submitted for publication), but in contrary to the present study, it will primarily focus on the seedlings stage and over a period of few years.

Our results suggest that silver fir will be mainly threatened by an increase in summer drought events. The speed of climate change and magnitude of the expected changes raise questions about the fate of silver fir populations, especially in the Mediterranean region, which is the southern margin of the species range and is where many populations already experience warm and dry conditions. A significant fir dieback was observed during the last 12 years and was attributed to the cumulative effect of dry years following the warm year in 2003 (Cailleret et al., 2014; Davi and Cailleret, 2017). Silver fir will probably not be able to survive in most of the driest or intermediate humidity stands corresponding to the lower halves of the elevation range of the two altitudinal gradients that we studied. In these stands, natural or assisted species substitution could be recommended. At higher elevation or more humid sites, considering that climate will continue to change over long time scales even if the production of greenhouse gases is significantly reduced in the near future, foresters will also have to favor practices that reduce water stress.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.04.012.

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