

# Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient

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**Abstract** In high-elevation forests, growth is limited by low temperatures, while in Mediterranean climates drought and high temperatures are the main limiting factors. Consequently, the climate-growth relationships on Mont Ventoux, a mountain in the Mediterranean area, are influenced by both factors. Two co-occurring species were studied: silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.), whose geographical distribution depends on their low tolerance to summer drought at low altitude/latitude, and low temperatures (late frost and short length of the growing season) at high altitude/latitude. Firs and beeches distributed along an elevational gradient were investigated using dendroecological methods. Silver fir growth was found to be more sensitive to summer water stress than beech. On the other hand, beech growth was more impacted by extreme events such as the 2003 heat wave, and negatively related to earlier budburst, which suggests a higher sensitivity to late frost. These results are confirmed by the different altitudinal effects observed in both species. Beech growth decreases with altitude whereas an optimum of growth potential was observed at intermediate elevations for silver fir. Recent global warming has caused a significant upward shift of these optima. As found for the period 2000–2006, rising temperatures and

decreasing rainfall may restrain growth of silver fir. If these trends continue in the future beech might be favored at low altitudes. The species will have a reduced capacity to migrate to higher altitudes due to its sensitivity to late frosts, although an upward shift of silver fir is likely.

**Keywords** Growth · Altitude · *Abies alba* · *Fagus sylvatica* · Climate change · Drought

## Introduction

Tree growth will be modified in response to climate change. It is now well established that warmer temperatures (Christensen et al. 2007) would increase tree growth, due to a lengthening of the growing season (e.g. Menzel and Fabian 1999; Bronson et al. 2009; Delpierre et al. 2009) and higher metabolic rates during winter and spring (Paulsen et al. 2000), especially at high altitudes/latitudes (Theurillat and Guisan 2002). A positive impact of elevated CO<sub>2</sub> on tree growth is also expected due to higher photosynthesis rates (Hyvönen et al. 2007), even if some experimental studies did not confirm this hypothesis (Handa et al. 2006). On the other hand, these positive effects may be moderated by the likely increase in autotrophic respiration due to higher temperatures, and by the predicted decline in summer precipitation in the south of Europe (Christensen et al. 2007). First, tree water deficit negatively affects tree-ring formation by inhibiting cell division and enlargement (Zweifel et al. 2006). Second, it reduces carbon assimilation via a stomatal control of photosynthesis and transpiration (Breda et al. 2006). In addition, an earlier budburst may increase the probability of late frost impact in temperate, boreal or mountainous zones (Hanninen 2006). All these phenomena impact

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physiological processes and thus stem radial growth and tree vigor (Dobbertin 2005). But as some contradictory effects are expected, co-occurring species with different functional strategies can exhibit different responses to global change (Büntgen et al. 2007; Green 2007).

Silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.) often co-occur in the mountain vegetation belt. In this paper we studied both species at their Southern Alps margin: on Mont Ventoux, a French mountain located in the Mediterranean area. In this ecosystem, silver fir and beech are recolonizing planted pine stands (Chauchard et al. 2007) and are undergoing rapid environmental changes because both warming and drought trends were considerable. During the twentieth century, warmer temperatures and nitrogen deposition has led to an increase in radial growth of silver fir (Bert 1992; Pinto et al. 2007) and beech (Badeau 1995). However, in the Mediterranean region, with the accumulation of summer droughts, new forest decline have also been observed (Jump et al. 2006; Sarris et al. 2007; Piovesan et al. 2008). On Mont Ventoux observed trends could be the consequence of the contradictory effects of both reduced frost and increased drought. Consequently, a better understanding of the species-specific effects of climate is needed to determine costs and benefits for beech and silver fir in this context and to predict future competitive ability.

The assessment of climate-growth relationships provides understanding of the effect of averaged climate and extreme events. To our knowledge, climatic responses of silver fir and beech have been analyzed many times, but separately (Bert 1992; Badeau 1995; Desplanque et al. 1998; Rolland et al. 2000; Dittmar et al. 2003; Lebourgeois et al. 2005; Manetti and Cutini 2006; Di Filippo et al. 2007; Lebourgeois 2007). The impact of extreme events has also been studied alone, for example by focusing on the consequences of the summer 2003, which impacted forest productivity throughout Europe (Ciais et al. 2005; Granier et al. 2007; Pichler and Oberhuber 2007). Assessing the variability of tree-ring components of silver fir and beech along an elevational gradient can consequently be useful to reveal different growth responses to climate, and their sensitivity to frost and drought (Guehl 1985; Badeau 1995; Dittmar et al. 2006; Geßler et al. 2007). With increasing altitude, reduced temperatures, shorter growing season, increased exposure to wind and reduced nutrient supply should negatively impact growth rates (Coomes and Allen 2007; Körner 2007). However, in the Mediterranean region where summer drought is the main limiting factor, low elevation sites may also be affected by declining precipitation.

The aims of this study were: (1) to describe if these co-occurring species are impacted in a same way by monthly-averaged climate and climatic events, by respectively

analyzing climate-growth relationships and the effects of the 2003 heat wave for both species; (2) to examine the different altitudinal effects on tree growth and if the conclusion agrees with the first analysis; and (3) to investigate if recent climate change has differently impacted growth of both species according to altitude.

## Materials and methods

### Study site

The study was conducted on Mont Ventoux (44°11'N; 5°17'E), a calcareous mountain located in the southwestern Alps, 1,909 m above sea level (a.s.l.). Originally forested, Mont Ventoux suffered massive deforestation from the 12th century onwards as the wood from the trees was used to serve the demands for shipbuilding, firewood and charcoal and because of grazing. In 1850, it was almost entirely deforested and mixed *Abies alba*—*Fagus sylvatica* forests were reduced to small forest islands. A decrease in grazing combined with reforestation efforts undertaken in the 20th century (using pines) made it possible for post-pioneers (e.g. *Sorbus aria*, *Acer opalus*) and shade-tolerant species (such as silver fir and beech) to gradually recolonize the planted stands. Substrates range between limestone lithosol to one meter deep colluvium. However, soil water content is probably low considering the percentage of coarse material (between 50 and 80%), high slope (25° on average) and water infiltration into the calcareous bedrock. On the north-facing slope of Mont Ventoux (weather station of Mont Serein, 1,445 m a.s.l., 1993–2006), mean annual temperature has been 6.8°C. The distribution of rainfall (1,300 mm on average) is characteristic of a Mediterranean climate: the driest season is summer and rainfall occurs mostly in autumn. The elevational effect on temperature on the studied gradient was assessed in 2007 and 2008 by five HOBO Pro V2 microloggers located at 995, 1,117, 1,225, 1,340 and 1,485 m. The number of late frost days was calculated from April to June. As the altitudinal effect on rainfall varies between years, we used longer data (2000–2005) from seven meteorological stations distributed throughout Mont Ventoux (100, 300, 430, 792, 1,100, 1,445, and 1,455 m).

### Study species

Silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.) are two shade-tolerant species which need high atmospheric humidity due to their weak tolerance to summer drought (Geßler et al. 2007; Lebourgeois 2007). In France, both species are distributed in mountainous regions (Pyrenees, Vosges, Jura, Massif-Central, Alps) while beech

is found in plain in northern regions as well. Their ranges are currently expanding in mountainous regions due to pastoral abandonment and forest maturation (Chauchard et al. 2007). On Mont Ventoux, beech is present in the form of coppice or high forest, between 950 and 1,500 m a.s.l. on the north- and south-facing slopes (Ladier et al. 2007). On the northern slope fir is generally associated with beech. This affinity reveals that both species are generally influenced in the same way by environmental conditions. However, their wood production mechanisms belong to two different functional groups, and silver fir needles persist 7–9 years on the twig in contrast to deciduous beech. Concerning phenology, beech budburst on the study site generally begins 2 weeks earlier than silver fir.

### Tree-ring processing

73 firs and 77 beeches were sampled along a continuous elevational transect from 970 to 1,530 m (a.s.l.) on the north-facing slope of Mont Ventoux. The continuous transect followed the same slope orientation (NNW) and was chosen to minimize non-climatic variations, such as soil heterogeneity and management. For the same goal, and to have a reasonable sample size for the dendroclimatic analysis, dominant and codominant trees were sampled, explaining the variability in ages (Table 1). Suppressed trees were excluded from the study because of their high sensitivity to competition. For the analysis the individuals were ranged in five classes of increasing altitudes (F1–F5 for silver fir and B1–B5 for beech). Cores were extracted in autumn 2006 and 2007 with an increment borer, 1.3 m

above the ground and perpendicular to the slope to avoid compression wood (for silver fir) and tension wood (for beech). After preparation with a razor blade, cores were scanned at 1,200 dpi. Ring limits were pointed using the semi-automatrical software CooRecorder v5.3 and coordinates were transcribed into the nearest 0.01 mm ring-width using CDendro v5.3 (CDendro 5.3 & CooRecorder 5.3; Cybis Elektronik & Data AB, Sweden). Individual series were checked for missing rings and dating errors and mean chronologies were calculated using CDendro v5.3. Classical dendrochronological parameters were respectively computed for all the individual series and for the mean chronologies (Fritts 1976). Mean sensitivity (MS) was calculated to characterize relative intensity of year to year changes in growth. Calculation of the first autocorrelation coefficient (A1) was made for each tree to assess the influence of the previous year's growth upon the current year.

To study growth trends, basal area increments (BAI, mm<sup>2</sup>) were calculated from ring widths (RW, mm) assuming a circular outline of stem cross-sections. When a core did not reach the pith, the total missing width was estimated using the curvature of the innermost rings of the sample. The number of years estimated to the pith is based on the growth rate after the missing segment (Esper et al. 2003). Age effect was removed using the mean regional age curve (RC) of BAI of both species (Fig S1). This theoretical growth curve is exclusively dependent on the cambial age of the tree and is assumed to be correct for a given species in a given area (Bert 1992; Esper et al. 2003). In addition to the study sampling, 227 firs cored in 2008

**Table 1** Characteristics of selected elevational levels (F1 and B1: low-altitude to F5 and B5: high altitude) and statistics for tree-ring chronologies (mean followed by standard deviation in parentheses)

	Altitude (m)	Mean altitude (m)	N	Age (years)	Height (m)	MS	A1	RW (mm)	BAI (mm <sup>2</sup> )	GI
Silver fir <i>Abies alba</i>										
Total	970–1,530	1,214.5 (152.4)	73	72.6 (35.3)	13.1 (3.5)	0.20	0.63	1.84 (0.66)	767.4 (493.0)	1.06 (0.65)
F1	970–1,040	1,005.8 (26.9)	13	56.1 (22.5)	10.9 (2.9)	0.21	0.54	1.71 (0.48)	511.4 (259.2)	0.74 (0.40)
F2	1,040–1,140	1,096.7 (28.2)	14	57.8 (13.0)	12.0 (2.5)	0.20	0.61	1.91 (0.55)	744.8 (378.2)	1.22 (0.66)
F3	1,140–1,240	1,193.2 (28.2)	13	54.5 (22.2)	14.9 (3.2)	0.19	0.56	2.59 (0.79)	1185.9 (724.1)	1.60 (0.83)
F4	1,240–1,350	1,285.9 (34.9)	16	80.5 (36.5)	14.1 (3.3)	0.20	0.63	1.76 (0.55)	787.9 (459.1)	0.85 (0.36)
F5	1,350–1,530	1,428.4 (50.2)	17	105 (41.2)	13.2 (4.3)	0.20	0.77	1.36 (0.26)	633.3 (340.7)	0.72 (0.30)
Common beech <i>Fagus sylvatica</i>										
Total	1,000–1,520	1,260.7 (149.5)	77	88.2 (19.1)	12.2 (2.2)	0.30	0.67	1.01 (0.32)	295.7 (154.1)	0.90 (0.42)
B1	1,000–1,100	1,042.4 (30.0)	15	97.3 (8.1)	12.1 (1.2)	0.31	0.72	0.99 (0.24)	333.5 (157.8)	1.01 (0.43)
B2	1,100–1,230	1,177.1 (37.0)	18	68.2 (28.8)	10.7 (2.0)	0.30	0.58	1.32 (0.36)	360.8 (171.3)	1.15 (0.44)
B3	1,230–1,330	1,278.2 (26.5)	16	93.9 (8.1)	12.5 (2.9)	0.30	0.68	0.89 (0.29)	268.2 (157.3)	0.79 (0.42)
B4	1,330–1,420	1,375.1 (31.4)	13	94.1 (6.8)	13.3 (1.5)	0.30	0.68	0.89 (0.24)	265.9 (135.1)	0.73 (0.37)
B5	1,420–1,520	1,461.3 (38.6)	15	91.7 (10.6)	12.9 (1.9)	0.32	0.69	0.89 (0.24)	253.7 (112.4)	0.74 (0.31)

N number of trees selected, MS mean sensitivity, RW mean ring-width, BAI mean basal area increment, GI mean radial growth index, A1 first-order autocorrelation coefficient

(Cailleret et al. 2010) and 84 beeches cored in 2007 close to the study site were used to process these curves. A mean radial growth index (GI) was calculated for each tree.

$$GI = \sum_{t=1}^{t=n} \frac{BAI(x, t)}{BAI(RC, t)}$$

where  $BAI_{(x,t)}$  and  $BAI_{(RC,t)}$  are the BAI of the tree  $x$  at the cambial age  $t$ , and the corresponding theoretical value of BAI given by the regional curve. A GI superior to 1 indicates that the tree had a better growth than the average. The date effect, i.e. the effect of recent environmental changes, was also removed because RC was performed using both old and young trees, which have grown under different conditions, and not using old trees alone. This procedure makes it possible to test the effect of altitude but not to compare growth of both species.

Recent change of growth optima along the altitudinal gradient with date was assessed by comparing GI for the whole period (all years) and GI for the 2000–2006 period. Linear regressions between BAI and years were fitted for each individual and for the master chronology of both species to identify significant temporal growth trends between 2000 and 2006. Even though the regression included only seven points, a significant negative trend ( $p < 0.1$ ) is a sound indication of decline in tree growth (Pedersen 1998; Dobbertin 2005; Piovesan et al. 2008).

### Climate-growth relationships

Analyses of the climate-growth responses were conducted using detrended series. Ring widths were first detrended with a negative exponential or linear function and then with a cubic spline with 50% frequency response for 75 years using the ARSTAN software (Cook 1985). Autoregressive modelling of residuals (ARMA) and bi-weight robust estimation of the mean were used to calculate chronology indices for each ring component. Pearson correlation coefficients between annual growth indices and monthly precipitation and temperatures were then calculated separately using the statistical software R (R for Windows version 2.8.0; R Development Core Team 2008). Climate-growth relationships were calculated using meteorological data from Carpentras (99 m a.s.l.), the closest station with long-term meteorological time series (1964–2006). Carpentras and Mont Ventoux differ in altitude but they belong to the same climate sub-unit according to monthly precipitation patterns as defined by Guiot (1986). Each growth index was related to monthly mean, maximum and minimum temperatures and monthly rainfall from the previous July to August of the growth year (i.e.  $14 \times 4$  variables). Consequently, current climate and climate feedback due to the previous year were taken into account.

Effect of budburst date on growth was studied by matching spring phenological data with the increment index for the year 2006. First, as spring phenology varies with altitude (Dittmar and Elling 2006), a potential budburst date for each elevational level was estimated as the average of observed dates for trees located at this level. Secondly, a “phenological discrepancy” ( $\Delta B_d$ ) was calculated for each tree based on the difference between potential and observed date to determine which trees had an early budburst ( $\Delta B_d < 0$ ) and which had a delayed one ( $\Delta B_d > 0$ ). Finally, the difference between individual growth index and the average of indices of trees situated at the same level was calculated for each tree to extract elevational and current climate effects on growth. A growth index ratio superior to 0 indicated that this tree proportionally had a better increment in 2006 than its neighbours at the same elevational level. We then analysed if differences in growth between individuals are linked to differences in budburst dates and altitude using generalized linear models.

## Results

### Characteristics of the tree-ring chronologies

Numerical features of tree-ring chronologies are summarized in Table 1. Elevational levels were slightly different between silver fir and beech. For example, the range of F1 (silver fir of the lowest altitude class) was from 970 to 1,040 m a.s.l. whereas B1 (beech of the lowest altitude class) was from 1,000 to 1,100 m a.s.l.. These differences do not reflect a differential distribution of each species on Mont Ventoux, but rather differences along the transect where trees were sampled. Ages were also heterogeneous, although beeches sampled were on average older than firs (88.2–72.6;  $p = 0.001$ ; unpaired  $t$ -test). Mean sensitivity (MS) was lower for silver fir ( $0.20 \pm 0.04$ ) than for beech ( $0.30 \pm 0.05$ ) and no statistical differences between elevational levels were found ( $p > 0.1$ ; unpaired  $t$  test). First-order autocorrelation coefficients were high, not statistically different between silver fir and beech (0.63 and 0.67 respectively;  $p = 0.19$ ;  $df = 115$ ), and were also positively correlated with age ( $r^2 = 0.47$  and  $r^2 = 0.22$ ;  $p < 0.001$ ). The well-synchronization between chronologies of both species (RW;  $r^2 = 0.41$ ), and the high mean series correlation ( $r^2 = 0.58$  for silver fir;  $r^2 = 0.52$  for common beech) indicated a common growth forcing.

### Contrasting radial growth-climate relationships

Growth responses to climate showed species-specific differences (Table 2). While silver fir was only negatively

**Table 2** Summary of the significant correlation between monthly meteorological data and annual growth index of the five elevational level chronologies

		<i>Abies alba</i>												<i>Fagus sylvatica</i>															
		Year <i>n</i> -1						Year <i>n</i>						Year <i>n</i> -1						Year <i>n</i>									
		J	A	S	O	N	D	J	F	M	A	M	J	J	A	J	A	S	O	N	D	J	F	M	A	M	J	J	A
<i>P</i>	N5					+		-						+									+						
	N4					+							+	+									+						
	N3												+	+										+					
	N2						+						+	+	+	+					+							+	
	N1												+	+	+	+													
<i>T<sub>mean</sub></i>	N5			-				+			+				-	-				-							+		
	N4			-				+			+				-	-				-									
	N3			-				+							-	-				-									
	N2														-	-				-									
	N1			-											-	-				+									
<i>T<sub>max</sub></i>	N5			-				+			+				-	-	+			-									
	N4			-				+			+				-	-				-									
	N3			-											-	-				-									
	N2			-											-	-				-							-		
	N1			-											-	-				-									
<i>T<sub>min</sub></i>	N5		-	-				-							-	-				-							+		
	N4		-	-				+							-	-				-							+		
	N3		-	-											-	-				-									
	N2		-	-											-	-				-									
	N1		-	-											-	-				-							+		

+, expresses a positive relation; -, indicates an inverse relation. Grey and white boxes indicate that the corresponding correlation coefficient attains 95 and 90% of probability respectively. N1 corresponds to the lowest elevational level, and N5 to the highest altitudinal level

affected by high temperatures during September of the previous year, negative correlations between beech growth and temperatures were significant for July and August. Moreover, a weak positive effect of rainfall was only found for beech at low altitudes, indicating a negative impact of previous summer drought. Winter conditions seemed to have no clear explanatory impact, except for beech with a negative effect of November temperatures at high altitude (B4 and B5), and a positive one at low altitude (B1). A positive effect of temperature was also found for silver fir in February of the current year. The effect of maximum temperatures in April on radial growth differed between the two species. Particularly at high elevation and for codominant trees (data not shown), positive responses were observed for silver fir in contrast to beech, which was negatively influenced by high temperatures in April. This effect can be linked to budburst, which largely depends on spring meteorological conditions. In 2006, differences in radial growth between trees were related to differences in budburst date. Beech trees with delayed leaf-out had better growth than those whose budburst was earlier whatever altitude ( $p < 0.05$ ; Table 3). For silver fir, radial increment was slightly negatively related with a positive budburst discrepancy. This trend seemed to be stronger at low altitude (Table 3).

During the beginning of summer (May–June) beech radial growth was observed to be independent of rainfall except in B2; whereas a positive impact of May temperatures appeared at high altitude. For silver fir, growth was more dependent on summer drought, indicated by the positive correlations between growth indices and rainfall in June, July, and even in May for trees at low elevations. Silver fir growth was also negatively correlated with temperature, especially at low altitudinal sites.

Altitudinal effect on growth

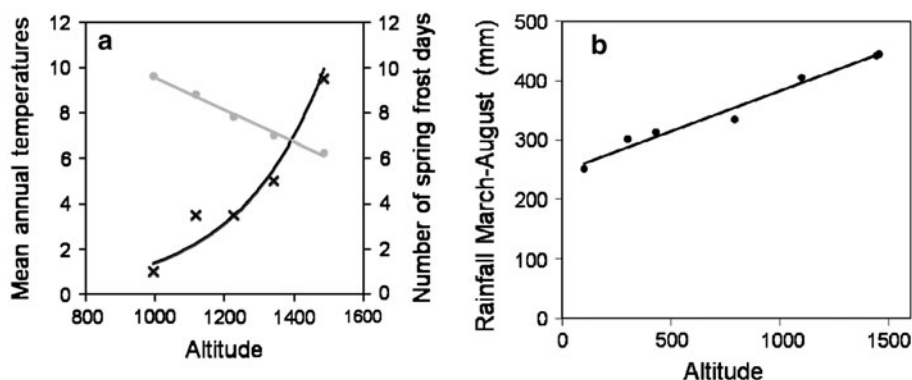
In the years 2007 and 2008 mean temperatures decreased on the north-facing slope by 0.71°C for every 100 m rise in altitude, and the mean number of spring frost days increased exponentially with up to 9.5 frost days per year at 1,500 m (a.s.l.) (Fig. 1a). For the period 2000–2005 spring and summer rainfall (March–August) increased in average 14 mm per 100 m (Fig. 1b). GI was used to analyze the altitudinal effect. Elevational effects on radial growth were different between species. For silver fir the maximum value was observed at an intermediate altitudinal level (F3) (mean GI = 1.60; Fig. 2a). Minima were observed for the low-elevational (F1) (0.74) and for the high-elevational level group (F5) (0.72). Growth indices of beech trees



**Table 3** Coefficients of the best generalized linear models chosen by AIC in a stepwise algorithm

Species	Variables	Estimate	Error	<i>t</i> value	Pr(>  <i>t</i>  )
<i>Abies alba</i> AIC = 20.31	Intercept	-6.37e-2	0.268	-0.251	0.802
	ΔBd	-0.131	7.12e-2	-1.842	0.071
	Altitude	4.97e-5	2.17e-4	0.228	0.820
	ΔBd × Altitude	1.13e-4	6.19e-5	1.823	0.074
<i>Fagus sylvatica</i> AIC = -9.06	Intercept	-7.55e-17	2.77e-2	-2.73e-15	1.000
	ΔBd	2.32e-2	1.04e-2	2.224	0.030

Models were fitted on individual growth index difference for *Abies alba* and *Fagus sylvatica*



**Fig. 1** **a** Altitudinal effect on mean annual temperature (grey circles) and on the number of spring frost days (black crosses) in 2007 and 2008 along the gradient studied on the north-facing slope of Mont Ventoux. The number of spring frost days was calculated as the average of the number of frost days between April and June for the

years 2007 and 2008. The slope of the linear regression between mean temperature and altitude is  $-0.71^{\circ}\text{C}/100\text{ m}$ . **b** Elevational effect on spring and summer (March–August) rainfall on the Mont Ventoux for the period 2000–2005. The slope of the linear regression between rainfall and altitude is  $+14\text{ mm}/100\text{ m}$

located at B2 were significantly different from those growing at higher altitude (B3, B4 and B5), but not to those located at B1 (Fig. 2b) indicating a global negative relationship between altitude and tree-ring growth.

#### Climate change and growth trends

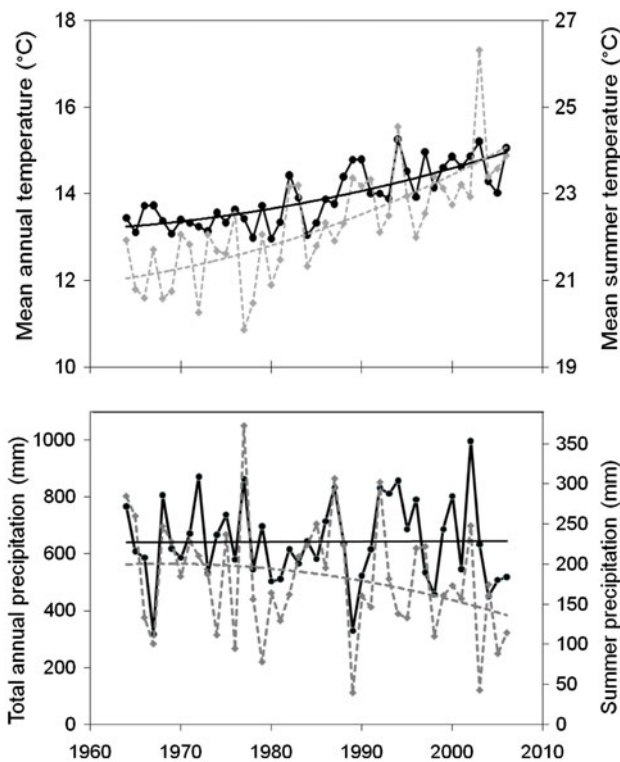
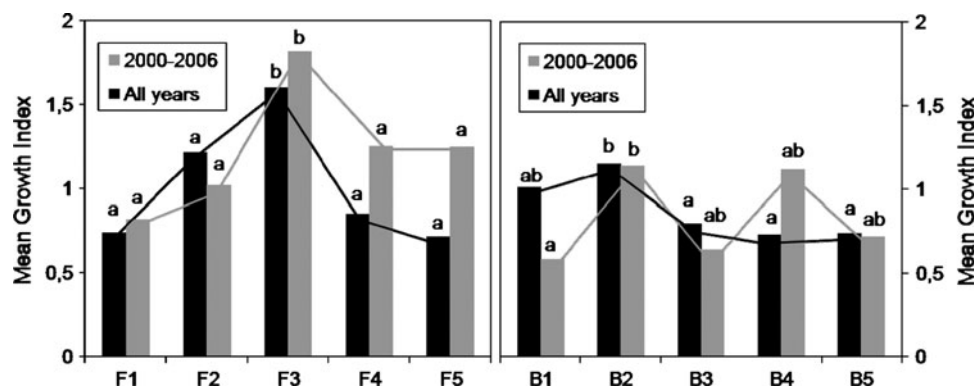
Since 1964 there was a clear warming trend in mean annual temperatures ( $r^2 = 0.60$ ,  $p < 0.001$ ), which corresponds to an increase of  $0.4^{\circ}\text{C}$  per decade and was more pronounced during summer ( $0.6\text{--}0.7^{\circ}\text{C}$  by decade; Fig. 3). Since the 1980s this warming has been associated with a decrease in summer rainfall (Fig. 4).

The effects of altitude on growth (GI) in the 2000–2006 period differed from the period studied as a whole (Fig. 2a, b). When comparing present and past growth (grey and black lines), an upward shift of growth potentials appears. For beech, lower GI values were found for trees at level B1, while differences between B2 and B3, B4 and B5 were not significant anymore (Fig. 2b). The upward shift was more obvious for silver fir (Fig. 2a). Growth optimum was still located at F3. Even if not significant, trees located at

higher altitudes (F4 and F5) seemed to show higher GI values compared with those at lower altitudes (F1 and F2).

As in most of Europe, weather conditions in the 2003 summer on Mont Ventoux were exceptional. At the weather station of Mont Serein (1,445 m a.s.l.) temperatures during June till August were  $3.3^{\circ}\text{C}$  above average ( $19.3^{\circ}\text{C}$  compared to  $16^{\circ}\text{C}$ ). Rainfall corresponded to 67% of the mean (92.8 mm compared to 138.8 mm) but could have been partly counterbalanced by high rainfall in April (172.4 mm compared to 124.1 mm). However, in 2003 BAI of beech and silver fir was close to the average of the 2000–2006 period (respectively 102 and 104% compared to the mean; Fig. 4). Nevertheless, an important decrease in BAI was found in 2004, where silver fir and beech growth were 16% and 29% respectively below average compared to the reference period. A negative relationship between altitude and 2004 increment was observed for silver fir ( $p < 0.001$ ;  $r = -0.43$ ) but not for beech ( $p > 0.1$ ). This growth decline does not only depend on a post-effect of 2003 drought, since meteorological conditions during the 2004 growing period were also particular. A dry period was recorded at the beginning of summer, with only 7.3 mm of

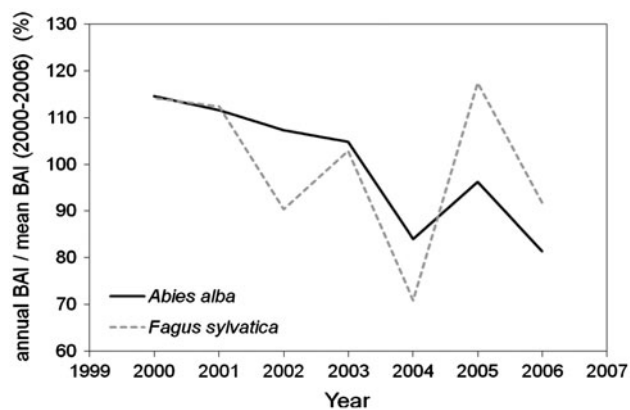
**Fig. 2** Altitudinal effect on predicted mean annual growth index of *Abies alba* (a) and *Fagus sylvatica* (b) for the whole period studied (black histogram) and for the period 2000–2006 (grey histogram). Elevational levels are abbreviated as in Table 1. Different letters indicate significant differences between means for the same period ( $p < 0.1$ , Tukey's HSD)



**Fig. 3** Climate trends in the studied area (measured at the Carpentras meteorological station at 99 m) between 1964 and 2006. Mean annual (in black) and mean summer (June–August; in grey) temperature increases were statistically significant ( $p < 0.1$ ). The decrease in summer rainfall (in grey) was significant at the  $p < 0.1$ , while no trend appeared for annual rainfall (in black)

rainfall during June and July, instead of 86.7 mm on average, but with normal temperatures.

Since the beginning of the 21st century there has been a significant decrease in BAI: 38 of the 73 firs (52%) had a negative slope over time, whereas only 5 trees had a positive slope (Table 4). This trend was also found for the master chronology whose slope was negative (BAI;  $-65.5 \text{ mm}^2/\text{year}$ ;  $p = 0.006$ ). No significant trend was observed for the growth of 70% of the beeches (54 of 77), and 25% had a negative slope. The non-significant slope of



**Fig. 4** Temporal trend in mean annual growth for *Abies alba* (solid line) and *Fagus sylvatica* (grey dashed line) between 2000 and 2006. To compare both species, basal area increment values were standardized by dividing them by mean basal area increment during this period

the average chronology ( $p = 0.43$ ) emphasized these results.

## Discussion

### Growth of both co-occurring species

Values of mean sensitivity and of mean series correlation were high and in agreement with previous studies (Desplanque et al. 1998; Dittmar et al. 2003; Lebourgeois et al. 2005; Lebourgeois 2007), which demonstrated a high suitability for dendroclimatic analysis for both species (Table 1). Silver fir was observed to be less sensitive to environmental changes than beech, which is likely due to the persistence of needles in winter and to a higher maximal root depth (Stokes et al. 2007), yielding higher growth inertia.

High autocorrelation values indicated that the tree-ring width of both species was influenced by growth conditions of previous years (Table 1). High temperatures during July to September of the previous year negatively impact wood

**Table 4** Comparison of linear basal area increment trend for the 2000–2006 period

Species	Individual chronologies		Master chronology	
	Range of slopes	Direction	Slope	<i>p</i> (linear regression)
<i>Abies alba</i>	–355 to +136	38 (–), 30 (=), 5 (+)	–65.5	0.006
<i>Fagus sylvatica</i>	–69 to +145	19 (–), 54 (=), 4 (+)	–10.7	0.43

Slope values are in mm<sup>2</sup>/year

Direction of slopes: (–)/(+), significant negative/positive trend ( $p < 0.1$ ); (=), no significant trend

production of the next year (Table 2), and more precisely earlywood production (Desplanque et al. 1998; Lebourgeois et al. 2005; Di Filippo et al. 2007), by changing the dynamic of carbohydrate storage, decreasing the root elongation and inducing leaf fall. Other mechanisms can also be envisaged such as delayed bud differentiation or abnormal losses of hydraulic conductivity (Selås et al. 2002; Lebourgeois 2007). No strong influence of winter conditions (January–March) was observed. Silver fir resists winter frosts well (Guehl 1985; Aussenac 2002), whereas beech develops mechanisms to recover hydraulic conductivity after winter cavitation (Cochard et al. 2001).

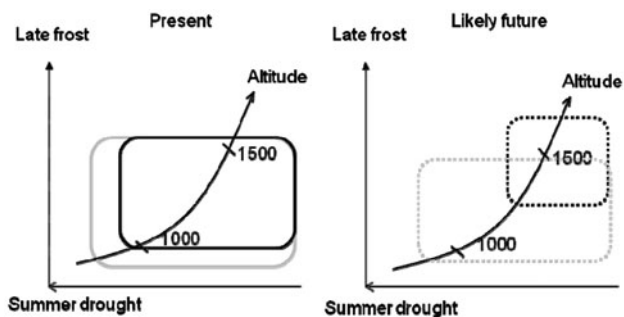
During the growing period, meteorological conditions differently impact the radial growth of both species. It is commonly accepted that high temperatures in April positively influence tree growth by causing earlier budburst and cambium activation, which lengthen the growing season and increase carbon assimilation (Davi et al. 2006; Delpierre et al. 2009). In this study, the same trend was observed for silver fir as in other dendroclimatic studies (Bert 1992; Manetti and Cutini 2006). However, for beech, whose budburst began 2 weeks before silver fir, a significant negative effect of maximal temperatures in April was observed for trees growing at high altitude. This report was not attributed to different evolutionary adaptation along the altitudinal gradient. As trees from the elevational range were originated from same relict populations that survive during last exploitation phases, genetic diversity should be reduced such as the adaptation processes since this period. The most convincing hypothesis is that an earlier budburst increases the risk of late frost damage on open buds and young leaves. These spring frosts can kill leaves blocking carbon assimilation and thus provoking a decrease in radial growth (Dittmar et al. 2006; Awaya et al. 2009). Budburst could also be advanced due to high temperatures in autumn. According to Chuine and Cour (1999), the more chilling units are cumulated, the less forcing units are subsequently needed for budburst, which can also explain the negative relationship between November temperatures and beech growth at high altitude. This explanation is confirmed by the results obtained by comparing radial growth of trees with different budburst date (Table 3). In 2006, beeches whose leaf-out was earlier had lower growth

than those whose budburst was later. Analysis of minimal temperatures at the meteorological station located at 1,445 m strengthens this conclusion. Negative temperatures were indeed recorded during 2006 beech budburst: six in April, four in May and one in June. To conclude, beech seems to be more sensitive to spring frost than silver fir.

The beginning of the current summer (May–July) differently affects wood production of both species. Drought during the first half of summer (May–July) negatively influenced ring-width of silver fir, particularly latewood (Lebourgeois 2007). These results can be explained by a high vulnerability to drought-induced cavitation, which involves a rapid and complete stomatal closure to avoid xylem embolism (Guicherd 1994; Aussenac 2002), and by an inhibition of cell division and enlargement (Zweifel et al. 2006). In contrast, beech growth indices were not related to summer rainfall and a positive effect of May temperatures was found at high altitude. This correlation with temperature shows that the conditions at the beginning of the growing season are important for cambial activity and wood production (Skomarkova et al. 2006; Čufar et al. 2008).

Mean radial increment variations with altitude were consistent with previous dendroclimatic results. Until the end of the 20th century, silver fir growth optimum was at intermediate altitudes (between 1,140 and 1,240 m a.s.l.) with lower values at lower and higher elevation. For beech, growth changes along the elevational gradient were less clear. Tree-ring growth analysis seemed to indicate that the optimum was between 1,100 and 1,230 m a.s.l., with a mean radial growth between 1,000 and 1,100 m not significantly different from the optimum, while height growth patterns seemed more confused. Below 1,000 m, beech trees are very scattered. This under representation at lower elevations was probably due to low recolonization rates from upper refuge sites. Presence of beech down to an altitude of 800 m is possible (Fig. 5). Coomes and Allen (2007) have recently reported a decrease in potential growth rate with altitude caused by reduced temperatures and shorter growing season. However, in their study water limitation at low elevations was not as important as on Mont Ventoux. In the Mediterranean region, where summer drought is the main growth limiting factor, trees





**Fig. 5** Present (left, continuous rectangle) and likely future (right, dashed rectangle) distribution range of silver fir (black) and common beech (grey). The two major limiting factors are late frost (number and/or intensity), and summer drought (frequency, intensity and/or duration). The curve is the elevational gradient studied

located on low elevational sites may be more constrained than those on upper sites because of the positive effect of altitude on water availability: less evaporation and more precipitation (Fig. 1b).

#### Climate change effects

Climate in south-eastern France showed an increase in mean annual and especially summer temperatures since the 1960s, which was associated with a decrease in summer rainfall since the 1980s (Fig. 3). It is well known that global warming and nitrogen deposition have increased tree radial growth (Hyvönen et al. 2007). Constant age methods have demonstrated this increase for both species (Bert 1992; Badeau 1995). However, our results also show that the effect of altitude on radial growth has changed. For the 2000–2006 period, trees growing in high altitudinal sites showed a high increase in radial growth, whereas trees at lower elevations did not grow better. This shift in growth optima to higher altitudes is consistent with the upward shift of species range recently observed and attributed to global change (Beckage et al. 2008; Lenoir et al. 2008; Jump et al. 2009). The intensity of factors limiting growth at low elevation (drought) has increased, whereas those which restrict carbon assimilation at upper elevation sites (low temperatures) have decreased. However, this upward shift can be mitigated by species-specific effects. For example, at high elevations, changes in budburst date could be connected with changes in late frosts damage probabilities and in competitiveness, which could alter beech vitality.

Since the beginning of 21st century, with the increase in summer drought frequency and intensity, most of the silver firs showed a decline of their growth (Table 4) and vitality. In the worst cases this led to mortality. For beech no significant trend was evident in this study. Even if several authors have already found a decrease in beech growth at its southern range edge (Peñuelas and Boada 2003; Jump

et al. 2006; Piovesan et al. 2008), beech is able to survive periods of reduced water availability (Dittmar et al. 2003), which also explains why other authors have found an increasing growth potential for beech (Geßler et al. 2007).

It is predicted that climate change will cause an increase in the frequency of extreme events, such as heat waves (Meehl and Tebaldi 2004). The 2003 summer was exceptional due to the intensity and duration of high temperatures (Schär et al. 2004; Rebetez et al. 2006). In France, the South-East was the region with the highest rainfall deficit (50–70% below average; Landmann et al. 2003). Nevertheless, no significant growth decrease was observed that year for both study species on Mont Ventoux. This result does not agree with studies on beech in Catalonia (Jump et al. 2006) or in north-eastern France (Granier et al. 2007) where tree growth was significantly reduced. The study of vegetative response to 2003 heat wave in the Swiss Alps revealed that trees located in the mountain zone (700–1,400 m) showed a decrease in growth, whereas an increase was observed in the subalpine zone (1,400–2,100 m; Jolly et al. 2005). This demonstrates that the impact of these extreme events on radial growth depends on the site- and species-specific responses to climatic factors (Pichler and Oberhuber 2007). Lag-effects of this heat wave cannot be deduced in this study due to the occurrence of severe drought in spring 2004, in summer 2005 and 2006. Moreover post-drought growth reductions occurring the following year (2004) were more detectable in beech.

#### Probable modification of species' range

The elevational gradient can be schematized as a curve where the two major limiting factors progress exponentially with altitude (Fig. 5). The number of frost days and their intensity increase exponentially with the upward shift in altitude (Fig. 1a). As elevation decreases, the frequency, intensity and duration of summer drought increase exponentially due to the combination of rising temperatures and decreased rainfall (Fig. 1a, b). Therefore, the future distribution of both species can change. In Mediterranean area, rising temperatures and decreasing rainfall (4–27%) are predicted (Christensen et al. 2007). Along with these trends a growth decline is expected for silver fir, and the species could disappear at the lowest altitudes and on soils with low water content, replaced by more drought tolerant species such as *Fagus sylvatica*, *Quercus pubescens* or *Acer opalus* (Fig. 5). Beech vitality would probably be less effected, except if the expected increase in intensity, frequency and duration of heat-waves occur (Meehl and Tebaldi 2004). It is commonly accepted that both warming and a decrease in anthropogenic pressure may favor the upward expansion of species distribution. Although a rise of 70 m in altitude has already been observed for beech in

the Montseny Mountains (Peñuelas and Boada 2003), an upward shift of beech would be limited by the likely increase in late frost damage (Hanninen 2006; Augspurger 2009). At higher altitude silver fir could completely take advantage of higher carbon assimilation due to rising temperatures and lengthening of the growing season (winter and summer photosynthesis). Factors limiting its shift would be mainly seed dispersion, along with edaphic and topographic conditions. If climatic events are not taken into account silver fir is predicted to face higher risks than common beech (Ohlemüller et al. 2006). However, the probable increase in late frost and heat-wave frequency and intensity would put beech at a disadvantage. These results need to be completed by considering other dynamic processes (regeneration, herbivory, intra- and interspecific competition, seed production and dispersion), and can be mitigated in some sites by changes in soil with altitude.

Co-occurring species can show quite divergent responses to climate despite occupying nearby niches and can be differently impacted by environmental changes such as those induced by global change. Using tree rings as proxy of tree growth give interesting results but further research is needed to investigate these relationships for different-aged trees, and under others environmental conditions (with different growth-limiting factors).

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