



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



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## ARTICLE INFO

### Article history:

Received 6 December 2016

Received in revised form 9 April 2017

Accepted 10 April 2017

Available online 26 April 2017

### Keywords:

Radial growth

Climate

Altitudinal gradient

*Abies alba*

Mediterranean region

## 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<sub>2</sub> rise: +40% since pre-industrial 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 ≈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:

$$CA\_GI_{ij} = \left( BA_{ij}^{obs} - BA_{i(j-1)}^{obs} \right) / \left( BA_{ij}^{RC} - BA_{i(j-1)}^{RC} \right) \quad (1)$$

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

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