Annals of Forest Science (2020) 77:54
https://doi.org/10.1007/s13595-020-00958-w

RESEARCH PAPER

Climate warming differently affects *Larix decidua* ring formation at each end of a French Alps elevational gradient

Philippe Rozenberg[1] · Thibaud Chauvin[1] · Margarita Escobar-Sandoval[1,2] · Frédéric Huard[3] · Vladimir Shishov[4] · Jean-Paul Charpentier[1] · Anne-Sophie Sergent[5] · J. Jesus Vargas-Hernandez[6] · Alejandro Martinez-Meier[5] · Luc Pâques[1]

Received: 12 December 2019 / Accepted: 28 April 2020

Abstract

• ***Key message*** **The ongoing global warming tends to reduce *Larix decidua* radial growth and ring wood density at the bottom of an elevational gradient in the French Alps, while it has a less marked effect at the top.**
• ***Context*** The ongoing climate warming affects most tree species across their biogeographic distribution range. The bottom and the top of an elevational gradient are appropriate environments to observe the effect of climate warming in contrasted temperature conditions.
• ***Aims*** To retrospectively study the effect of the ongoing climate warming on *Larix decidua* trees located in warm and cold conditions, i.e., at the bottom (1200 m) and the top (2300 m) of an elevational gradient, respectively.
• ***Methods*** Dendroecological analysis of two groups of *Larix decidua* trees located at very low (1200 m) and very high (2300 m) elevations. Construction of climatic response curves for annual ring variables. Decomposition of the variance of the response models into their high and low frequency components.
• ***Results*** At Briançon, in the French Alps, the increase of the daily maximum temperature during the last 50 years is already almost 3 °C for the March–October period. The results reveal contrasted behaviors at both ends of the investigated elevational gradient. Basal area increment, ring width, and their earlywood and latewood components increase or level off at the top of the gradient, while they all strongly decrease at the bottom. At the bottom, the low frequency warming effect explains the recent ring width decrease, with no influence of the high frequency temperature variation. At the top, both the low frequency warming effect

Handling Editor: Patrick Fonti

This article is part of the topical collection on *Wood formation and tree adaptation to climate*

✉ Philippe Rozenberg
philippe.rozenberg@inrae.fr

Thibaud Chauvin
thibaud.chauvin@hotmail.fr

Margarita Escobar-Sandoval
margarita.escobar-sandoval@inrae.fr

Frédéric Huard
frederic.huard@inrae.fr

Vladimir Shishov
vlad.shishov@gmail.com

Jean-Paul Charpentier
jp.charpentier2301@laposte.net

Anne-Sophie Sergent
ansosergent@gmail.com

J. Jesus Vargas-Hernandez
jjesus.vargashernandez@gmail.com

Alejandro Martinez-Meier
martinezmeier.a@inta.gob.ar

Luc Pâques
luc.paques@inrae.fr

[1] INRAE, UMR 0588 BIOFORA, 2163 Avenue de la Pomme de Pin, CS 40001, 45075 Ardon Cedex 2, Orléans, France

[2] Facultad de Ingeniería, Universidad de Ciencias y Artes de Chiapas, Unicach Villacorzo, Villacorzo, Chiapas, México

[3] INRAE, US 1116 AgroClim, 228 route de l'Aérodrome CS 40509, 84914 Avignon Cedex 9, France

[4] Math Methods and IT Department, Institute of Economics and Trade, Siberian Federal University, L. Prushinskoi st., 2, Krasnoyarsk 660075, Russia

[5] INTA, EEA Bariloche, Grupo de Ecología Forestal, San Carlos de Bariloche, Río Negro, Argentina

[6] Ciencias Forestales, Colegio de Postgraduados, Montecillo, 56230 Texcoco, Edo. de México, México

and the high frequency temperature effect explain each about half of the ring width variation encompassed by the model. Latewood density displays the same trend as ring width, while earlywood density decreases at both ends of the gradient.

- ***Conclusion*** Such opposed trends of the radial growth time trends between the top (2300 m) and the bottom (1200 m) of the gradient reflects the respectively favorable and unfavorable effects of climate warming at such ends of this *Larix decidua* elevational gradient. We propose that the strong ring width decrease observed at the warmer bottom announces a coming dieback. The corresponding wood density decrease will affect wood hydraulic properties in a way that is unclear.

Keywords Climate warming · Elevational gradient · *Larix decidua*

1 Introduction

Broad scale forest die-off triggered by more frequent and intense drought associated to the global warming has been widely documented during the recent years (Allen et al. 2015). In general, mountain forests are recognized to be more fragile and more sensitive to disturbances than lowland forests (Tse-ring et al. 2010). The maximum warming associated to climate change is expected to occur in artic regions and in mountain regions at medium to high elevations (Kotlarski et al. 2015; Wang et al. 2014) and thus may jeopardize the future of mountain forests. In some areas of the Alps, temperature already augmented twice as fast as the average increase in the northern hemisphere during the previous century (Rebetez and Reinhard 2008). This current warming rate is greater at upper elevation (Mountain Research Initiative EDW Working Group et al. 2015).

Several recent studies reported climate change–related declines in several European mountain tree species, i.e., Scots pine (*Pinus sylvestris* L.) in South-Western and North-Eastern Germany (Taeger et al. 2013); mountain pine (*Pinus mugo* ssp. Uncinata (DC.) Domin) in Western Tatra Mountains, Slovakia (Solár 2013); Norway spruce (*Picea abies* (L.) H. Karst.) in Austria (Vospernik and Nothdurft 2018); and silver fir (*Abies alba* Mill.) in Spain, Italy, Romania, and France (Gazol et al. 2015; Cailleret et al. 2014). These declines are generally observed at the bottom and could correspond to a contraction of the warm edge of these species elevational distributions.

Unlike these species, and to our knowledge, *Larix decidua* (*Larix decidua* Mill.) showed no particular climate change–related decline so far. Larch is a light-demanding pioneer species with a distribution that benefited from agricultural activities and especially grazing (Heinz H. Ellenberg 1988; Schulze et al. 2007) and growing well on soils with a high water supply (Fourchy 1952; Keller et al. 1997). But one modeling study shows that its distribution is threatened by climate change (Dyderski et al. 2018). Indeed, *Larix decidua* is regulating water loss during atmospheric drought more efficiently than *Picea abies* (Peters et al. 2019). It is able to preserve a comparatively high transpiration rate even during periods of moderate water deficit, thanks to its high capacity of water uptake (Anfodillo et al. 1998; Badalotti et al. 2000). However, this species is also known to be nearly as sensitive to soil water deficit as Norway spruce (Vanoni et al. 2016; Schuster and Oberhuber 2013; Lévesque et al. 2013; Charra-Vaskou et al. 2012). Decreased water availability and increased atmospheric demand constrain *Larix decidua* from low to higher than expected elevations in dry Alpine valleys (Obojes et al. 2018; Schuster and Oberhuber 2013; Eilmann and Rigling 2012): low elevation *Larix decidua* stands are sensitive to water stress (M. Saulnier et al. 2019). The bottom and the top of the elevational distribution of a mountain tree species are appropriate environments to observe the effect of climate warming in much contrasted temperature conditions. The climate warming tends to impose more intense drought stress to the trees located at the lower end of an elevational gradient, while it tends to improve the growing conditions at the top. Global warming could increase tree radial growth at high elevation, while it would decrease it at low elevation (Primicia et al. 2015; Sidor et al. 2015; Marqués et al. 2016), as already observed for *Larix decidua* in an Inner Alpine dry valley (Obojes et al. 2018).

In the southwestern part of its Alpine natural area, *Larix decidua* elevational distribution ranges from as low as 1200 m to as high as 2500 m, making it one of the mountain species with the largest temperature variation along its elevational gradients (Fourchy 1952). *Larix decidua* is an important forest tree species throughout the Alps and in some regions of central Europe. As one of the very few deciduous conifer species, it confers a very distinctive appearance to the Alpine landscapes (Garbarino et al. 2013). It produces a durable, high quality wood and plays an important ecological, economic, and cultural role all over its natural area (Riou-Nivert 2001). In this study, we retrospectively investigated the annual ring response of adult *Larix decidua* trees to climatic variation during the last 50 years in the French Alps. We selected three as low and two as high as possible sampling plots in the region of Briançon, France, where we found the longest *Larix decidua* elevational gradients.

We hypothesize that during the last 50 years, radial growth increased at the top, while it decreased at the bottom of the *Larix decidua* elevational gradient. We completed the information brought by basal area increment and ring width with the early- and latewood components, and the corresponding density variables of the annual radial growths. Ring density is a proxy of the proportion of cell wall and lumen area in a wood volume, and provides information on wood hydraulic properties (Dalla-Salda et al. 2011). The large anatomical variation between early- and latewood (Zobel 1989) suggests that both parts of the ring play very different hydraulic roles (Zimmermann 1983), as shown in Douglas fir for vulnerability to cavitation (Guillermina Dalla-Salda et al. 2014). Therefore, it seems relevant and interesting to investigate *Larix decidua*'s response to climate not only at the ring level, but also at the early- and latewood levels. We studied the relationships between these annual ring variables and the corresponding climatic time series from the closest Météo-France weather station. We postulate that the global warming explains the radial growth increase at the top and the radial growth decrease at the bottom of the gradient. Finally, we discuss to what extent the observed variations are possible predictors of future changes.

2 Material and methods

2.1 Sample collection

We collected the wood samples in November 2016 at two of the three low elevation plots and in June 2017 for the two high elevation plots, coupled with the sampling of the third low elevation plot (Rozenberg et al. 2020). All plots are located in the *forêt communale* of St-Martin-de-Queyrières, near Briançon, Hautes-Alpes, France. The forest is owned by the village of St-Martin-de-Queyrières and managed by the Office National des Forêts (French National Forest Service) since the middle of the nineteenth century. It is a North, North-West facing slope ranging from 1200 to 2500 m and covered mostly by pure uneven-aged larch forests with some patches of *Abies alba*, *Pinus sylvestris*, *Pinus cembra*, and *Pinus uncinata*. The forest is mostly naturally regenerated with occasional plantations of local origins in case of regeneration failure. The soil types found along the slope are more or less complex succession and associations of Calisol, Eutric Brunisol, Colluviosol, and Regosol. The forest is subjected to low intensity periodic thinning done according to the management plan (Table 1).

We collected 144 5-mm breast height increment cores with a power-driven increment borer, following a perpendicular to the slope orientation to avoid compression wood. The trees were all adult, dominant trees with no visible major defect. The freshly collected increment cores were stored in polycarbonate honeycomb boxes, brought back to the laboratory, where they were oven-dried and sawn to a 2-mm uniform thickness. Then, they were resin-extracted with a 48-h pentane bath. They were dried again and then X-rayed using the indirect procedure invented by Polge in 1966 and continuously improved since then (Polge 1978; Mothe et al. 1998). Finally the X-ray films were scanned at 4000 dpi to acquire the microdensity profiles using the WINDENDRO software (Windendro 2008e Regent instruments Canada nc.; http://www.regent.qc.ca/products/dendro/DENDRO.html).

The microdensity profiles were visually checked and compared with the sawn samples then cross-dated using pointer years. Some profiles had to be discarded because ring boundaries were blurred by a very strong grain angle. When the increment core missed the pith, we estimated the number of missing rings using the curvature of the innermost rings of the increment core. Then, tree age was estimated by arbitrarily adding 10 years to the number of rings counted from pith. We assumed that 10 was the average number of years taken by the trees to reach the increment core collection height, breast height.

2.2 Annual radial growth variables

The raw microdensity profiles were imported into R (R Core Team 2018), and the following conventional annual radial growth variables were calculated using specially designed R functions, i.e., ring width, basal area increment (ring area, BAI), earlywood width, latewood width, earlywood density, latewood density, and standard deviation of ring microdensity (ring standard deviation). Earlywood-latewood boundary was calculated using the conventional extreme average method based on the mean of the extreme ring density values (Rozenberg et al. 2002). Basal area increment was calculated as $\mathrm{BAI}_i = \pi \times \left(r_i^2 - r_{i-1}^2\right)$, where BAI_i is the basal area increment of the ith ring from the pith, and r_i^2 and r_{i-1}^2 are the radius of the ith and $(i-1)$th rings from the pith. The radii are calculated as cumulated ring width. BAI is a dendroecological approach based on the assumption that it expresses a constant growth distributed all around the growing stem (Biondi and Qeadan 2008).

2.3 Detrending

Our objective is to ensure that the main trends in our results and conclusions are not biased but robust. Besides the conventional ring variables based on the earlywood-latewood model (Ruiz Diaz Britez et al. 2014), we introduced BAI. Endogenous and exogenous factors may affect radial variation of any annual radial growth variable. To study relationships with climate, we need to keep as far as possible the climatic signal in our time series, but eliminate other possibly confounding sources of variation. We especially need to eliminate the low frequency cambial age effect, which is generally assumed to be the major confounding effect, but keep the low frequency climatic effects like the possible uniform effect of climate change and global warming (Cook et al. 1990). We tested separately each non-climatic effect available (cambial age, *Larix decidua* bud moth defoliation, and heartwood-

Table 1 Location of sampling sites

Plot name	Latitude	Longitude	Elevation (m)	Slope aspect	Elevation (class)	Number of validated annual ring time series	Estimated mean age (years)
Crête des Queyrelets	N 44.787515	W 6.601709	2350	North	High	27	106
Fond Froid	N 44.813903	W 6.618727	2320	North, North-West	High	30	91
Le Villaret	N 44.857215	W 6.592905	1140	North, North-West	Low	15	92
Torrent de Queyrières	N 44.831536	W 6.5791	1120	North-West, West	Low	30	89
Tunnel de Rochebaron	N 44.85263	W 6.583611	1140	North-West	Low	29	89
Total number						131	

sapwood), and we adjusted from the effects that proved to affect significantly the radial variation of the ring variables. Larvae of larch bud moth (*Zeiraphera griseana*) episodically defoliate alpine stands of *Larix decidua* during considerable outbreaks striking most of the time at 8–10-year intervals, with a maximum at 1800 m altitude (Baltensweiler et al. 2008; Dormont et al. 2006). The defoliation reduces photosynthesis, decreases carbohydrates production, and lowers annual ring growth. Such reduction of annual ring growth leaves a typical mark in annual ring time series (Battipaglia et al. 2014; Mélanie Saulnier et al. 2017; Cerrato et al. 2019). To separate bud moth outbreak-induced growth decreases from those produced by climatic factors or by other biotic factors, we used a 15-year moving window approach (Büntgen et al. 2009). We tested the heartwood-sapwood effect with a one-way ANOVA. We found that only the cambial age significantly affected radial variation. A one-way ANOVA showed that the cambial age effect was significantly different between the elevational classes (Fig. 4). Then, we adjusted linearly all the ring variables from the cambial age effect estimated at both elevational levels by *regional curve standardization* (RCS) procedure (Esper et al. 2003). We compared three methods, i.e., *raw* (no detrending), *residual* RCS, and *ratio* RCS (Esper et al. 2003). The terms *residuals* and *ratio* refer to the terminologies used in Esper et al. (2003). We obtained age-related curve for both elevations (Fig. 4). For each individual time series (or individual tree), we obtained an adjusted value of tree-ring growth by subtracting (residuals) or dividing (ratio) the observed value by age-depended estimation for each year. We obtained the residual and ratio RCS chronologies by time-depended averaging of individual series. Figure 5 shows raw, residual, and ratio detrended time series for ring width at low and high elevations. We compared the results obtained with the three types of times series, the two adjusted and the one non-adjusted. For ring width, earlywood width, and latewood width, we found very similar results that lead to mostly identical conclusions with the three methods (Fig. 6). For BAI, the results obtained with the raw and residual RCS time series were similar, while the ratio RCS method appeared to be obviously not adapted. The possible bias associated to the ratio RCS applied to specific ring variables has already been reported (Cook and Peters 1997). For ring, earlywood, and latewood density, the results obtained with the raw and residual RCS time series were similar, while the ratio RCS time series were apart and probably biased. The corresponding results are not shown in Section 3, since the objective of the article is not to work on method development but on larch response to climate. A small selection of these methodological results is provided in the Appendix section.

The cambial age effect shown in Fig. 4 is high near the pith and gradually decreases with the ring number counted from the pith (Zobel and Sprague 1995). In this study, we used the last 50 rings counted from the bark (from 1967 to 2016), in trees that are generally much older than 70 years (estimated age is between 89 and 106). It means that in our time series, the cambial age effect is certainly lower than the climatic effect. In Section 3, we present the results based on the residual RCS detrended time series for both the conventional ring variables and BAI, knowing that in this study, both raw and residual RCS methods lead to the same conclusions.

2.4 Climatic data

Climatic data are daily values of minimum and maximum temperatures and precipitations coming from the closest Météo-France weather station (French national weather service). This weather station was first located in Briançon (N 44.905856, W 6.633046, 1306 m) and started to record data in 1966. In 2003, a new station was created and started to record climatic data in Villard-St-Pancrace (N 44.864861, W 6.61541, 1276 m), 4.8 km south of the Briançon weather station. From 2004 to 2010, both weather stations have been operating together. In 2010, the Briançon weather station stopped operating. Only the Villard-St-Pancrace weather station continued to record climatic data since then. The climatic time series during the Briançon-Villard-S-Pancrace common recording periods show that there is nearly no difference between both sites for maximum and minimum temperatures and very little for the precipitations (Fig. 9).

We grouped the data from the two weather stations to create a unique climatic database going from 1966 to 2017. We used this database to study the annual variation of the three climatic variables available from 1966 to 2017. For each climate variable, we tested a large number of intra-annual periods, and we selected the annual periods for which the climate-time relationships were maximum (Fig. 8). The corresponding models describe the effect of climate change on the three climatic variables available, i.e., minimum and maximum temperature, and precipitation in the Briançon region.

2.5 Variation of ring variables against time

The mean adjusted annual radial growth variables and BAI were plotted against time (years) at each elevational level for the period 1945–2016. We estimated the Spearman correlation coefficient (rho) among the ring variables for the same 1945–2016 period. We chose the Spearman non-parametric rank correlation instead of the Pearson, because the first method is more flexible for data that are not necessarily normally distributed, or for relationships which are not strictly linear, such as with time series data.

We tested the relationships between climate and annual radial growth variables at each elevational level using also the Spearman correlation coefficient, using for the ring variable time series from 1966 to 2016, corresponding to the climatic variable time series. While we found no significant relationships with precipitation, we found significant relationships with both temperature variables and stronger relationships with maximum than with minimum temperature. Thus, we decided to do the dendroecological analysis with maximum temperature only.

We created two maximum temperature time series going from 1966 to 2017 for the two elevational classes (*low* and *high* elevation) by linearly adjusting the temperature time series of the elevational effect as in Latreille et al. (2017). The parameters of the elevational temperature model are based on temperature data recorded from 2008 to 2016 in four INRA field weather stations installed in four elevational plots located a few kilometers away in the forest of Villard-St-Pancrace, at 1350, 1700, 2000, and 2300 m elevation.

2.6 Data analysis

We tested the variation with time (annual periods) of minimum and maximum temperature from 1966 to 2017 with linear regression analysis for varying annual periods. The duration and dates of the tested annual periods varied from 2 to 12 months, starting from January 1 to December 31, respectively, with a 1-week step variation from one tested period to the other. For each climatic variable, we selected the period maximizing the coefficient of correlation of the time-trend relationship ("maximizing period"). We estimated the confidence interval at 95% of the beginning and ending dates of the maximizing period.

The relationships between annual radial growth variables and climate were tested at each elevational level using simple linear regression. The effect of low and high frequency climate variation was tested using the analysis of variance (ANOVA):

$$x_{ijk} = \mu + y_i + z_j + \varepsilon_{ijk}$$

where x_{ijk} is the annual radial growth variable, μ is the mean, y_j is the year variable, z_j is the annual climate variable, and ε_{ijk} is the residual. The part of the variation explained by the linear year (y_j) effect is the *low frequency* warming effect (Fig. 1), while the part of the variation explained by the annual climatic variable (maximum temperature here) is the remaining *high frequency* effect.

We used this ANOVA model to decompose the model variance into its two components, the global warming (GW) effect and the high frequency temperature (HFT) effect. We used the R gvlma package to test and validate the linear model assumptions.

3 Results

3.1 Climate change

There are significant linear time trends for the three climatic variables. These relationships are quite strong for minimum temperature (Adj. R-square = 0.48), strong for maximum temperature (Adj. R-square = 0.62), and low (but significant) for precipitation (Adj. R-square = 0.09). The periods maximizing the relationships are very similar for minimum and maximum temperature (from the beginning of March to the end or the middle of October, respectively), while it is very different for precipitation (from the beginning of January to the beginning of April). They correspond to a 0.0281-°C and 0.058-°C annual increase for minimum and maximum temperature, respectively, and to a significant but very low 0.0154 mm annual decrease for precipitation.

3.2 Annual radial growth variable time series

From 1945 to around 1985, adjusted BAI increases in a parallel way at both low and high elevations, with BAI growth being faster at the low elevation. Then after 1985, low elevation BAI starts to level off and finally decreases after 2000. During the same period, high elevation BAI continues to increase. Adjusted ring width is mostly stable at the high elevation except for a marked decrease during the early 1970s, while at the low elevation, it steadily decreases from the beginning (1945) to the end (2016) of the study period.

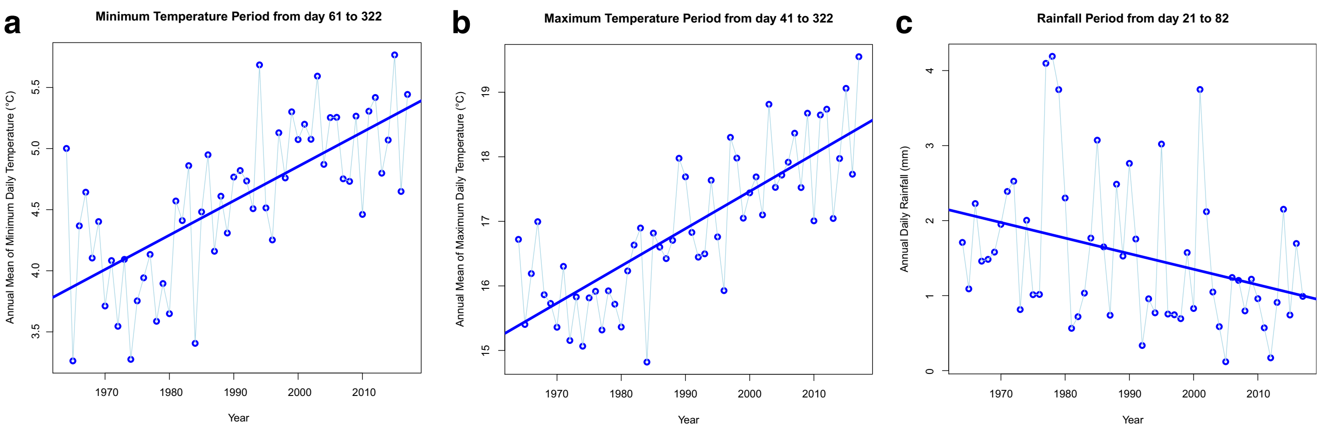


Fig. 1 Chart of the strongest significant linear relationships between minimum and maximum temperature, and precipitation (rainfall and snow) across time (year) for the maximizing annual periods based on the Météo-France weather data of Briançon (1306 m) and Villard-St-Pancrace (1276 m). The equations and adjusted R-squares of the corresponding linear regressions are printed below each chart

Earlywood width and latewood width show mostly similar trends (Fig. 6). The high and low elevation lines cross during the 1990s: low elevation radial growth becomes lesser than high elevation after this period. Both curves merge and cross between 1995 and 2005. Earlywood density is mostly stable from 1945 to the beginning of the 1990s at both elevations, with the low elevation earlywood being generally higher than high elevation. Then, both high and low elevation earlywood density strongly decreases from the beginning of the 1990s to 2005, where they seem to mostly stabilize again until 2016. Latewood density show a different trend, with high elevation latewood density being mostly stable or slightly increasing, and low elevation latewood density showing a trend very similar to low elevation earlywood density. Ring density variation is intermediate between that of earlywood and latewood densities (Fig. 6). From 1945 to approximately 1985 (earlywood density, Fig. 2), 1990 (ring density, Fig. 6), and 2000 (latewood density, Fig. 2), density is lower at the high elevation than at the low elevation. This tendency strongly changes afterwards, temporarily for earlywood density, more clearly for ring density, and considerably for latewood density (Figs. 2 and 6).

3.3 Relationships among the ring variables

At the low and high elevations, ring width, and BAI are quite strongly positively correlated (0.82 and 0.74, respectively). Both variables are positively correlated with latewood density, with this correlation being stronger at the low elevation, especially for ring width. The sign of the moderate correlation between earlywood density and ring width changes with elevation: it is positive at the low and negative at the high elevation. The same trend is observed for BAI but with a much weaker relationship at the low elevation (Table 2).

3.3.1 Relationships between annual radial growth variables and annual temperature

Table 3 and Fig. 3 show the strongest significant relationships that we found between the annual radial growth variables and mean maximum daily temperature of the period maximizing the relationship (the annual period maximizing the coefficient of correlation of the time-trend relationship). We found similar but weaker relationships with minimum temperature, and no significant relationship with precipitations. Table 3 shows the results for all the ring variables, while Fig. 3 shows the same results for a selection of four variables (basal area increment, ring width, earlywood density, and latewood density).

Table 3 shows that it is possible to find very strongly significant relationships with maximum temperature for all the ring variables at both elevations. There are significant relationships for a large number of periods and sometimes for all the tested period. This is the case, for example, for latewood density at the low elevation (Fig. 7). The maximizing periods are different between variables and elevations. At the low elevation, all the relationships are negative and generally quite strong to very strong (Spearman's coefficient of correlation ranging between − 0.72 and − 0.86 except for basal area increment, − 0.50). At the high elevation, all the relationships are quite strong to strong (from 0.60 to 0.90), stronger than at the low elevation, with six positive relationships and two negative (for mean ring density and earlywood density).

Figure 3 shows the corresponding relationships for the four selected variables. Patterns of earlywood width and latewood width are very similar to that of ring width, while the pattern of ring density is very similar to that of earlywood density (not shown). The pattern of ring density standard deviation is very similar to that of latewood density (not shown). All the relationships are linear.

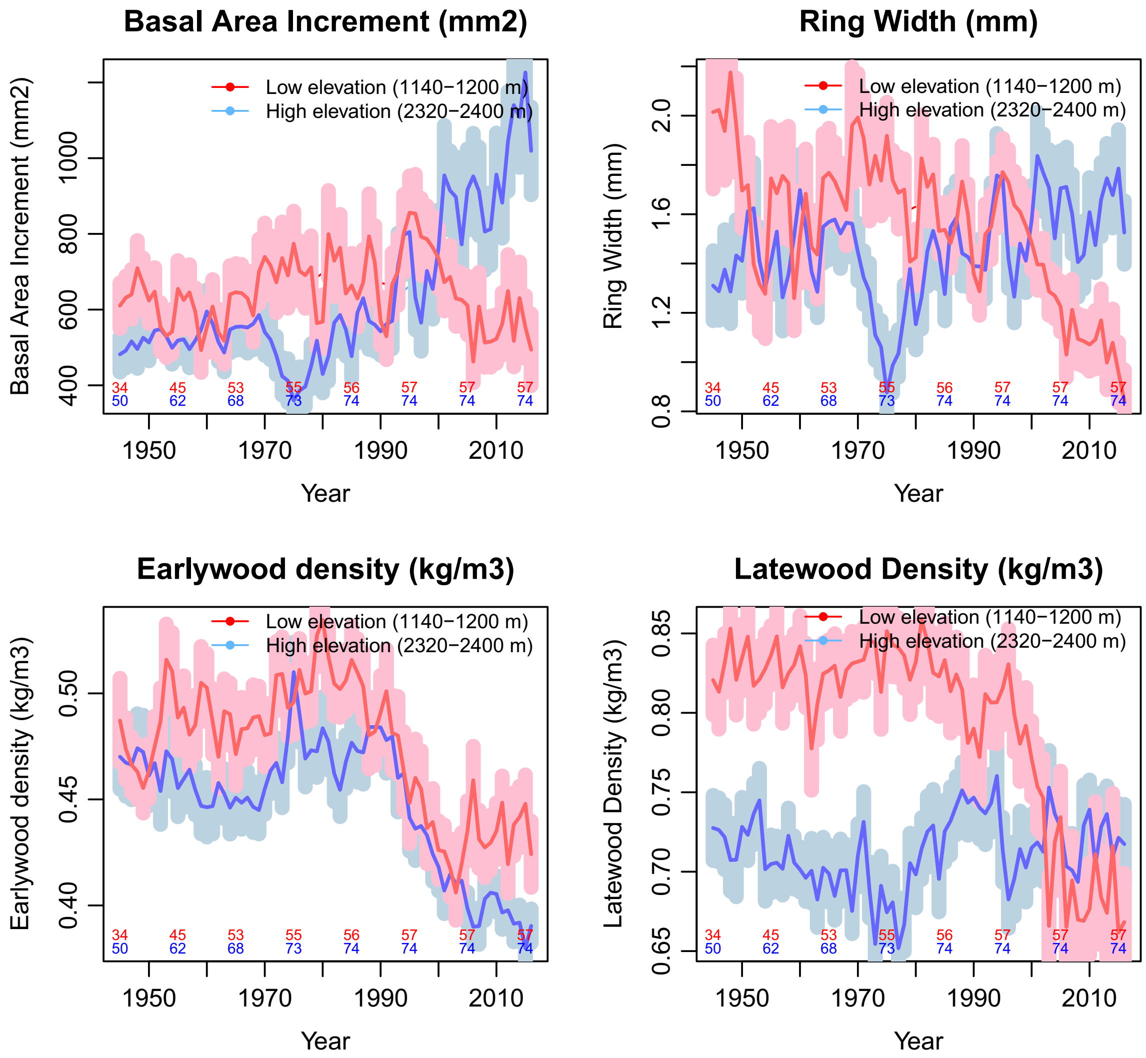


Fig. 2 Average variation across time of four adjusted annual radial growth variables at the low (red line) and high (blue line) elevation. Light colors represent the 95% confidence interval around the mean. The red and blue numbers are the number of trees used in the calculation of the mean at each year and elevational level (same color code)

3.4 Variance decomposition based on the ANOVA model for four selected variables

The results in Table 4 show the variance decomposition based on the ANOVA model for the low frequency "global warming" effect (the part of the variation explained by the linear relationship between annual temperature and year) and the remaining high frequency "annual temperature" effect. There are strong differences between elevations and ring variables. The global warming effect explains most part of the variation at the low elevation for ring width and early- and latewood density, and at the high elevation for BAI and earlywood density. For ring width and latewood density at the high elevation, and for BAI at the low elevation, both global warming and high frequency effects explain analogous parts of the total variance.

The total *R*-square of the models in Table 4 are of the same magnitude order than those of the models presented in Fig. 3, with small differences due to the fact that not exactly the same annual values or the same models are used in both analyses. For example, for ring width at the high elevation, *R*-square is 0.40 in Fig. 3, while it is 0.42 in Table 4. Nevertheless, both analyses show the same trends with similar between-traits and between-elevation level differences.

4 Discussion

The climate dataset of the Briançon, Villard-St-Pancrace Météo-France weather stations shows that the average temperature of a large part of the year including the *Larix decidua* growing season (March–October) linearly increased between 1967 and 2017 (Fig. 1). Two warm years (1966 and 1969) preceded the cold period from 1970 to 1980. The temperature of these two warm years is nevertheless at the same level than

Table 2 Spearman's correlation coefficients among the four selected ring variables at both elevation levels. All correlation coefficients are significant at the 0.001 (***), 0.01 (**), or 0.05 (*) level, except when indicated (NS)

High elevation Low elevation	Ring width	Basal area increment	Earlywood density
Basal area increment	0.82*** 0.74***		
Earlywood density	− 0.67*** 0.53***	− 0.84*** 0.19*	
Latewood density	0.41*** 0.85***	0.45** 0.57**	− 0.04 NS 0.76***

the temperature of the coldest years after 1998. The succession of cold and relatively cold years from 1970 to 1980 reduced the radial growth of the corresponding annual rings in the limiting conditions of the high elevation plots, but not in the warmer conditions of the bottom of the gradient (Fig. 2). For the whole study period, the maximum temperature increase exceeded 3 °C (0.58 °C by 10 years during the last 50 years). According to the French national weather service Météo-France, the average increase of maximum temperature is 0.32 °C/10 years for France (Impacts du changement climatique: Atmosphère, Températures et Précipitations 2020). This result is consistent with the faster warming observed in the Western Alps than in lower elevation regions for maximum temperature (Rebetez and Reinhard 2008). For minimum temperature, the values are approximately the same: 0.28 °C/10 years at Briançon, Villard-St-Pancrace, and 0.29 °C/10 years for France. A similar trend was recently observed in Switzerland (Vitasse et al. 2018).

The variation of the annual ring time series during the same period (Fig. 2) shows very different temporal trends at the low (under 1300 m) and high (about 2300 m) elevations. At the low elevation, ring width decreases from more than 2.5 mm to less than 1 mm, while at the high elevation, it remains stable around 1.5 mm. BAI better represents the overall tree growth potential than ring width and its components (Biondi and Qeadan 2008), which nevertheless remain pertinent at least for comparison with previously published results.

Table 3 Correlations (Spearman's correlation coefficient) between the ring variables and the mean maximum temperature of periods selected for maximizing the ring-climate relationship.

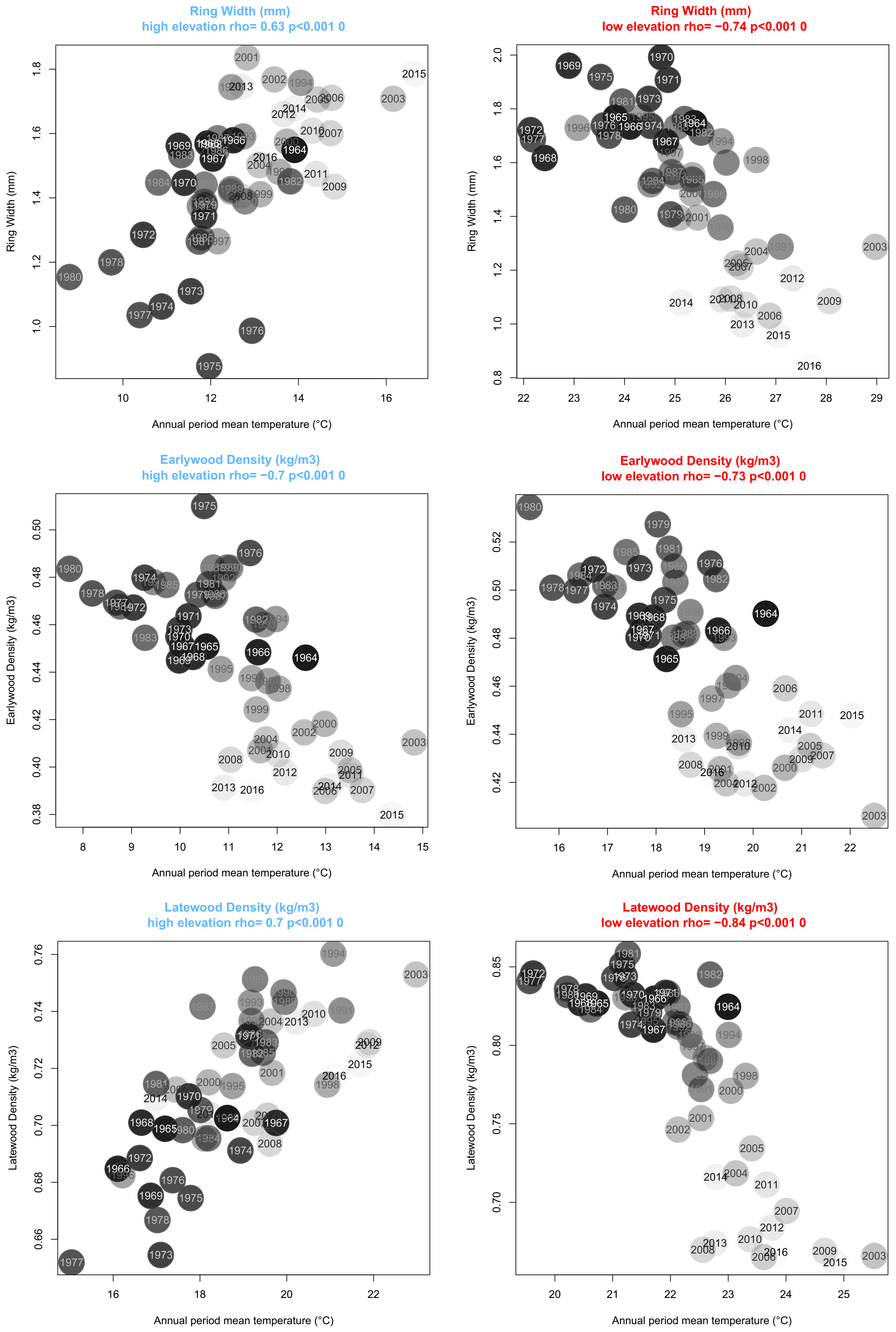
Ring variables	High elevation	Low elevation
Basal area increment	0.78***	− 0.49***
Ring width	0.63***	− 0.74***
Earlywood width	0.61***	− 0.72***
Latewood width	0.60***	− 0.78***
Ring density	− 0.64***	− 0.81***
Earlywood density	− 0.70***	− 0.73***
Latewood density	0.70***	− 0.84***
Ring standard deviation	0.90***	− 0.72***

***means that all the correlations are significant at the 0.001 probability level

Earlywood and latewood densities display different trends reflecting distinct determinisms (Fig. 2). The pattern of mean ring density (Fig. 6) is very similar to that of earlywood density. Before 1990, mean earlywood density was 0.47 kg/dm^3 (standard deviation 0.016) at the high elevation and 0.50 (0.016) at the low elevation. After the 2000s, it decreased to respectively 0.39 (0.016) and 0.42 (0.016) kg/dm^3. The relatively uniform latewood density trend suggests no global warming effect on this trait at the high elevation. In contrast, the strong latewood density decreases at the low elevation from the 1980s to the beginning of the 2000s (Fig. 2, from 0.82 (0.016) to 0.68 (0.016) kg/dm^3) indicates a major global warming effect in the warmer conditions of the bottom of the *Larix decidua* distribution. Another obvious consequence is the alteration of the elevational trend of wood density. During the period preceding the observed warming, wood density tends to be lower at the higher than at the lower elevation. This well-known trend (Zobel 1989; Rossi et al. 2014; Apiolaza 2012) is reversed afterwards, especially for latewood density (Fig. 2; see also Fig. 6).

The strong and continuous radial growth decrease at the low elevation for all variables (ring, early- and latewood width, and from 1990 for BAI) is consistent with predictions (Primicia et al. 2015; Sidor et al. 2015; M. Saulnier et al. 2019) and with observations of different species including *Larix decidua* (Obojes et al. 2018; Jiao et al. 2019; Zhu et al. 2018; Marqués et al. 2016). However, we find contradictory trends for the high elevation radial growth between BAI and ring width, even if partly explained by the geometrical relationship between both traits. While ring width remains rather stable all across the study period, high elevation BAI increases

Fig. 3 A selection of relationships between four ring variables (basal area ▶ increment, ring width, earlywood, and latewood densities) and mean maximum temperature of the selected maximizing annual periods at both low and high elevation. Rho is the Spearman correlation coefficient and p is the associated probability. p = 0 corresponds to significance levels below 10^{-12}. The gradient of gray of the year points corresponds to between-year time variation from 1967 (dark gray) to 2016 (light gray)


Ring Width (mm)
high elevation rho= 0.63 p<0.001 0
Ring Width (mm)
1.0
1.2
1.4
1.6
1.8
10
12
14
16
Annual period mean temperature (°C)
Ring Width (mm)
low elevation rho= −0.74 p<0.001 0
Ring Width (mm)
0.8
1.0
1.2
1.4
1.6
1.8
2.0
22
23
24
25
26
27
28
29
Annual period mean temperature (°C)
Earlywood Density (kg/m3)
high elevation rho= −0.7 p<0.001 0
Earlywood Density (kg/m3)
0.38
0.40
0.42
0.44
0.46
0.48
0.50
8
9
10
11
12
13
14
15
Annual period mean temperature (°C)
Earlywood Density (kg/m3)
low elevation rho= −0.73 p<0.001 0
Earlywood Density (kg/m3)
0.42
0.44
0.46
0.48
0.50
0.52
16
17
18
19
20
21
22
Annual period mean temperature (°C)
Latewood Density (kg/m3)
high elevation rho= 0.7 p<0.001 0
Latewood Density (kg/m3)
0.66
0.68
0.70
0.72
0.74
0.76
16
18
20
22
Annual period mean temperature (°C)
Latewood Density (kg/m3)
low elevation rho= −0.84 p<0.001 0
Latewood Density (kg/m3)
0.70
0.75
0.80
0.85
20
21
22
23
24
25
Annual period mean temperature (°C)

and thus follows the predicted (Primicia et al. 2015; Sidor et al. 2015; M. Saulnier et al. 2019) and sometimes observed (Bošeľa et al. 2014; Zhu et al. 2018; Yin et al. 2018) global warming–related growth trend.

A radial growth decrease often precedes forest tree mortality (Cailleret et al. 2017, 2019). Therefore, the growth decrease observed at the low elevation could be interpreted as a warning signal for coming diebacks related with increased drought stress during the growing season. In our case, a wood density decrease also accompanies the observed low elevation growth decline. In general, a radial growth drop-off is related to a density increase (Zobel 1989). Nevertheless, the summer 2003 heat wave and drought in France induced in Douglas fir a mean density decrease of the 2003 ring explained by a smaller proportion of lower density latewood (Martinez Meier et al. 2008). To our knowledge, few results are available concerning variation with time of ring density variables in forest mountain species. Wood density of four dominant European species decreased by 8 to 12% during the last 100 years (Pretzsch et al. 2018). Several studies suggest that the global warming tends to decrease minimum ring and/or earlywood density (Camarero and Gutiérrez 2017; Fonti and Babushkina 2016). In our case, earlywood (at both elevations) and latewood (at the low elevation only) densities strongly decreased during the study period, with most part of the decrease observed during a 20 to 25-year period between the mid-1980s and the mid-2000s. Then, the three ring density variables seem to level off after 2005. Only latewood density at the high elevation remains more or less stable all along the study period (Fig. 2). Water stress is known to affect ring density: for example, a major heat wave induced the formation of a narrower, less dense ring with incomplete latewood in Douglas fir (Martinez Meier et al. 2008). Wood density is mainly related with the proportion of cell wall and lumen area in the xylem. It is generally accepted that the variation of wood density has an effect on conduction properties and on resistance to drought (Dalla-Salda et al. 2011). During the growing season, stomata of anisohydric species like *Larix decidua* remain open even when temperature increases up to critical levels. Because of its high water uptake capacity, *Larix decidua* can preserve a rather high transpiration rate even during periods of limited water deficit (Anfodillo et al. 1998). Transpiration peak, water availability fall, and carbohydrates rerouting to vital functions rather than to tracheid cell wall thickening could explain the observed density decrease.

The distribution of the tested periods for the relationship between latewood density and temperature at the low elevation is shown in Fig. 7. The maximum correlation coefficient in this distribution corresponds to the selected response curve. The heat map in Fig. 7 and all the heat maps for the other ring variables (not shown) reveal that there is a wide range of periods generating significant correlations nearly as high as the maximizing one. A variation of more or less 50 to 100 days of the beginning and ending dates of the maximizing periods does not decrease much the value of the correlation coefficient. In other words, the average temperature of a wide range of periods explains more or less the same, large part of the inter-annual variation of ring characteristics. With Fig. 3, we show the selected temperature response curves for BAI, ring width, earlywood density, and latewood density. The earlywood width trend is very similar to that of ring width, and the ring density trend is very similar to the earlywood density one (Fig. 6). Other studies of climate-growth relationships based on monthly mean temperature seem to have always found lower values of correlation coefficients than in this study (M. Saulnier et al. 2019; Danek et al. 2018; Carrer and Urbinati 2004; Rolland et al. 1998). All the relationships are obviously linear, except maybe the latewood density low elevation relationship, which shows a relatively clear negative sigmoidal trend, not tested in this study.

In Table 4, we split the explained variation for the ring variables into two components, i.e., the low frequency *year* effect, which is equivalent to the linear global warming effect highlighted in Fig. 1, and the high frequency residual effect, equivalent to the part of the between-year temperature variation not explained by this linear global warming effect. We show that the weight of these two components is very different between both elevation levels. The global warming effect

Table 4 Variance decomposition based on the ANOVA model. The values are the proportions of the total variance explained by each effect (low frequency "Global warming" and "high frequency temperature") and by the complete model ("Total," equal to model R-square)

Variance decomposition	High elevation			Low elevation		
	Global warming	High frequency temperature	Total (*R*-square)	Global warming	High frequency temperature	Total (*R*-square)
Ring width	0.24	0.18	0.42	0.74	0.02	0.76
Basal area increment	0.74	0.03	0.77	0.12	0.12	0.23
Earlywood density	0.57	0.06	0.63	0.58	0.07	0.65
Latewood density	0.18	0.33	0.52	0.74	0.06	0.8

alone explains most part of the annual ring linear variation for all the traits except BAI at the low elevation, while it explains much less at the high elevation. More generally, it means that the global warming alone explains all or nearly all of the strong ring width and density linear decrease at the warm bottom of the *Larix decidua* elevational gradient, as well as the earlywood density linear decrease and the BAI linear increase at the top. It means that the global warming is the main driver of larch radial growth decrease during the last 50 years at the warm bottom of the study site. For ring width, latewood width, and latewood density at the high elevation, about half or more of the variation is explained by the high frequency year effect. In this cold-limiting environment, we hypothesize that the high frequency inter-annual effect of climate partly masks the potentially favorable effect of the global warming. Studies at larger geographical scales are necessary to estimate the geographical extension and the variation of such trends.

At the species level, wood density is generally positively related with resistance to drought (Hacke et al. 2001). Nevertheless, the same relationship becomes more complex at the intra-species level and when wood density is decomposed into its annual ring components. Early-, latewood, and even the transition between early- and latewood may play different roles in resistance to drought (Dalla-Salda et al. 2011; Dalla-Salda et al. 2014). Wood microdensity depicts the proportion of cell wall in a small (between micrometers and millimeters) wood volume. A wood density decrease can be explained by a cell wall width decrease, a lumen area (and a tracheid diameter) increase, or a combination of both. For example, according to a multi-site multi-species study in the northern hemisphere, tracheid size has the main effect on earlywood density, while cell wall width determines latewood density (Bjorklund et al. 2017). The consequences on wood hydraulic properties are different. Thus, it is difficult at this stage to infer precisely the effect of a wood density decrease on *Larix decidua* hydraulic properties and on its resistance to drought. Should we expect coming to a hydraulic failure at the bottom of the *Larix decidua* elevational distribution? Direct studies using resistance to drought traits like resistance to cavitation could bring light to the consequences of the observed wood density decrease.

The main environmental variable consistently decreasing with elevation is temperature. However, many other environmental variables vary with elevation. Among them, soil properties sometimes play a very important role on water availability and could explain part of the observed behaviors.

Can we do something to lower the risk of sub-vitality or even mortality? At short term, reducing competition is a way to mitigate the effect of drought (Gleason et al. 2017). At longer term, a possible solution is to stimulate substitution by assisted migration of more drought-adapted origins or species. Up to which elevation will the lower end of the *Larix decidua* distribution climb? Larger geographical studies along continuous elevational gradients are necessary to identify the critical limit, remembering that this elevational threshold will ascent with global warming.

5 Conclusion

The warming trend observed in the Briançon region is faster than in lowland areas and faster for maximum than for minimum temperature. It explains most part of the growth and density decrease observed at the warm bottom of the studied *Larix decidua* elevational gradient. Such recent, fast, and marked decrease can be interpreted as a warning signal for coming diebacks related with increased drought stress during the growing season. A parallel growth increase is observed for BAI at the cold end of the *Larix decidua* elevational gradient, where global warming is supposed to improve growing conditions, but not for ring width and its earlywood and latewood components. BAI and ring width seem to bring relevant complementary information.

Acknowledgments The authors thank the INRAE experimental unit UE GBFOR and the INRAE plateau technique PHENOBOIS (formerly GENOBOIS), INRAE Val de Loire, Orléans (Frédéric Millier), France, for the field and laboratory work along the larch altitudinal gradient. We also want to thanks the municipalities of Villard-St-Pancrace, St-Martin-de-Queyrières, and Puy-St-André, as well as the local forest service, ONF Hautes-Alpes, Briançon, France. The study experimental site "Gradient Altitudinal Mélèze" is part of the "Zone Atelier Alpes."

Authors' Contribution This study is part of an international project about response of mountain forests to climate. Philippe Rozenberg designed and directed the study and analyzed the data. Luc Pâques participated to the design and the direction of the study. With Thibaud Chauvin, Margarita Escobar, Jean-Paul Charpentier, Vladimir Shishov, Jesus Vargas Hernandez, Anne-Sophie Sergent, and Alejandro Martinez-Meier, they planned, organized, and realized the different steps of the study, including the field activities. Frédéric Huard was in charge of the climatic data production and analysis. On top of this, Thibaud Chauvin, Margarita Escobar, and Anne-Sophie Sergent participated to the data analysis. All the authors participated to the design and the writing of the article.

Funding information This project was funded by the following projects: Ministry of Ecology GICC GRAAL 10-MCGOT-GICC-8-CVS-139, France; Region Centre Val-de-Loire Studium Fellowship Vladimir Shishov, Orléans, France, European Union MSCA-RISE-2014-645654-TOPWOOD; and M16A01 ECOS Nord–CONACYT bilateral France-Mexico.

Data availability The datasets generated and/or analyzed during the current study are available in the Data INRAE repository, https://doi.org/10.15454/PPTBPY

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

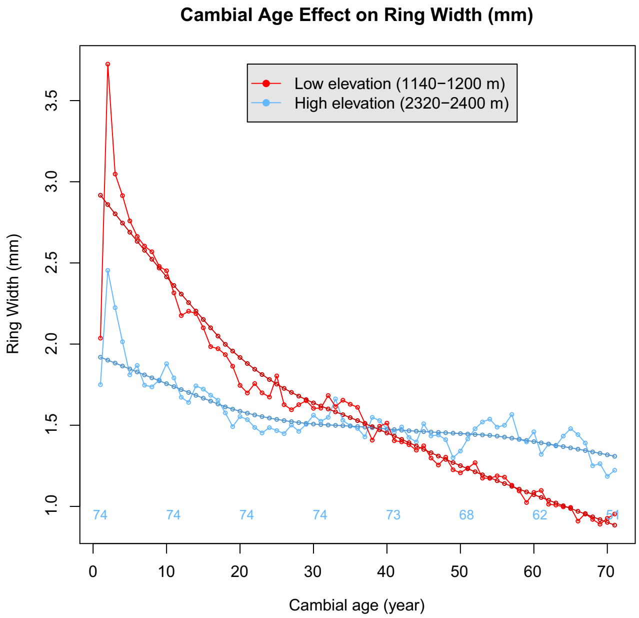


Fig. 4 Cambial age time series for ring width

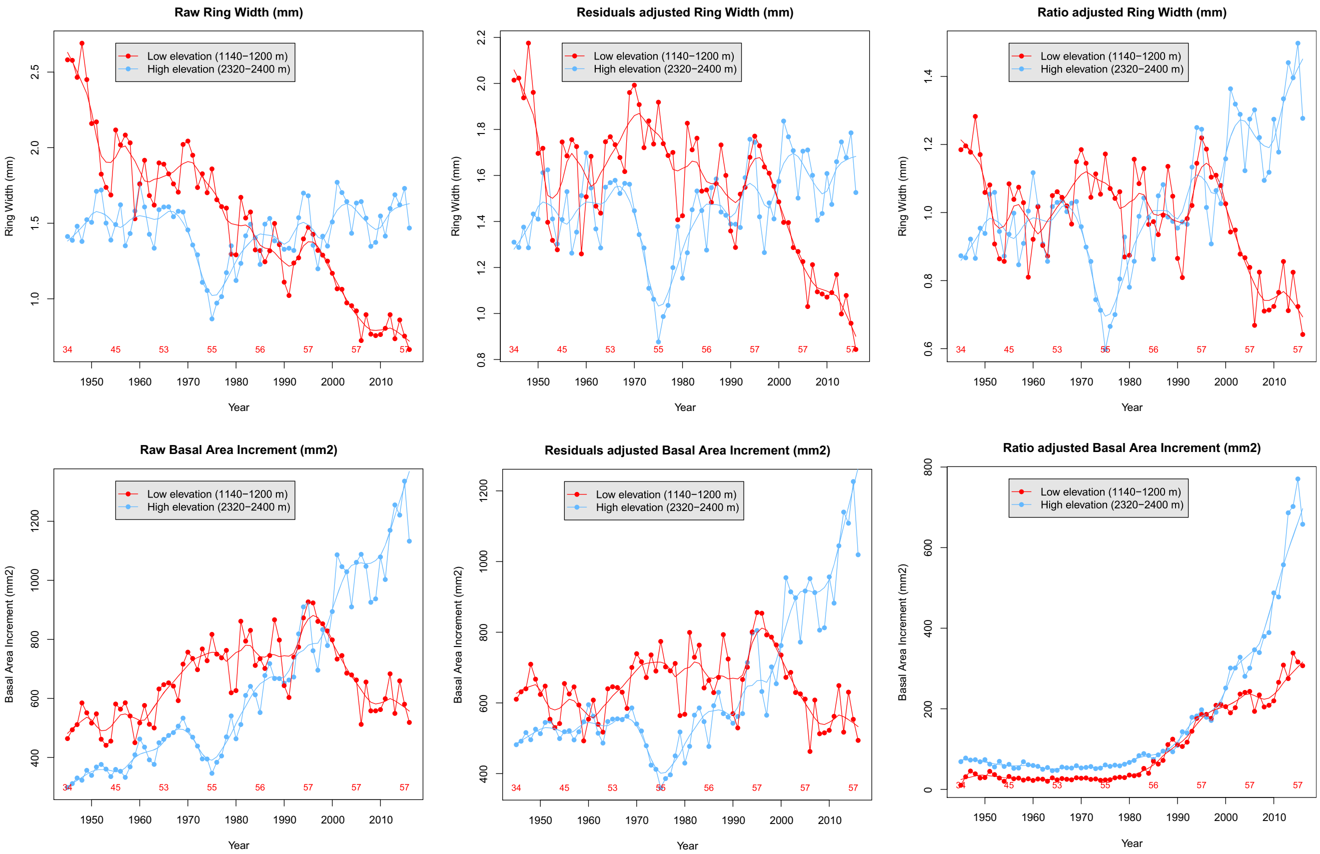


Fig. 5 Comparison of the raw and detrended time series for ring width and BAI

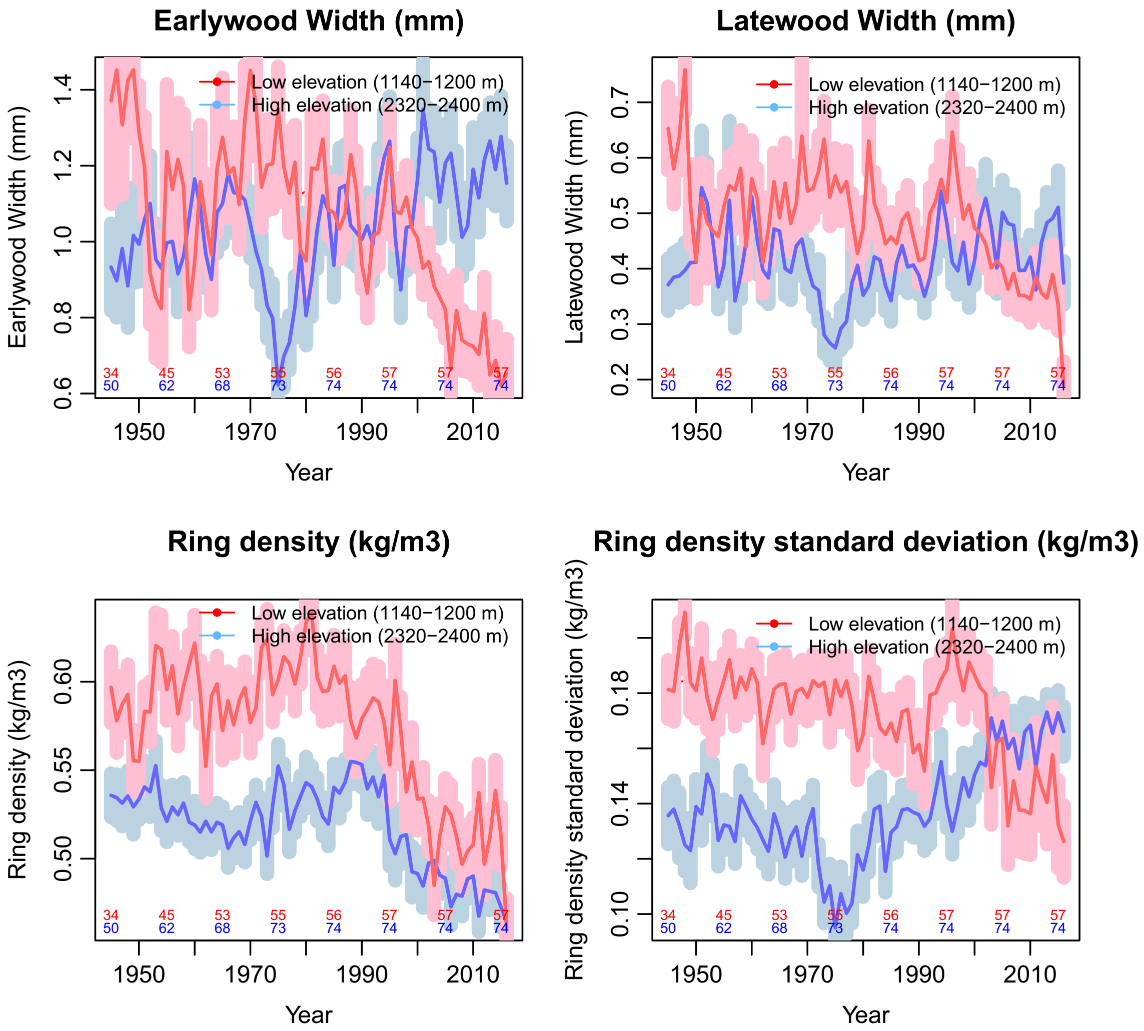


Fig. 6 Same as Fig. 2 of the article for the other four ring variables (earlywood and latewood width, mean ring density, and ring density standard deviation). Average variation across time of four adjusted annual ring variables at the low (red line) and high (blue line) elevation. Light colors represent the 95% confidence interval around the mean. The red and blue numbers are the number of trees used in the calculation of the mean at each year and altitudinal level (same color code)

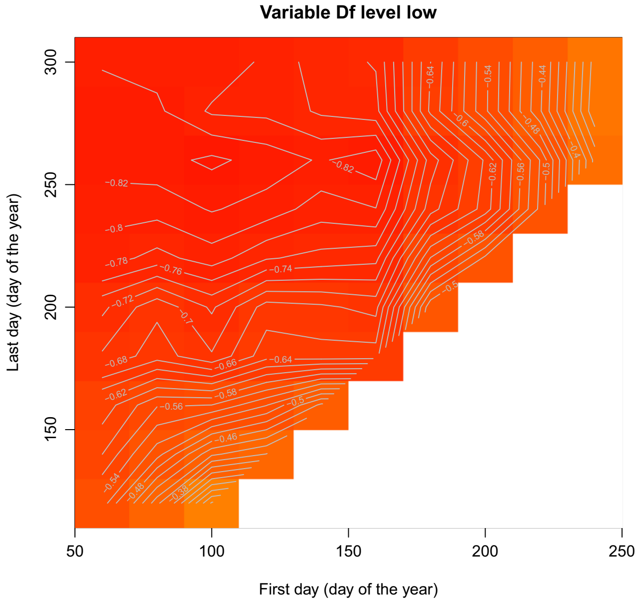
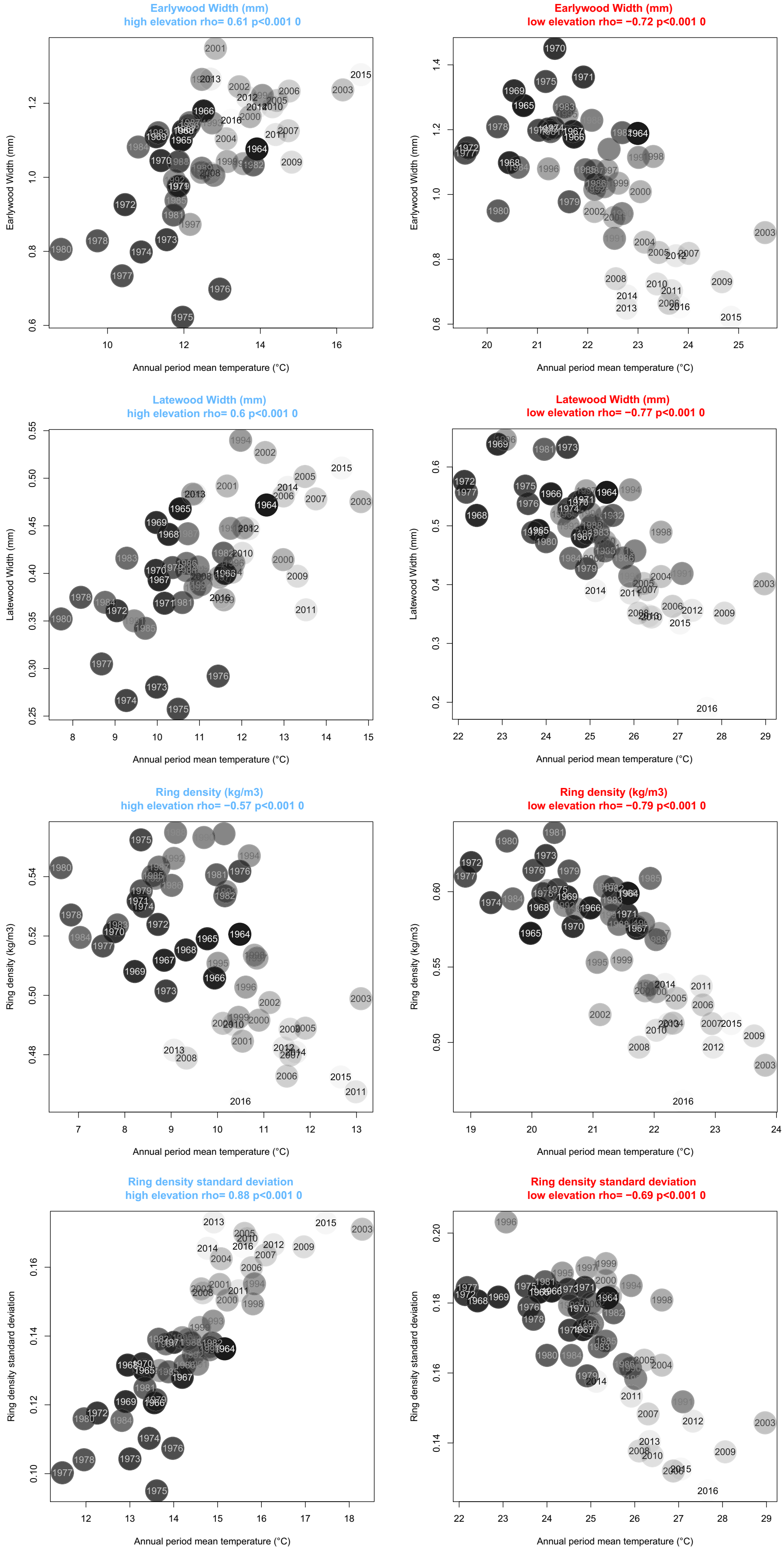


Fig. 7 Heat map and level curves of the correlation coefficients of the response curves obtained for the tested periods for latewood density (Df) at the low elevation level


Earlywood Width (mm)
high elevation rho= 0.61 p<0.001 0
Earlywood Width (mm)
low elevation rho= −0.72 p<0.001 0
Earlywood Width (mm)
Annual period mean temperature (°C)
0.6
0.8
1.0
1.2
1.4
10
12
14
16
20
21
22
23
24
25
Latewood Width (mm)
high elevation rho= 0.6 p<0.001 0
Latewood Width (mm)
low elevation rho= −0.77 p<0.001 0
Latewood Width (mm)
0.25
0.30
0.35
0.40
0.45
0.50
0.55
0.2
0.3
0.4
0.5
0.6
8
9
10
11
12
13
14
15
22
23
24
25
26
27
28
29
Ring density (kg/m3)
high elevation rho= −0.57 p<0.001 0
Ring density (kg/m3)
low elevation rho= −0.79 p<0.001 0
Ring density (kg/m3)
0.48
0.50
0.52
0.54
0.55
0.60
7
8
9
10
11
12
13
19
20
21
22
23
24
Ring density standard deviation
high elevation rho= 0.88 p<0.001 0
Ring density standard deviation
low elevation rho= −0.69 p<0.001 0
Ring density standard deviation
0.10
0.12
0.14
0.16
0.18
0.20
12
13
14
15
16
17
18
22
23
24
25
26
27
28
29

◀ **Fig. 8** Same as Fig. 3 in the article for the other four ring variables (earlywood and latewood width, mean ring density, and ring density standard deviation) and mean maximum temperature of the selected maximizing annual periods at both low and high elevation (periods' table and the relationships for the other ring variables are in the Appendix section). Rho is the Spearman correlation coefficient and p is the associated probability. $p = 0$ corresponds to significance levels below 10–12. The gradient of gray of the year points corresponds to between-year time variation from 1967 (dark gray) to 2016 (light gray)

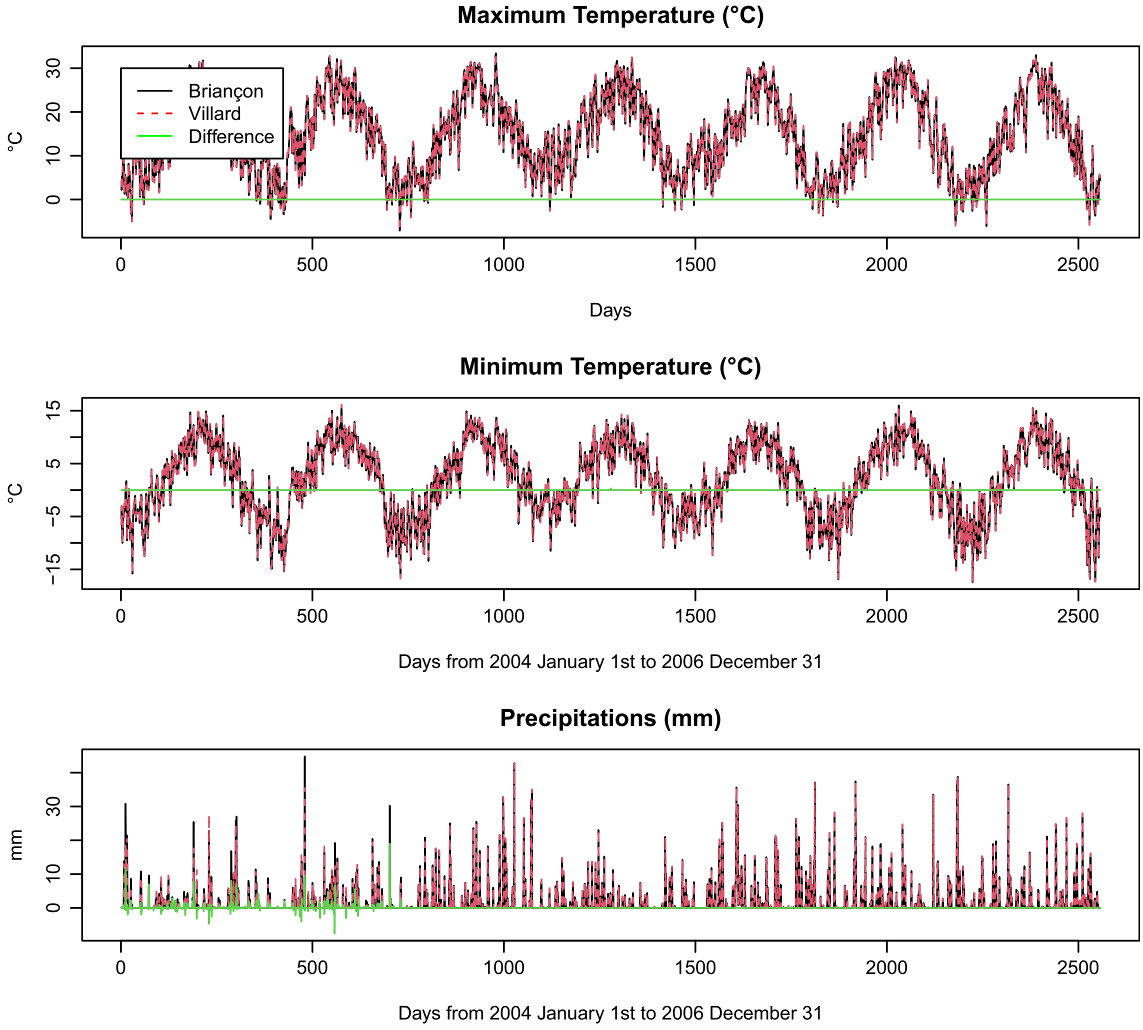


Fig. 9 Météo-France Briançon and Villard-Saint-Pancrace climatic time series during the 2004-2010 period

References

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8):art129. https://doi.org/10.1890/ES15-00203.1

Anfodillo T, Rento S, Carraro V, Furlanetto L, Urbinati C, Carrer M (1998) Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in Larix decidua Miller, Picea Abies (L.) Karst. and Pinus cembra L. Ann Sci For 55(1-2):159–172. https://doi.org/10.1051/forest:19980110

Apiolaza LA (2012) Basic density of radiata pine in New Zealand: genetic and environmental factors. Tree Genet Genomes 8(1):87–96. https://doi.org/10.1007/s11295-011-0423-1

Badalotti A, Anfodillo T, Grace J (2000) Evidence of osmoregulation in Larix decidua at alpine treeline and comparative responses to water availability of two co-occurring evergreen species. Ann For Sci 57(7):623–633. https://doi.org/10.1051/forest:2000146

Baltensweiler W, Weber UM, Cherubini P (2008) Tracing the influence of larch-bud-moth insect outbreaks and weather conditions on larch tree-ring growth in engadine (Switzerland). Oikos 117(2):161–172. https://doi.org/10.1111/j.2007.0030-1299.16117.x

Battipaglia G, Buentgen U, McCloskey SPJ, Blarquez O, Denis N, Paradis L, Brossier B, Fournier T, Carcaillet C (2014) Long-term effects of climate and land-use change on larch budmoth outbreaks in the French Alps. Clim Res 62(1):1–14. https://doi.org/10.3354/cr01251

Biondi F, Qeadan F (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree Ring Res 64(2):81–96. https://doi.org/10.3959/2008-6.1

Bjorklund J, Seftigen K, Schweingruber F, Fonti P, von Arx G, Bryukhanova MV, Cuny HE, Carrer M, Castagneri D, Frank DC (2017) Cell size and wall dimensions drive distinct variability of earlywood and latewood density in Northern Hemisphere conifers. New Phytol 216(3):728–740. https://doi.org/10.1111/nph.14639

Bošeľa M, Petráš R, Sitková Z, Priwitzer T, Pajtík J, Hlavatá H, Sedmák R, Tobin B (2014) Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. Environ Pollut 184 (janvier):211–221. https://doi.org/10.1016/j.envpol.2013.08.036

Britez RD, Manuela A-SS, Meier AM, Bréda N, Rozenberg P (2014) Wood density proxies of adaptive traits linked with resistance to drought in Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). Trees 28(5):1289–1304. https://doi.org/10.1007/s00468-014-1003-4

Büntgen U, Frank D, Liebhold A, Johnson D, Carrer M, Urbinati C, Grabner M, Nicolussi K, Levanic T, Esper J (2009) Three centuries of insect outbreaks across the European Alps. New Phytol 182(4):929–941. https://doi.org/10.1111/j.1469-8137.2009.02825.x

Cailleret M, Nourtier M, Amm A, Durand-Gillmann M, Davi H (2014) Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann For Sci 71(6):643–657. https://doi.org/10.1007/s13595-013-0265-0

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B et al (2017) A synthesis of radial growth patterns preceding tree mortality. Glob Chang Biol 23(4):1675–1690. https://doi.org/10.1111/gcb.13535

Cailleret M, Dakos V, Jansen S, Robert EMR, Aakala T, Amoroso MM, Antos JA et al (2019) Early-warning signals of individual tree mortality based on annual radial growth. Front Plant Sci 9. https://doi.org/10.3389/fpls.2018.01964

Camarero JJ, Gutiérrez E (2017) Wood density of silver fir reflects drought and cold stress across climatic and biogeographic gradients. Dendrochronologia 45 (octobre):101–112. https://doi.org/10.1016/j.dendro.2017.07.005

Carrer M, Urbinati C (2004) Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85(3):730–740

Cerrato R, Cherubini P, Büntgen U, Coppola A, Salvatore MC, Baroni C (2019) Tree-ring-based reconstruction of larch budmoth outbreaks in the Central Italian Alps since 1774 CE. IForest Biogeosci Forestry 12(3):289. https://doi.org/10.3832/ifor2533-012

Charra-Vaskou K, Charrier G, Wortemann R, Beikircher B, Cochard H, Ameglio T, Mayr S (2012) Drought and frost resistance of trees: a comparison of four species at different sites and altitudes. Ann For Sci 69(3):325–333. https://doi.org/10.1007/s13595-011-0160-5

Cook ER, Peters K (1997) Calculating unbiased tree-ring indices for the study of climatic and environmental change. The Holocene 7(3):361–370. https://doi.org/10.1177/095968369700700314

Cook, E. R., L. A. Kairiukstis, éd. 1990. Methods of dendrochronology: applications in the environmental sciences. Springer Netherlands. https://www.springer.com/gp/book/9780792305866.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Dalla-Salda G, Martinez-Meier A, Cochard H, Rozenberg P (2011) Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (Pseudotsuga menziesii (Mirb.)). Ann For Sci 68(4). https://doi.org/10.1007/s13595-011-0091-1

Dalla-Salda G, Fernández ME, Sergent A-S, Rozenberg P, Badel E, Martinez-Meier A (2014) Dynamics of cavitation in a Douglas-fir tree-ring: transition-wood, the lord of the ring? J Plant Hydraulics 1(0):005. https://doi.org/10.20870/jph.2014.e005

Danek M, Chuchro M, Walanus A (2018) Tree-ring growth of larch (Larix decidua Mill.) in the Polish sudetes—the influence of altitude and site-related factors on the climate–growth relationship. Forests 9(11):663. https://doi.org/10.3390/f9110663

Dormont L, Baltensweiler W, Choquet R, Roques A (2006) Larch- and pine-feeding host races of the larch bud moth (Zeiraphera diniana) have cyclic and synchronous population fluctuations. Oikos 115(2):299–307. https://doi.org/10.1111/j.2006.0030-1299.15010.x

Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Glob Chang Biol 24(3):1150–1163. https://doi.org/10.1111/gcb.13925

Eilmann B, Rigling A (2012) Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiol 32(2):178–187. https://doi.org/10.1093/treephys/tps004

Heinz H. Ellenberg. 1988. *Vegetation ecology of Central Europe*. Cambridge University Press. https://books.google.com/books/about/Vegetation_Ecology_of_Central_Europe.html?id=LQNxbuyPxawC.

Esper J, Cook ER, Krusic PJ, Peters K, Schweingruber FH (2003) Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. Tree Ring Res 59(2):81–98

Fonti, Patrick, Elena A Babushkina 2016. Tracheid anatomical responses to climate in a forest-steppe in Southern Siberia. Dendrochronologia, Russian tree-ring research, 39 (septembre): 32-41. https://doi.org/10.1016/j.dendro.2015.09.002.

Fourchy, Pierre. 1952. Ecologie du mélèze particulièrement dans les Alpes françaises. In *Etudes sur l'Ecologie et la Sylviculture du Mélèze (Larix europeae D. C.)*, 13:144. Annales de l'école nationale des eaux et forêts et de la station de recherches et expériences 1. Ecole Nationale des eaux et forêts, Nancy, France. http://hdl.handle.net/2042/33551.

Garbarino M, Lingua E, Weisberg PJ, Bottero A, Meloni F, Motta R (2013) Land-use history and topographic gradients as driving factors of subalpine Larix decidua forests. Landsc Ecol 28(5):805–817. https://doi.org/10.1007/s10980-012-9792-6

Gazol A, Julio Camarero J, Gutiérrez E, Popa I, Andreu-Hayles L, Motta R, Nola P et al (2015) Distinct effects of climate warming on populations of silver fir (Abies alba) across Europe. J Biogeogr 42(6): 1150–1162. https://doi.org/10.1111/jbi.12512

Gleason KE, Bradford JB, Bottero A, D'Amato AW, Fraver S, Palik BJ, Battaglia MA, Iverson L, Kenefic L, Kern CC (2017) Competition amplifies drought stress in forests across broad climatic and compositional gradients. Ecosphere 8(7):e01849. https://doi.org/10.1002/ecs2.1849

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126(4). https://doi.org/10.1007/s004420100628

Impacts du changement climatique: Atmosphère, Températures et Précipitations (2020) Ministère de la Transition écologique et solidaire. Consulté le 24 février 2019. http://www.ecologique-solidaire.gouv.fr/impacts-du-changement-climatique-atmosphere-temperatures-et-precipitations.

Jiao L, Jiang Y, Zhang W, Wang M, Wang S, Liu X (2019) Assessing the stability of radial growth responses to climate change by two dominant conifer trees species in the Tianshan Mountains, northwest China. For Ecol Manag 433 (février):667–677. https://doi.org/10.1016/j.foreco.2018.11.046

Keller T, Guiot J, Tessier L (1997) Climatic effect of atmospheric CO2 doubling on radial tree growth in South Eastern France. J Biogeogr 24(6):857–864. https://doi.org/10.1046/j.1365-2699.1997.00140.x

Kotlarski S, Lüthi D, Schär C (2015) The elevation dependency of 21st century European climate change: an RCM ensemble perspective. Int J Climatol 35(13):3902–3920. https://doi.org/10.1002/joc.4254

Latreille A, Davi H, Huard F, Pichot C (2017) Variability of the climate-radial growth relationship among Abies alba trees and populations along altitudinal gradients. For Ecol Manag 396(Supplement C): 150–159. https://doi.org/10.1016/j.foreco.2017.04.012

Lévesque M, Saurer M, Siegwolf R, Eilmann B, Brang P, Bugmann H, Rigling A (2013) Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Glob Chang Biol 19(10): 3184–3199. https://doi.org/10.1111/gcb.12268

Marqués L, Camarero JJ, Gazol A, Zavala MA (2016) Drought impacts on tree growth of two pine species along an altitudinal gradient and their use as early-warning signals of potential shifts in tree species distributions. For Ecol Manag 381 (décembre):157–167. https://doi.org/10.1016/j.foreco.2016.09.021

Martinez Meier AG, Sanchez L, Dalla Salda G, Pastorino MJM, Gautry JY, Gallo LA, Rozenberg P (2008) Genetic control of the tree-ring response of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) to the 2003 drought and heat-wave in France. Ann For Sci 65(1):102

Mothe F, Duchanois G, Zannier B, Leban JM (1998) Microdensitometric analysis of wood samples: data computation method used at INRA-ERQB (CERD programme). Annales des Sciences Forestieres 55(3):301–313

Mountain Research Initiative EDW Working Group, Pepin N, Bradley RS, Diaz HF, Baraer M, Caceres EB, Forsythe N et al (2015) Elevation-dependent warming in mountain regions of the world. Nat Clim Chang 5(5):424–430. https://doi.org/10.1038/nclimate2563

Obojes N, Meurer A, Newesely C, Tasser E, Oberhuber W, Mayr S, Tappeiner U (2018) Water stress limits transpiration and growth of European larch up to the lower subalpine belt in an inner-alpine dry valley. New Phytol 220(2):460–475. https://doi.org/10.1111/nph.15348

Peters RL, Speich M, Pappas C, Kahmen A, von Arx G, Pannatier EG, Steppe K, Treydte K, Stritih A, Fonti P (2019) Contrasting stomatal sensitivity to temperature and soil drought in mature alpine conifers. Plant Cell Environ 42(5):1674–1689. https://doi.org/10.1111/pce.13500

Polge H (1978) Fifteen years of wood radiation densitometry. Wood Sci Technol 12(3):187–196. https://doi.org/10.1007/BF00372864

Pretzsch H, Biber P, Schütze G, Kemmerer J, Uhl E (2018) Wood density reduced while wood volume growth accelerated in Central European forests since 1870. For Ecol Manag 429 (décembre): 589–616. https://doi.org/10.1016/j.foreco.2018.07.045

Primicia I, Camarero JJ, Janda P, Čada V, Morrissey RC, Trotsiuk V, Bače R, Teodosiu M, Svoboda M (2015) Age, competition, disturbance and elevation effects on tree and stand growth response of primary Picea abies forest to climate. For Ecol Manag 354 (octobre): 77–86. https://doi.org/10.1016/j.foreco.2015.06.034

Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. Theor Appl Climatol 91(1):27–34. https://doi.org/10.1007/s00704-007-0296-2

Riou-Nivert, Philippe. 2001. *Le mélèze*. Les guides du sylviculteur. Paris: Institut pour le Développement Forestier (IDF).

Rolland C, Petitcolas V, Michalet R (1998) Changes in radial tree growth for Picea abies, Larix decidua, Pinus cembra and Pinus uncinata near the alpine timberline since 1750. Trees 13(1):40–53. https://doi.org/10.1007/PL00009736

Rossi S, Cairo E, Krause C, Deslauriers A (2014) Growth and basic wood properties of black spruce along an alti-latitudinal gradient in Quebec, Canada. Ann For Sci 72(1):77–87. https://doi.org/10.1007/s13595-014-0399-8

Rozenberg P, Van Loo J, Hannrup B, Grabner M (2002) Clonal variation of wood density record of cambium reaction to water deficit in *Picea abies* (L.) Karst. Ann For Sci 59(5-6):533–540

Rozenberg P et al (2020) Climate warming differently affects *Larix decidua* ring formation at each end of a French Alps altitudinal gradient. V1. Data INRAE repository. [Dataset]. https://doi.org/10.15454/PPTBPY

Saulnier M, Roques A, Guibal F, Rozenberg P, Saracco G, Corona C, Edouard J-L (2017) Spatio-temporal heterogeneity of larch budmoth outbreaks in the French Alps over the last 500 years. Can J For Res, janvier. https://doi.org/10.1139/cjfr-2016-0211

Saulnier M, Corona C, Stoffel M, Guibal F, Edouard J-L (2019) Climate-growth relationships in a *Larix decidua* Mill. network in the French Alps. Sci Total Environ 664 (mai):554–566. https://doi.org/10.1016/j.scitotenv.2019.01.404

Schulze E-D, Mischì G, Asche G, Börner A (2007) Land-use history and succession of Larix decidua in the Southern Alps of Italy–an essay based on a cultural history study of Roswitha Asche. Flora - Morphology, Distribution, Functional Ecology of Plants 202(8): 705–713. https://doi.org/10.1016/j.flora.2007.05.003

Schuster R, Oberhuber W (2013) Drought sensitivity of three co-occurring conifers within a dry inner alpine environment. Trees 27(1):61–69. https://doi.org/10.1007/s00468-012-0768-6

Sidor CG, Popa I, Vlad R, Cherubini P (2015) Different tree-ring responses of Norway spruce to air temperature across an altitudinal gradient in the Eastern Carpathians (Romania). Trees 29(4):985–997. https://doi.org/10.1007/s00468-015-1178-3

Solár J (2013) Effect of climate change on mountain pine distribution in western tatra mountains. Climate Change - Realities, Impacts Over Ice Cap, Sea Level and Risks. https://doi.org/10.5772/54724

Taeger S, Zang C, Liesebach M, Schneck V, Menzel A (2013) Impact of climate and drought events on the growth of Scots pine (Pinus sylvestris L.) provenances. For Ecol Manag 307:30–42. https://doi.org/10.1016/j.foreco.2013.06.053

Tse-ring, Karma, Eklabya Sharma, Nakul Chettri, Arun Shrestha. 2010. Climate change vulnerability of mountain ecosystems in the Eastern Himalayas. Climate Change Impact and Vulnerability in the Eastern Himalayas. GPO Box 3226, Kathmandu, Khumaltar, Lalitpur, Nepal: International Centre for Integrated Mountain Development.

Vanoni M, Bugmann H, Nötzli M, Bigler C (2016) Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. For Ecol Manag 382 (décembre):51–63. https://doi.org/10.1016/j.foreco.2016.10.001

Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric For Meteorol 248 (janvier):60–69. https://doi.org/10.1016/j.agrformet.2017.09.005

Vospernik S, Nothdurft A (2018) Can trees at high elevations compensate for growth reductions at low elevations due to climate warming? Can J For Res 48(6):650–662. https://doi.org/10.1139/cjfr-2017-0326

Wang Q, Fan X, Wang M (2014) Recent warming amplification over high elevation regions across the globe. Clim Dyn 43(1):87–101. https://doi.org/10.1007/s00382-013-1889-3

Yin D, Xu D, Tian K, Xiao D, Zhang W, Sun D, Sun H, Zhang Y (2018) Radial growth response of Abies georgei to climate at the upper timberlines in Central Hengduan Mountains, Southwestern China. Forests 9(10):606. https://doi.org/10.3390/f9100606

Zhu L, Cooper DJ, Yang J, Zhang X, Wang X (2018) Rapid warming induces the contrasting growth of Yezo spruce (Picea jezoensis var. microsperma) at two elevation gradient sites of northeast China. Dendrochronologia 50 (août):52–63. https://doi.org/10.1016/j.dendro.2018.05.002

Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. Berlin, German Federal Republic: Springer-Verlag.

Zobel BJ (1989) Wood variation: its causes and control. Springer

Zobel B, Sprague J (1995) Juvenile wood in forest trees. Springer-Verlag, Berlin Heidelberg New York