Temperature rather than individual growing period length determines radial growth of sessile oak in the Pyrenees

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ABSTRACT

Tree growth and leaf phenology are both affected by global warming. Mountain ecosystems are of paramount importance for studying phenological and growth responses of trees to the gradual variation of temperature. However, the relationship between growing season length and tree growth has been little studied at the level of individual trees. Here, we investigated the relationships between leaf phenology, growing degree-days and radial growth of sessile oaks growing in nine populations along an elevational gradient of 1500 m in the French Pyrenees. In each population, leaf unfolding in spring and leaf coloration in autumn were monitored between 2005 and 2015 on 25-30 trees having contrasting spring phenology (*i.e.* early *vs.* late flushing trees). These trees were cored in 2013 to analyse annual tree-ring widths. While trees displayed consistent phenological ranks for both leaf unfolding and leaf coloration within their population over the years, the growing period length decreased with increasing elevation, from about 210 days at the lowest elevation (131 m a.s.l.) to 140 days at the highest elevation (1630 m a.s.l.). For a given year, individual leaf coloration dates correlated positively with leaf unfolding dates at lower elevations, but negatively at higher elevations. Radial growth was positively correlated with growing degree-days at higher elevations, but negatively correlated at lower elevations, likely because higher temperatures are often associated with severe droughts in the lowlands of this region. No clear relationship was found between growing period length and radial growth of oaks within their population. This indicates that climatic conditions during the growing period have a more important impact on the secondary growth of sessile oaks than the growing period length. Our findings suggest that the lengthening of the growing period of trees in response to global warming does not necessarily lead to higher radial growth and productivity.

1. Introduction

Ecosystems of temperate regions respond to the cyclic and seasonal changes of temperature. Trees of boreal and temperate forests have developed a period of rest, the dormancy, during the cool winter season. A period of active growth begins in late winter or spring when climatic conditions become more favourable and lasts until the end of the growing season in autumn, marked by leaf senescence for deciduous species. The timing when deciduous trees start and end their photosynthetic activity appears to have a strong impact on tree growth and thus on carbon fluxes at the global scale (Richardson et al., 2009; Richardson et al., 2010). Because tree phenology is particularly sensitive to temperature (Lieth, 1974), global warming causes pronounced phenological shifts (Menzel et al., 2020; Vitasse et al., 2021) and thus

major changes in water and carbon fluxes (Richardson et al., 2013). However, it is unclear to what extent these phenological changes impact productivity at the tree level, as tree growth is also sensitive to other abiotic and edaphic factors. For example, a long period of high vapour pressure deficit reduces stomatal conductance and photosynthesis, and hence carbon assimilates (Grossiord et al., 2020).

The number of studies documenting plant phenological shifts in response to climate change has massively increased over the recent years (reviewed in Piao et al., 2019). Thus, an extension of the growing season due to increasing temperature has been reported in numerous studies (Meier et al., 2021; Menzel & Fabian, 1999; Morin et al., 2010; Piao et al., 2019; Schwartz, 2013). However, phenological studies have rarely focused on individual trees but rather on tree populations. For example, only a few studies focusing on spring and autumn leaf phenology have

Table 1

Description of the study sites in the Gave valley in the French central Pyrenees. Elevation is indicated in meters above sea level (m a.s.l.). North (N), south (S), west (W) and east (E) refer to the cardinal points for latitude, longitude and aspect of the slope. Average annual temperatures were estimated over the years 2005-2007, 2009 and 2011-2013 (corresponding to the years with complete temperature data for all the sites).

Site	Elevation (m a.s.l.)	Latitude	Longitude	Aspect	Average annual temperature (°C)
Laveyron	131	43°45' N	00°13' W	lowland	13.2
Ibos	387	43°15' N	00°00' W	S	12.6
Adé	427	43°08' N	00°00' W	S	12.4
Pierrefitte	627	42°56' N	00°03' W	S	11.7
Chèze	803	42°55' N	00°02' W	S	11.0
Bourdalats	1082	42°54' N	00°06' W	S	9.8
Gèdre bas	1235	42°47' N	00°01' E	S	9.7
Gèdre haut	1349	42°47' N	00°02' E	S	8.7
Péguère	1630	42°52' N	00°07' W	S	7.7

reported that individual trees maintain their phenological rank from year to year within the population – *i.e.* it is generally the same trees that flush the earliest year after year (Crawley & Akhteruzzaman, 1988; Delpierre et al., 2017). Furthermore, few studies have attempted to link leaf phenology with tree growth rates (e.g Čufar et al. 2015; Delpierre et al. 2017; Kolář et al. 2016). In particular, our understanding on how the relationship between leaf phenology and radial growth responds to temperature along elevation is limited. In this respect, mountain eco-systems are particularly interesting to study these effects, since the drastic change of topography and elevation offers a large gradient of temperature over short distance. Here, we took advantage of a strong temperature gradient induced by an elevational gradient of 1500 m to study these effects on nine populations of sessile oaks in the Pyrenees.

Sessile oak is a species of major ecological importance in European forests (Leuschner & Ellenberg, 2017b), which has a high cultural and economic value for several centuries (Eaton et al., 2016). It is considered a promising species for future forests in central and southern Europe due to its high resistance and resilience to drought (Leuschner & Ellenberg, 2017a). In this study, we aimed at understanding the effects of temperature on the relationship between leaf phenology and radial growth of sessile oak by combining observations of leaf unfolding in spring and leaf coloration in autumn with tree-ring widths measured at the individual tree level. Leaf unfolding and leaf coloration dates of 262 trees with contrasting spring phenology (*i.e.* either early or late flushing trees) were monitored across nine sites in the French Pyrenees during the period 2005-2015. Among them, 217 individuals were cored in 2013 for tree-ring analysis. To document the relationships between temperature, leaf phenology and radial growth, we addressed the following questions: (1a) Is the inter-annual leaf phenological sequence in spring and autumn consistent among individuals of sessile oak? Within populations, we expected the early flushing trees to be the earliest every year and similarly for leaf coloration (hypothesis 1a). (1b) Is there an intra-annual correlation between leaf unfolding and leaf coloration dates? We hypothesised that early (or late) flushing trees would be also early (respectively late) for leaf coloration within a given year (hypothesis 1b). (2) Does the length of the growing season increase with warmer temperature? We expected an extension of the growing season with increasing temperatures (hypothesis 2). (3a) Does radial growth increase with higher growing degree-days? We expected radial growth to increase with higher growing degree-days within populations, but potentially not for all elevations because precipitation may become a more important driver of growth than temperature at low elevations (hypothesis 3a). (3b) Is radial growth correlated with growing period length at the individual level? We anticipated to find an increased radial growth of individuals displaying a longer growing period within their population (hypothesis 3b).

2. Material and methods

2.1. Species and study area

Sessile oak (*Quercus petraea* (Matt.) Liebl.) is a temperate deciduous oak species widely spread across Europe, ranging from Great Britain to the North of the Iberian Peninsula and from eastern Poland to the Atlantic Ocean (Eaton et al., 2016). In the Pyrenees, sessile oaks are found from low elevation, where they form almost pure stands, up to 1800 m a.s.l. where the trees are more scattered (Alberto et al., 2011). The species naturally grows on south-facing slopes and prefers acidic soils (Eaton et al., 2016; Leuschner & Ellenberg, 2017b). Sessile oak is known as a rather drought tolerant species preferring well-drained soils.

The study area is located in the French central Pyrenees, in the Gave valley (south-west of France). It is located at the southern limit of the sessile oak distribution, which makes it particularly interesting for the study of phenological and growth responses to climatic conditions (Vitasse et al., 2009b). Nine natural populations of sessile oaks were monitored along an elevational transect ranging from 131 to 1630 m a.s.l. with increasing elevations from north to south, and with an elevation gain of *ca.* 200 m between populations. The transect was 109 km long with the eight highest sites comprised within 52 km. The lowest site (Laveyron; 131 m a.s.l.) was located 57 km further north to represent the population in the lowland, which grows in the warmest conditions (see Table 1 for the exact position of the sites and Fig. A.1 for a map of the study). The study region is characterised by a temperate oceanic climate (Dantec et al., 2015; Vitasse et al., 2009a). The average annual temperature ranges from 7.7°C at the highest elevation (1630 m a.s.l.) to 13.2°C at the lowest elevation (131 m a.s.l.), which represents an average decrease of –0.37°C per 100 m increase in elevation (Table 1). There is a generally increasing trend of temperature since the 1980s but no significant increase over the years of the study. The mean annual precipitation in the lowland of the study area was 1047 mm during the period 1981-2010 (Tarbes, 43°11′ N, 0°00′ E, 360 m a.s.l., Météo France 2021). The sites were located on different slopes within the Gave valley (see Fig. A.1) but all on south-facing slopes, with the exception of the lowest site, Laveyron at 131 m a.s.l., which has no particular exposure as it as situated in the plain in rather flat terrain.

2.2. Phenological data

From 2005 to 2015, leaf unfolding in spring was observed for *ca.* 25-30 dominant adult trees per site. No monitoring was conducted in 2008 and 2013. Since the monitoring has been setup for different projects over the time, phenological data are not available for all the years on all the trees. However, the dataset covers 262 trees along the elevational gradient, with an average of 5-6 years of observations per tree. Within
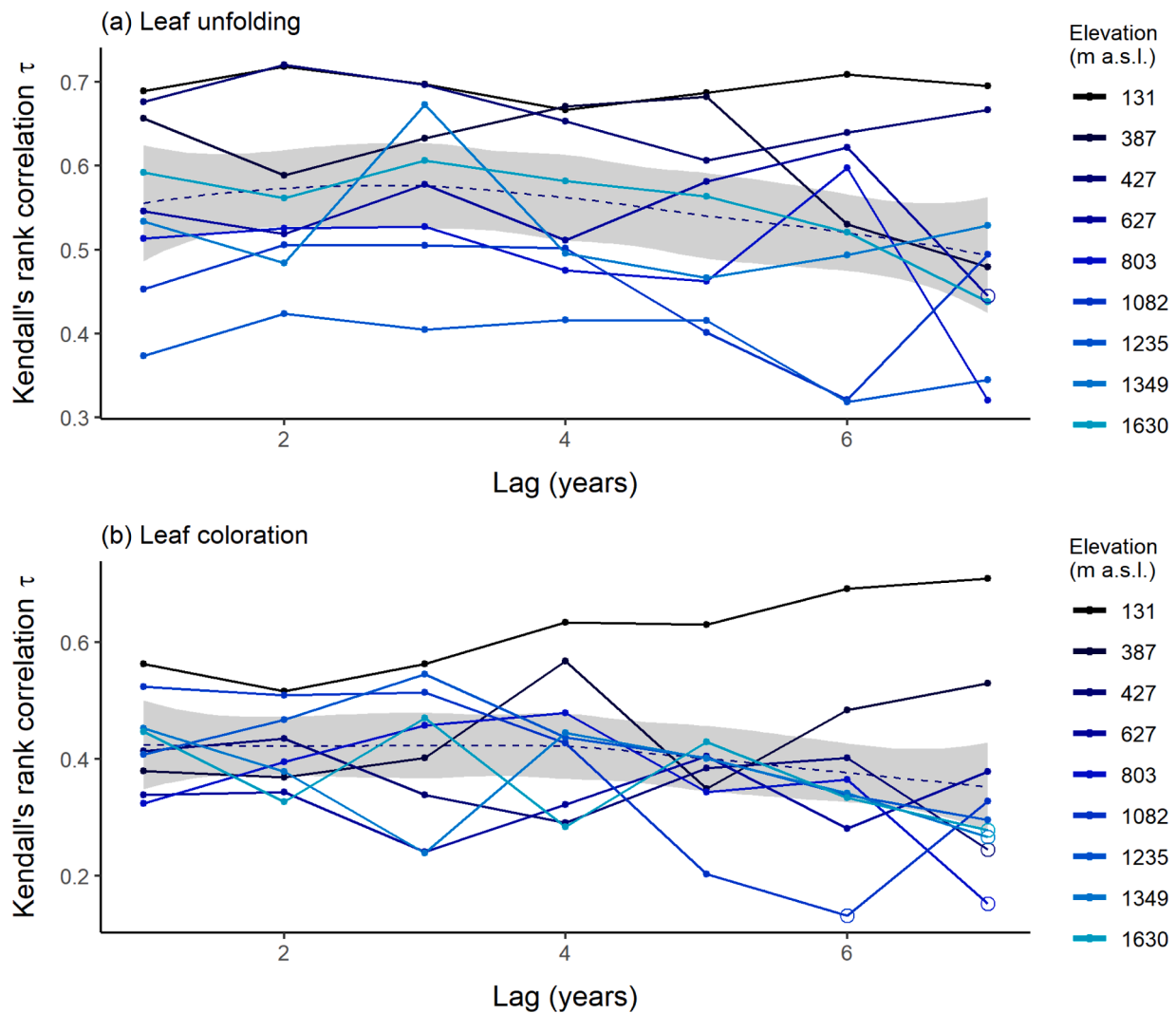
Fig. 1. Repetition of tree phenological ranks in sessile oak within their elevation for time lags from 1 to 7 years: (a) leaf unfolding (LU) date and (b) leaf coloration (LC) date. Significant τ values (P < 0.05) are shown as dots and non-significant values as open circles. Data from 258 tree individuals are shown spread over nine elevations (see legend) and monitored over the periods 2005-2007, 2009-2012 and 2014-2015 (9 years) for LU; 2005-2007 and 2009-2012 (7 years) for LC. One point represents one τ value estimated for all combinations of ranks of time lag n (*e.g.* lag 1 includes the comparisons 2005-2006, 2006-2007, 2009-2010, etc.) within an elevation. Smoothing lines are based on local polynomial regressions (dark blue dashed line) with 95% confidence intervals (grey area). See Methods for more details on the computation of Kendall's rank correlation τ.

each site, trees were chosen to be either particularly early or late in their leaf unfolding date to include the broadest variability in leaf unfolding dates. Stages of leaf unfolding were recorded every 5-10 days during the period of spring phenology. The date of leaf unfolding was recorded as the day of year (DOY) when 50% of the leaves of a tree were out of the bud. Because this stage may have occurred before or after a day of observation, the date of leaf unfolding was linearly interpolated for each tree between the two monitoring dates that encompass this stage (Alberto et al., 2011; Vitasse et al., 2009a). Leaf coloration was recorded from 2005 to 2012 (no data in 2008). Similarly, the interpolated value of leaf coloration date (in DOY) corresponded to the stage when 50% of the leaves of a tree were either coloured or shed, following the protocol set in Vitasse et al. (2009b). The growing period length was defined as the number of days between the dates of leaf unfolding and leaf coloration.

2.3. Ring-width data

In September 2013, 217 trees monitored for phenology were cored at a height of ca. 130 cm on the downhill side of the slope to avoid tension wood. One core per tree was extracted in each selected population. The

site at 387 m a.s.l. was dismissed because of its similarity with the site at 427 m a.s.l. in terms of elevation, temperature and topography. Dendrochronological data overlap with phenological data for 196 trees with an average of five overlapping years. Tree cores were then air dried, mounted, and sanded. The ring widths were finally measured in the lab to the nearest 0.01 mm on a Lintab 5 measuring system along with the TSAP-Win software (version 4.81, both from RINNTECH, Heidelberg, Germany). One chronology was established per site (16 to 30 trees per chronology) and samples were visually compared with the TSAP-Win software and statistically crossdated with the software COFECHA (Holmes, 1983). Because the trees were originally monitored for phenology since 2005 (see for example Vitasse et al., 2009a) and to follow the individuals already monitored, no particular size criteria was used for the choice of trees to core (see section 2.2 *Phenological data* for more details on the selection of the individuals) but the vast majority of the trees were either dominant or co-dominant and only three individuals had a lower position in the canopy.

To account for tree-specific trends in the tree-ring series (*e.g.* due to tree age and size), different detrending methods were applied to each ring-width series (*e.g.* spline, Friedman's super smoother) with the
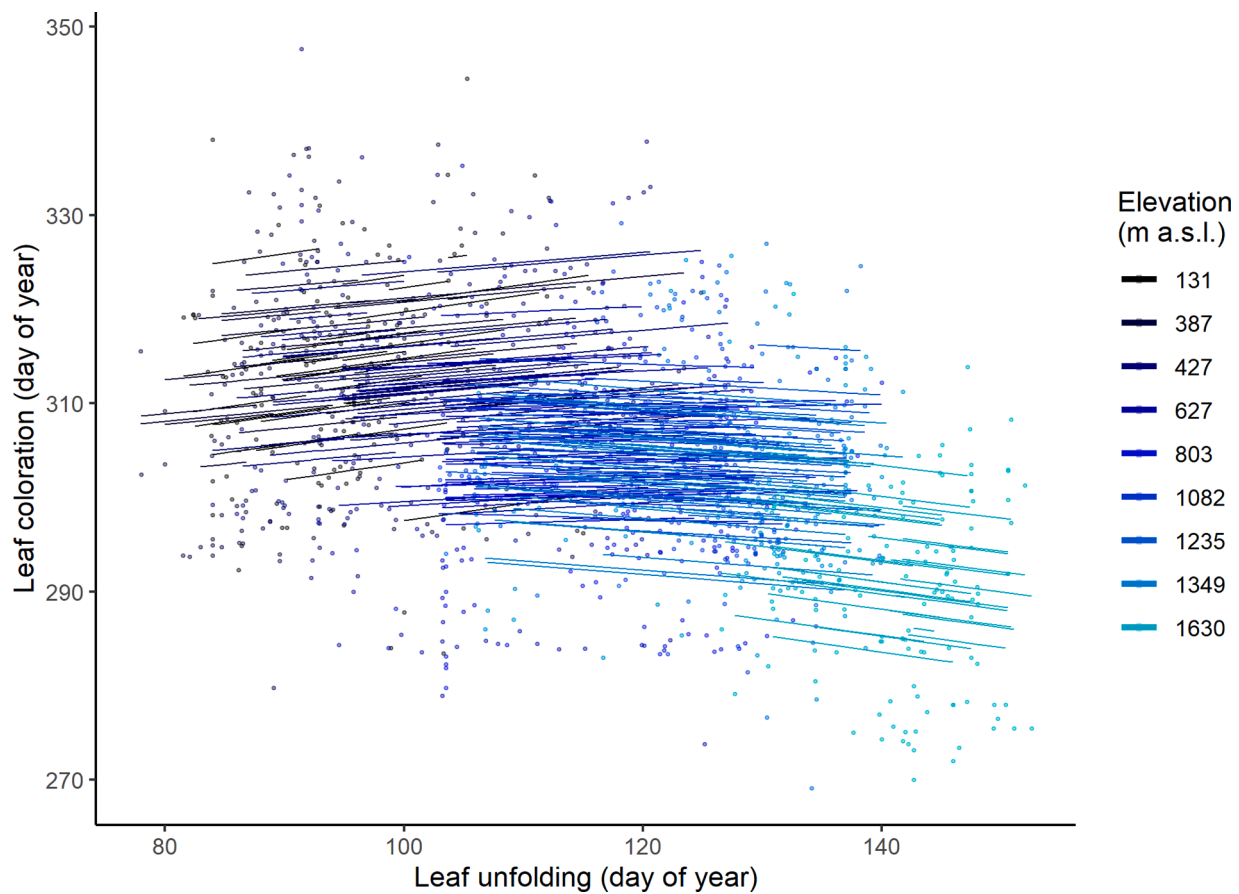
Fig. 2. Shift in the relationship between leaf unfolding (LU) and leaf coloration (LC) dates at the individual tree level depending on elevation. Data from 261 tree individuals of sessile oak are shown spread over nine elevations (see legend) and monitored over the periods 2005-2007 and 2009-2012 (7 years). One dot represents an observation of LU and LC for one tree and one year (1265 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in Table A.2 and following Eq. (2).

package *dplR* (version 1.7.0; Bunn, 2008) from the software R (R Core Team, 2019). After comparing the different detrending methods, the spline method with frequency response of 0.50 at a wavelength of 0.67 × series length in years resulted in the best visual fit of the series and was therefore used to calculate ring width indices (RWI). It removes the age trend but keeps the year-to-year variability. However, the detrending process has also the disadvantage of removing the shift in absolute growth rates along the elevational gradient. We therefore also used the raw ring width (RW) values without detrending in our analyses to assess the actual effect of elevation on growth irrespective of the age of the tree (see section 2.5 *Statistical analyses*).

2.4. Temperature data

Temperature was recorded hourly at every site during the whole duration of the study using temperature loggers (Hobo pro H23-002, Onset, USA). The sensors were set up at 1.50 m above ground in a meadow close to the forest border at each site. The sensors were protected from rain and solar radiation by a white solar radiation shield (RS3B, Onset, USA). In case of missing temperature records, temperature data were gap filled by linear models with data from the closest site (see Caignard 2018, for more details). For the site at 1630 m a.s.l., six months of data were missing in 2010 and the data (phenology and radial growth) corresponding to this period were therefore excluded from the analyses. Hence, the daily average temperature was extracted from the hourly measures.

As a proxy for temperature, the growing degree-days (GDD, in°C•days) were calculated per year by accumulating the daily mean

temperature above a threshold of 5°C during all days in the year from 1 January to 31 December, following the equation:

$$GDD = \sum_{DOY=1}^{DOY=365} f\left(T_{daily\ mean_{DOY}}\right) \tag{1}$$

with

$$f\left(T_{daily\ mean_{DOY}}\right) = \begin{cases} T_{daily\ mean_{DOY}} - 5\,°C, & T_{daily\ mean_{DOY}} \geq 5\,°C \\ 0\,°C, & T_{daily\ mean_{DOY}} < 5\,°C \end{cases}$$

where $T\ daily\ mean_{DOY}$ is the mean temperature in°C for each DOY. A 5°C threshold has been commonly used in other phenological studies on trees beyond which growth can be stimulated (*e.g.* Fu et al. 2013 Primault 1953; Vitasse et al. 2019). Because the leaf unfolding and leaf coloration dates varied considerably across elevations, we decided to include the entire year in the GDD index. Using this index rather than the annual average temperature is more relevant to get a value representative of the potential days of growth (*e.g.* negative temperature days do not decrease the index as in the case of the annual average temperature).

2.5. Statistical analyses

The rank of leaf unfolding was defined, per population, by classifying the individuals according to their date of leaf unfolding and by attributing them a rank. One new ranking was done for each year of data. To assess the consistency of inter-annual leaf unfolding dates, the population-specific ranks were then compared between pairs lagged from one to seven years using Kendall's rank correlation τ (Kendall,
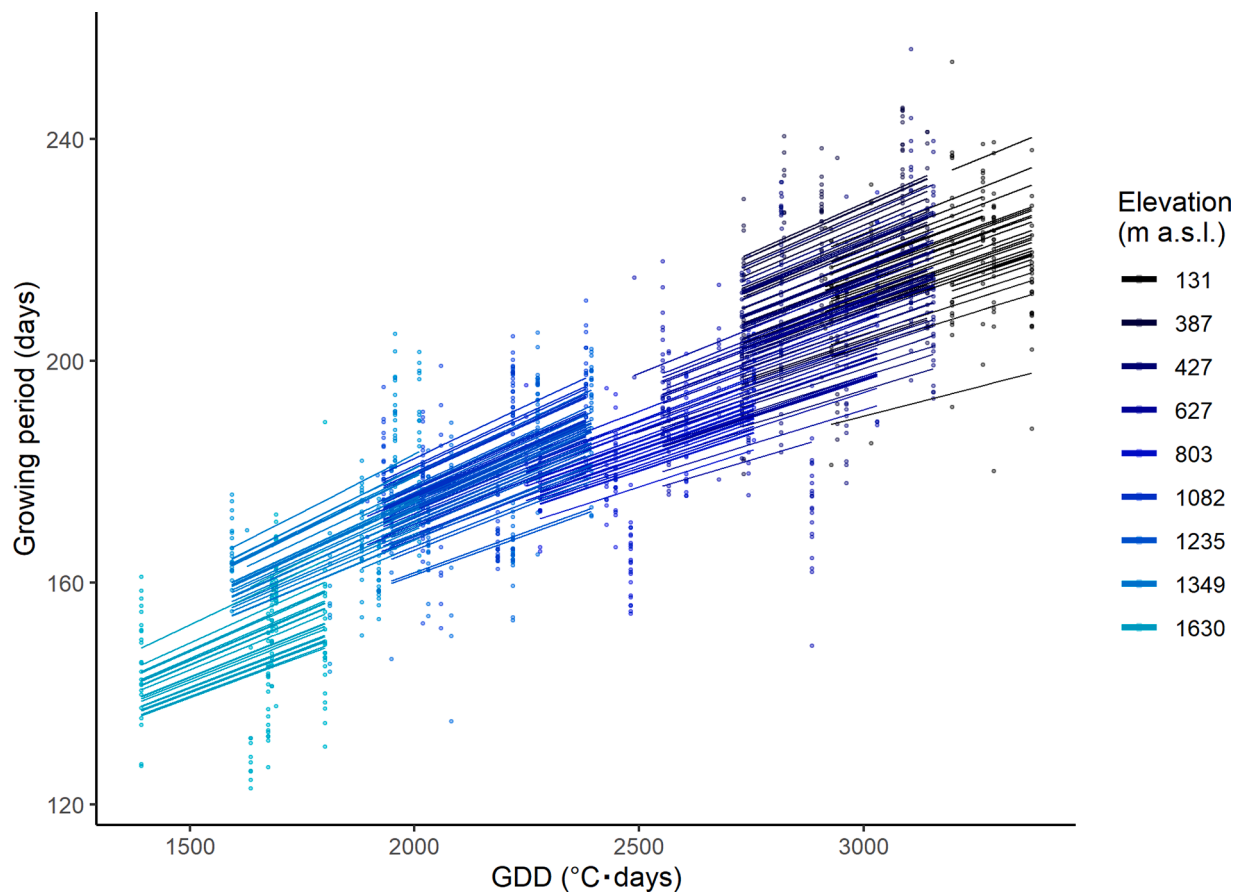
Fig. 3. Increase in growing period (GP) length with increasing accumulated growing degree-days (GDD) and decreasing elevation. Phenological data from 261 tree individuals of sessile oak are shown spread over nine elevations (see legend) and monitored over the periods 2005-2007 and 2009-2012 (7 years). GDD includes accumulated temperatures above 5°C from 1 January to 31 December (Eq. 1). One dot represents an observation of GP and GDD for one tree and one year (1264 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in Table A.3 and following Eq. (2).

1938). For example, lag one represented all the pairs of years with a difference of one year. We chose to limit the time lag to seven years because of the reduced sample size over seven years (lag seven is represented by only two pairs of years *i.e.* 2005-2012 and 2007-2014, see section 2.2 *Phenological data* for more details on the available data). We computed one τ value per population (25-30 individuals) and lag. The same analysis was computed for leaf coloration date. We then calculated the mean of all lags per elevation (*i.e.* same population) to summarize the results.

To test the hypotheses 1b, 2, 3a and 3b, we fitted six linear mixed-effects models. Mixed-effects models were chosen because phenological data and tree-ring width data per individual tree were not independent between the years. The mixed-effects models included a main effect for predictor variables x and elevation (m a.s.l.) and their interaction:

$$y_{ij} = (\beta_0 + u_{0,i}) + (\beta_1 + u_{1,i}) \cdot x_{ij} + (\beta_2 + u_{2,i}) \cdot elevation_i$$
$$+ (\beta_3 + u_{3,i}) \cdot x_{ij} \cdot elevation_i + \varepsilon_{ij} \quad (2)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

$$u_{0,i} \sim N(0, \sigma_{u0}^2), \ u_{1,i} \sim N(0, \sigma_{u1}^2), \ u_{2,i} \sim N(0, \sigma_{u2}^2), \ u_{3,i} \sim N(0, \sigma_{u3}^2),$$

where y_{ij} is the response variable (*i.e.* date of leaf coloration, length of growing period, RW or RWI) of tree i in year j, β are the coefficients, x is a predictor variable (*i.e.* date of leaf unfolding, GDD, or length of growing period), and elevation (m a.s.l) is the average elevation of the population to which tree i belongs. The errors (ε) and random effects (u_0,

u_1, u_2, u_3) follow a normal distribution with expected value 0 and variances σ^2, σ_{u0}^2, σ_{u1}^2, σ_{u2}^2, and σ_{u3}^2, respectively.

When fitting the models, we omitted all non-significant interactions but kept non-significant main effects (significance level at 5%), which allowed to test the hypotheses 1b, 2, 3a and 3b. Additionally, an auto-correlation parameter (Φ_1) was estimated for all models to account for temporal autocorrelation in the data. The latter was specified with an autocorrelation structure of order 1. We used tree identity as grouping factor for the random effects and the autocorrelation parameter. In some models, residuals and one or several random effects, respectively, tended to depart from a normal distribution. We tried to transform the response variable, but the models did not converge anymore due to their complexity. Since the models already included an autocorrelation parameter, random effects for the intercept and several variables, we decided to keep these models but to interpret the results carefully.

All statistical analyses were computed with the statistical software R (version 3.6.2; R Core Team, 2019). We fitted the mixed-effects models with the function *lme* of the package *nlme* (version 3.1-142; Pinheiro et al., 2019). The figures were created using the package *ggplot2* (version 3.2.1; Wickham, 2016).

3. Results

3.1. Inter-annual variations of leaf phenology

Overall, there was a repetition from year to year of the leaf unfolding and leaf coloration individual ranks within their population (*i.e.* the earliest trees within their population at the same elevation for one year
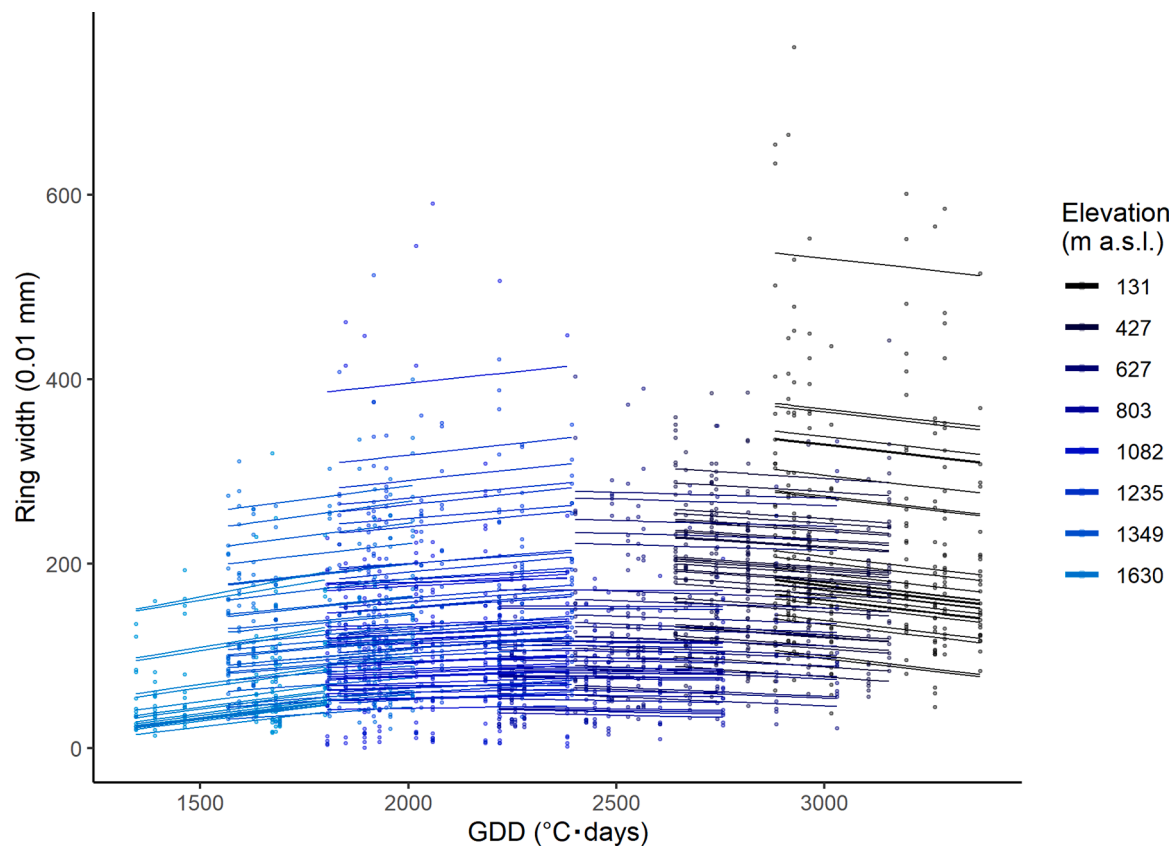
Fig. 4. Shift in the relationship between tree-ring width (RW) and accumulated growing degree-days (GDD) depending on elevation. GDD includes accumulated temperatures above 5°C from 1 January to 31 December (Eq. 1). Data from 197 tree individuals of sessile oak are shown spread over eight elevations (see legend) and measured over the period 2005-2013 (9 years). One dot represents an observation of RW and GDD for one tree and one year (1757 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in Table A.4 and following Eq. (2).

were usually the earliest in the following years). All rank correlations were positive and the large majority of the correlations were significant (P < 0.05; Fig. 1).

Leaf unfolding ranks tended to be more consistent from year to year than leaf coloration ranks (0.55 ± 0.11 *vs.* 0.42 ± 0.11; including all populations, mean of Kendall's τ ± standard deviation; Table A.1). For both leaf unfolding and leaf coloration, trees at the lowest elevation (131 m a.s.l.) presented the highest correlation (leaf unfolding: 0.69 ± 0.02 and leaf coloration: 0.62 ± 0.07; Table A.1; black lines, Fig. 1) but overall, all populations showed a relatively high correlation (all correlations above 0.39 ± 0.04 for leaf unfolding and all correlations above 0.33 ± 0.06 for leaf coloration; Table A.1).

This consistency of the ranks of leaf unfolding and leaf coloration dates remained over the years (*e.g.* a late flushing tree within its population for a given year was likely to display a late flushing behaviour in the following years, even seven years after; Fig. 1.a).

3.2. Intra-annual correlation between leaf unfolding and leaf coloration

A large variability in the dates of leaf unfolding and leaf coloration was observed across elevations (Fig. 2): leaf unfolding ranged from DOY 80 (131 m a.s.l.) to DOY 155 (1630 m a.s.l.) and leaf coloration ranged from DOY 270 (1630 m a.s.l.) to DOY 340 (131 m a.s.l.). This large variability was also visible at the intra-population level, *e.g.* for the two populations with the most extreme elevations: at 131 m a.s.l. leaf unfolding ranged from DOY 80 to DOY 115 and leaf coloration ranged from DOY 285 to DOY 340, and at 1630 m a.s.l. leaf unfolding ranged from DOY 130 to DOY 155 and leaf coloration ranged from DOY 270 to DOY 320 (Fig. 2).

In the mixed-effects model explaining the date of leaf coloration, the

estimate of the interaction between leaf unfolding and elevation was negative and significant (P < 0.001; Table A.2). According to the calculation of the partial derivative of the model (for further details see Meier et al., 2021), the effect changed at 870 m a.s.l. At lower elevations (< 870 m a.s.l.), leaf coloration date was positively correlated with leaf unfolding date (*i.e.* individuals with later flushing tended to have later leaf coloration within populations) whereas at higher elevation (≥ 870 m a.s.l.), a negative relationship was observed (*i.e.* individuals with earlier flushing tended to have later leaf coloration within population) (Fig. 2).

3.3. Relationship between leaf phenology and temperature

The length of the growing period increased with increasing GDD (*i.e.* a proxy for temperature; see Eq. 1) within the populations with an approximated extension of 2.8 days per 100°C•days (P < 0.001; Table A.3; Fig. 3). Across populations, the length of the growing period increased with decreasing elevation, from around 140 days at the highest elevation (1630 m a.s.l.) to more than 210 days at the lowest elevation (131 m a.s.l.; Fig. 3).

3.4. Relationship between temperature and radial growth

The relationship between GDD and radial growth varied with elevation. According to the calculation of the partial derivative of the mixed-effects model (Table A.4), the relationship changed at 624 m a.s.l. At lower elevation (< 624 m a.s.l.), radial growth decreased with increasing GDD whereas the opposite relationship was observed at higher elevation (≥ 624 m a.s.l.; Fig. 4). Similar results were obtained when computing the same model with the relative RWI instead of the
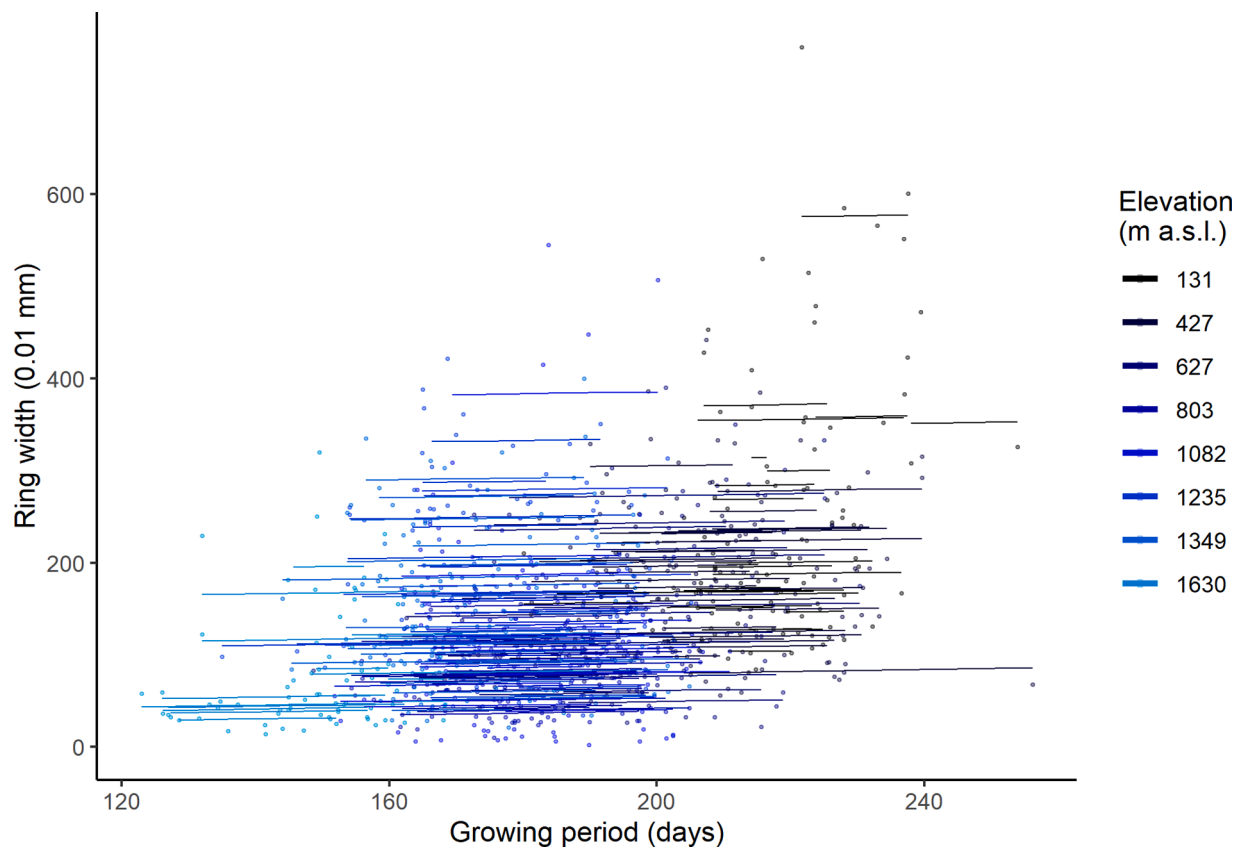
Fig. 5. Relationship between tree-ring width (RW) and growing period (GP) length. Data from 196 tree individuals of sessile oak are shown over eight elevations (see legend) and monitored over the periods 2005-2007 and 2009-2012 (7 years). One dot represents an observation of RW and GP for one tree and one year (975 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in the Table A.6 and following Eq. (2).

actual RW (Table A.5, Fig. A.2; see section 2.3 *Ring-width data* for the difference between RW and RWI). The interaction between elevation and GDD was significant in both models (P < 0.001; Table A.4 and Table A.5). In the model explaining RWI, the relationship became positive at an elevation of 980 m a.s.l. according to the calculation of the partial derivative.

3.5. Relationship between leaf phenology and radial growth

Unexpectedly, the effect of growing period length on radial growth was not significant within populations, *i.e.* trees that shared the same environmental conditions but unfolded their leaves earlier and coloured their leaves later, respectively, did not necessarily show higher radial growth (P = 0.353 for the variable growing period, Table A.6, Fig. 5). We computed a related model with the relative RWI instead of the actual RW and observed analogous results (P = 0.213 for the variable growing period, Table A.7, Fig. A.3). Radial growth, however, was negatively correlated with elevation (P < 0.001 in the model explaining RW, Table A.6; P = 0.127 in the model explaining RWI, Table A.7). Additionally, the interaction between growing period and elevation slightly influenced the radial growth in a positive way (P = 0.031 in the model explaining RWI, Table A.7; non-significant in the model explaining RW, Table A.6). Overall, we observed a large variability in tree-ring widths ranging from around 0.5 mm to 4 mm, and up to 6 mm in a few well growing trees at lower elevations (Fig. 5).

4. Discussion

4.1. Inter-annual variations of leaf phenology

We expected a consistent sequence of the phenological ranks at the inter-annual level within populations as already reported in previous studies (Crawley & Akhteruzzaman, 1988; Delpierre et al., 2017). This hypothesis was confirmed as we found a clear consistency from year to year in the sequence of both leaf unfolding and leaf coloration dates within populations (*i.e.* same elevation and same environmental conditions). The first trees to unfold their leaves in spring are mostly the same every year and similarly for leaf coloration. Crawley & Akhteruzzaman (1988) also observed for *Quercus robur* L. a consistency of the phenological ranks from year to year. However, leaf coloration ranks seemed to be repeated less consistently than leaf unfolding ranks. Using 35 populations of *Q. robur, Q. petraea* and *Fagus sylvatica* L. in France, Delpierre et al. (2017) showed that individual phenological ranks mostly repeated from year to year within a population, with a higher correlation found in leaf unfolding compared to leaf senescence, which is consistent with our findings. However, a study by Capdevielle-Vargas et al. (2015) that was conducted at the individual level on a population of *F. sylvatica* in southern Germany did not find a consistent inter-annual repetition of phenological ranks. The authors explained their results by plastic phenotypic responses of the trees, which could be a strategy to cope with changing environmental conditions. In our study, genetic variability is likely the main reason for these individual differentiations

as demonstrated by Alberto et al. (2011) using offspring of the very same populations as ours planted in a common garden. Our results reveal a lower phenological variability for populations inhabiting higher elevations. However, the availability of trees was not the same at each elevation. For example, at low elevation (131 m a.s.l.), the stand presented abundant trees in a vast forest and it was easier to select early and late flushing trees. In contrast, at high elevation (*e.g.* at 1630 m a.s.l.), the trees were more dispersed as we approached the upper elevational limit of the species and there was much less choice for selecting trees with contrasting phenology.

4.2. Intra-annual correlation between leaf unfolding and leaf coloration

We hypothesised that trees with early (or late) leaf unfolding would exhibit early (respectively late) leaf coloration within a given year. Our results showed that there was a significant correlation between leaf unfolding and leaf coloration dates at the individual tree level within a year but, surprisingly, this relationship changed along elevation. Although we observed that trees with early leaf unfolding were also early for leaf coloration at low elevation – in agreement with the experimental findings from Fu et al. (2014) for example – the opposite was observed at higher elevations ($\geq$ 870 m), *i.e.* trees with earlier leaf unfolding tended to exhibit later leaf coloration. This could be an effect of spring late frost that may more often hit the earliest flushing trees at high elevation. A new cohort of leaves may take two months to recover similar levels of canopy cover after a frost as shown in beech by Bascietto et al. (2018), which could subsequently delay the growing season and hence leaf senescence. However, this result needs further investigation as the phenological variation within population was also much lower at higher elevations (see section 4.1 *Inter-annual variations of leaf phenology*).

4.3. Relationship between leaf phenology and temperature

We expected that the growing season would extend with increasing temperatures. We indeed observed a positive correlation between growing period length and GDD as a proxy for temperature. Thus, the warmer the year, the longer was the canopy duration at all elevations. This relationship has already been observed based on experiments (Morin et al., 2010) or using a large *in situ* dataset (Piao et al., 2019), but not at the individual tree level with contrasting phenology as studied here. We observed a clear decrease in growing period length with increasing elevation. The lowest site (elevation 131 m a.s.l.) may be considered as quite distant from the other sites of the study (57 km from the site located at 387 m a.s.l.) but the eight other sites (*i.e.* elevations from 387 to 1630 m a.s.l.) are geographically reasonably close to each other (within a transect of 52 km) and are mainly differentiated by the elevational gradient. Precipitation changes with elevation and other environmental factors may change between sites (*e.g.* soil conditions) but here the strong positive correlation between growing period length and temperature (*i.e.* negative correlation with elevation) confirms that temperature is an important driver of the growing period length (Vitasse et al., 2009b).

Several studies have assessed the extension of the growing period in relation to temperature increase over the last decades (*e.g.* Menzel & Fabian, 1999; reviews from Linderholm, 2006 and Piao et al., 2019). In our study, seven years of observations is too short to detect phenological trends over time due to temperature increase. However, the elevational gradient represented here simulates a temporal gradient of temperature, also known as space-for-time substitution (*e.g.* in Caignard et al., 2017). In our study, the positive correlation found between the growing period and GDD suggests that further warming may continue to extend the

growing period of this species, at least at mid and high elevations where chilling requirement might still be fulfilled (Asse et al., 2018) and where severe drought will be less frequent and severe than at low elevation.

4.4. Relationship between temperature and radial growth

We expected to find a positive correlation between temperature and radial growth but potentially not at every elevation because of the influence of other climatic variables. We indeed found a significant correlation between GDD as a proxy for temperature over the year and radial growth. However, this correlation changed with elevation, being negative at lower elevations (< 624 m a.s.l.) and positive at higher elevations ($\geq$ 624 m a.s.l.). This change might be explained by drought limiting growth at low elevations and low temperature limiting growth at high elevations, respectively. At low elevations, water availability during spring-summer is critical and likely constrains growth whereas at high elevations lower temperatures reduce growth potential, as shown by Leal et al. (2007) for five common conifer species in the Austrian Alps. Periods of high temperatures are usually correlated with low precipitation in mountainous regions of the Iberian Peninsula (Fernández-Montes et al., 2017), where the Pyrenees are found. These periods of high temperatures and low precipitation, or droughts, often induce reduced radial growth in the lowlands (*e.g.* Sarris et al., 2007; Speer, 2010; Vitasse et al., 2019). At low elevations, the observed reduced growth when temperatures increased is likely underlying dry periods that are detrimental for tree growth in the lowlands. In contrast, at high elevations, where low temperature is a limiting factor for growth (Leal et al., 2007), tree growth may benefit from higher temperatures as it was observed in different dendroecological studies (*e.g.* Jochner et al., 2018; Vitasse et al., 2019).

We used the accumulated growing degree-days as an index for temperature and included all days of the year in the calculation. Including only the days in spring or a certain number of days prior to leaf unfolding could be more relevant when studying spring phenology (e.g. see Fu et al., 2013). However, we chose to include the same period for every elevation (i) due to the large variability of leaf unfolding from mid-March to the end of June and leaf coloration from the end of September to mid-December along the elevational gradient and (ii) to allow comparable results. In addition, the difference of accumulated growing degree-days among the sites would remain comparable irrespective of the period selected because it is mainly driven by the adiabatic lapse rate.

4.5. Relationship between leaf phenology and radial growth

We anticipated to find an increased radial growth of individuals showing longer growing periods. However, we did not find a clear relationship between radial growth and growing period length within populations, at any elevation. In agreement with our results, most of the studies investigating the link between radial growth and leaf phenology did not find a significant correlation between growing period length and radial growth (*e.g.* Čufar et al., 2015; Kolář et al., 2016; Liu et al., 2012). The length of the growing period is defined by the number of days between leaf unfolding and leaf coloration. Thus, it corresponds to the range of time in which a tree can potentially photosynthesize due to the presence of leaves. However, trees do not necessarily grow during the whole growing period and exhibit rather a high growth rate in spring and a relatively low growth rate during summer, especially when drought occurs (D'Orangeville et al., 2021; Etzold et al., 2021; Walthert et al., 2021). Nevertheless, when photosynthesis is still effective, the resources can be allocated to other organs without any radial growth, *e. g.* to seed production or root growth. Unlike our results, Delpierre et al.

(2017) observed an increased radial growth of individual trees of sessile oak within their population as the growing season lengthened. In their study, the authors observed that sessile oaks entering leaf senescence later tended to grow more but that the date of leaf unfolding did not have a significant effect on growth.

Our results suggest that the expected link between an increase of the growing season and an increase in radial growth is not so obvious as often assumed in modelling studies (see also Zohner et al., 2020). Further investigations should be conducted on different species and to test whether trees with longer growing seasons have higher reserves of non-structural carbohydrates.

Conclusion

Our study emphasizes relationships between growth, climate and phenology at the individual tree level, whereas most phenological studies to date have been based on population-level observations. We further provide a range of *in situ* phenological and growth responses to temperature across a natural distribution of oak populations along an elevational gradient of 1500 m. The present results confirm the importance of temperature as a driver for both leaf phenology and radial growth in sessile oak. Our findings further suggest that ranks of leaf unfolding and leaf coloration dates between individuals mostly repeat from year to year, likely due to a strong genetic component. Interestingly, our results also showed that radial growth was enhanced by higher temperatures at high elevations, but a negative association was found at low elevation, likely as a result of lower water availability often co-occurring with warmer periods. However, we did not detect a significant relationship between radial growth and growing period length within populations. This suggests that a longer growing season induced

by climate warming will not necessarily lead to higher productivity as often assumed in modelling studies. Further investigations, particularly experimental studies, would be necessary to clarify under which climatic conditions an extension of the growing season would lead to higher productivity. In addition, some studies demonstrated that radial growth is also influenced by temperature from multiple previous years (Zweifel & Sterck, 2018) and it remains to be examined for how long changes in phenology or extreme events such as frost and drought from previous years affect current year radial growth (see Vitasse et al., 2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix

Fig. A1, Fig. A2, Fig. A3, Table A1, Table A2, Table A3, Table A4, Table A5, Table A6, Table A7.

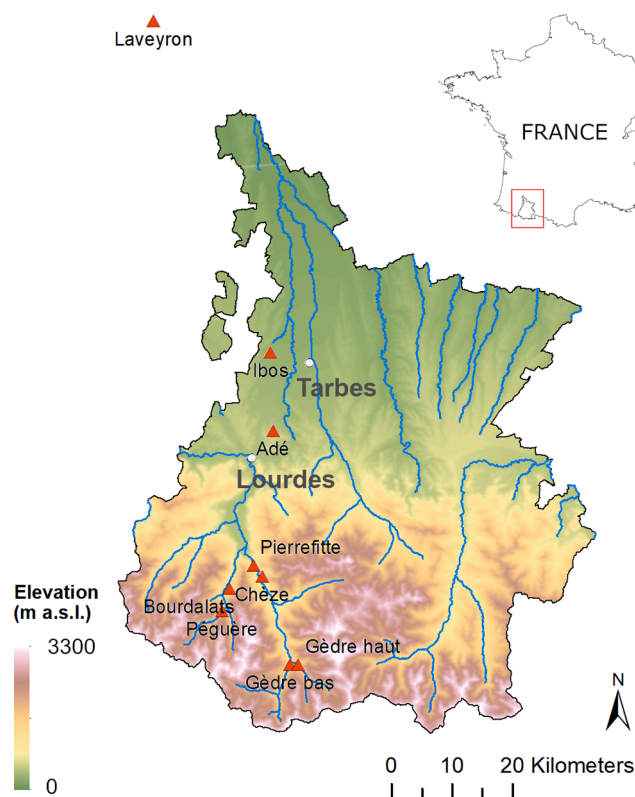**Fig. A.1.** Map of the study sites (red triangles) in the Gave valley in the French department *Hautes-Pyrénées*. See Table 1 for the exact position and elevation of the sites. The site *Laveyron* is located in the lowland (131 m a.s.l.), 57 km north from *Ibos* (represented with the correct scale on this map). © OpenStreetMap contributors and © IGN, 2020.
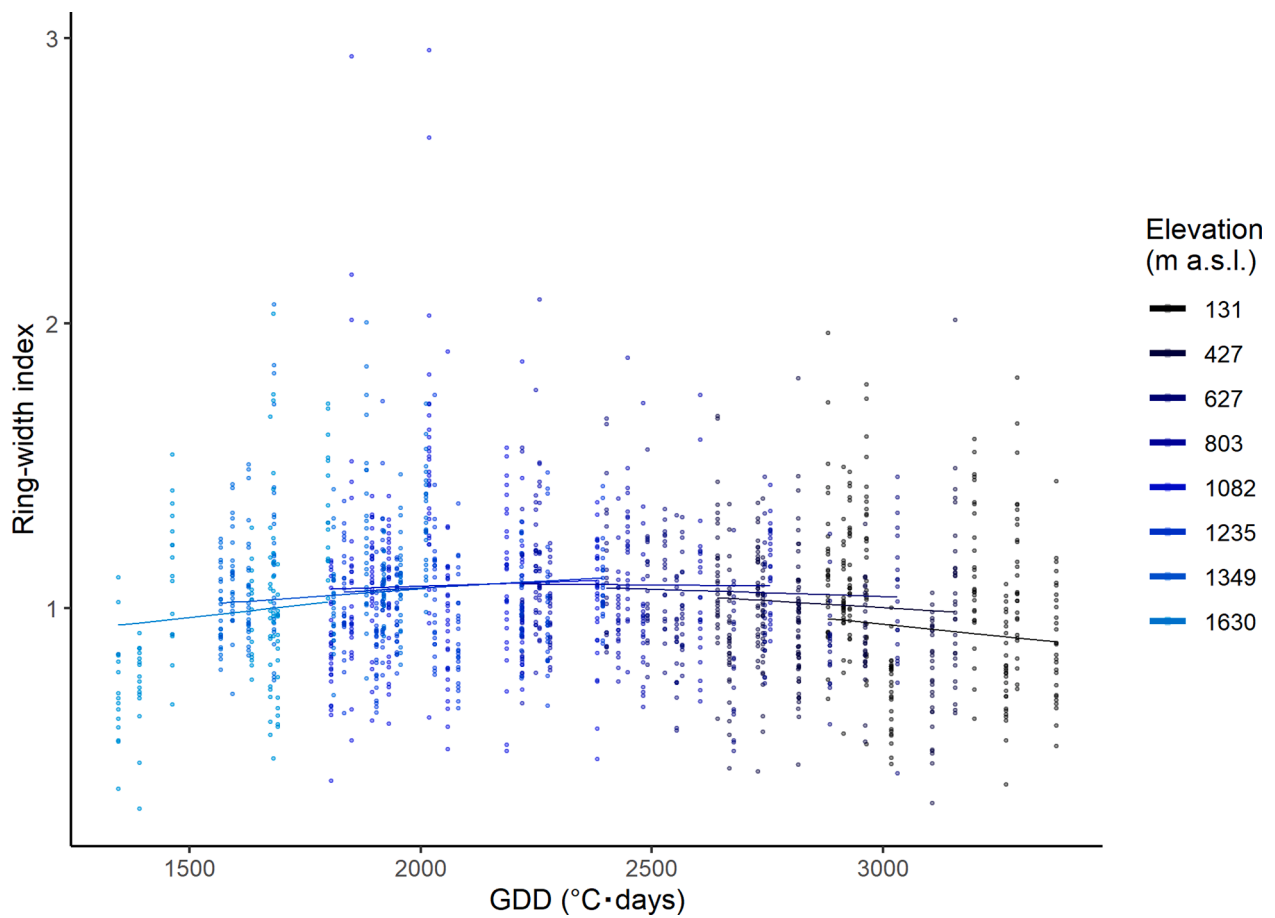
Fig. A.2. Shift in the relationship between ring-width index (RWI) and accumulated growing degree-days (GDD) depending on the elevation. Ring-width index was computed after detrending the raw ring-width series with the spline method (see Methods for more details). GDD includes accumulated temperatures above 5°C from 1 January to 31 December (Eq. 1). Data from 197 tree individuals of sessile oak are shown spread over eight elevations (see legend) and monitored over the period 2005-2013 (9 years). One dot represents an observation of RWI and GDD for one tree and one year (1757 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in Table A.5 and following Eq. (2). The lines overlap per site because of the small standard deviation of intercepts and slopes (Table A.5).
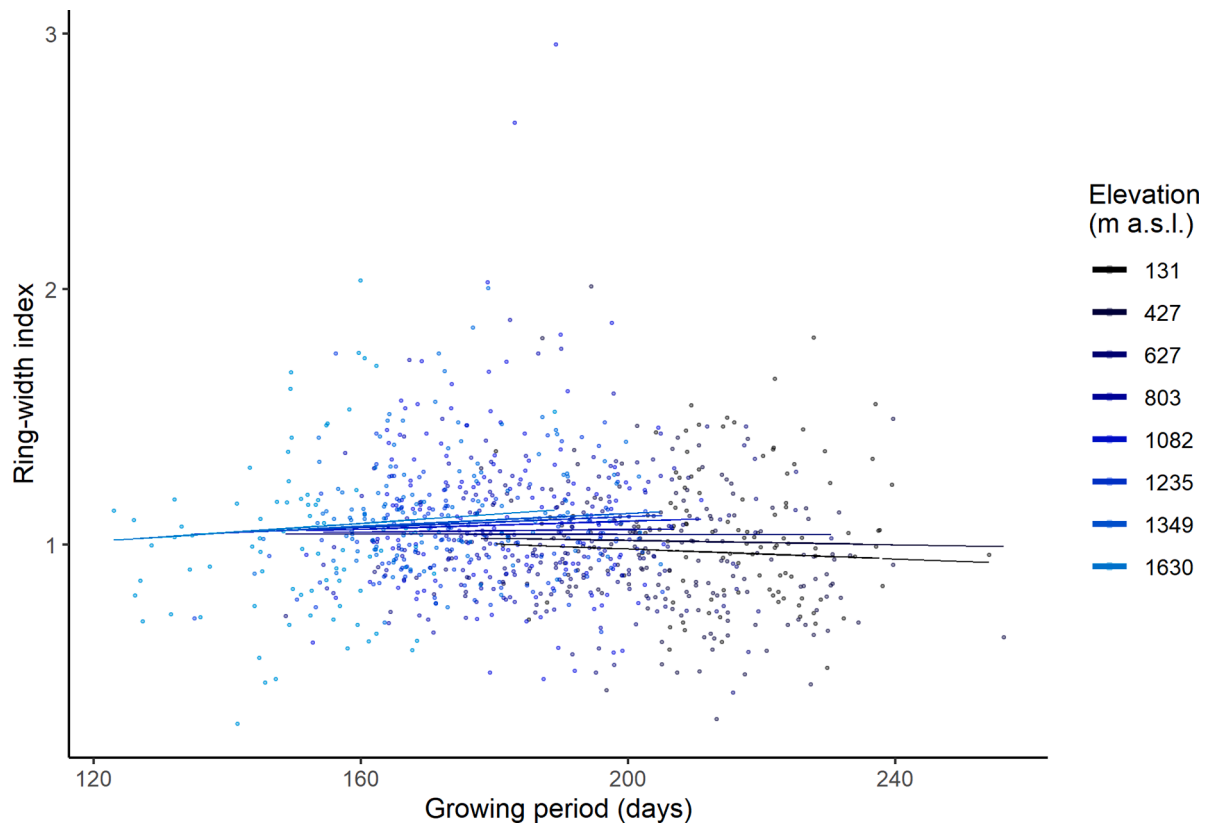
Fig. A.3. Relationship between ring-width index (RWI) and the growing period (GP) length. Ring-width index was computed after detrending of the raw ring-width series with the Spline method (see Methods for more details). Data from 196 tree individuals of sessile oak are shown spread over eight elevations (see legend) and monitored over the periods 2005-2007 and 2009-2012 (7 years). One dot represents an observation of RWI and GP for one tree and one year (975 observations). Regression lines are shown for the individual trees, fitted with the mixed-effects model described in Table A.7 and following Eq. (2). The lines overlap per site because of the small standard deviation of intercepts and slopes (Table A.7).

Table A.1

Mean Kendall's rank correlation $\tau \pm$ standard deviation (SD) per elevation and for two phenological phases in sessile oak: leaf unfolding (LU) date and leaf coloration (LC) date. Each tree was previously ranked per year within its elevation. Each value of τ was then estimated separately according to different time lags (from 1 to 7 years) and for every elevation. The means presented here include all the time lags from 1 to 7 years. See Fig. 1 for a visual representation of these τ values, separated per elevation and per time lag. Data cover the periods 2005-2007, 2009-2012 and 2014-2015 (9 years) for LU; 2005-2007 and 2009-2012 (7 years) for LC. See Methods for more details. In total, there are 1735 observations from 259 trees for LU and 1400 observations from 258 trees for LC spread over the nine elevations. Only significant τ values (P < 0.05) were included in the mean calculations presented in this table.

Elevation (m a.s.l.)	$\tau \pm SD$	
	LU	LC
131	0.694 ± 0.016	0.615 ± 0.071
387	0.605 ± 0.076	0.440 ± 0.086
427	0.665 ± 0.037	0.358 ± 0.070
627	0.543 ± 0.058	0.329 ± 0.055
803	0.488 ± 0.085	0.359 ± 0.107
1082	0.454 ± 0.070	0.376 ± 0.159
1235	0.385 ± 0.040	0.413 ± 0.082
1349	0.525 ± 0.069	0.360 ± 0.083
1630	0.551 ± 0.057	0.366 ± 0.080
All	0.547 ± 0.109	0.418 ± 0.108

Table A.2

Summary of the mixed-effects model (Eq. 2) explaining leaf coloration (LC, in day of year). LU for leaf unfolding (day of year), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (9 levels) and is included as a numeric variable. Data cover the periods 2005-2007 and 2009-2012. The random effect was omitted for elevation because the model did not converge.

	LC (response variable)		
	Fixed effects		Random effects
Predictor variable	Estimate ± SE	P	SD
Intercept	295.15 ± 5.87	< 0.001	6.97
LU	0.20 ± 5.68e-2	< 0.001	2.22e-3
Elevation	1.31e-2 ± 6.27e-3	0.037	-
LU:Elevation	-2.30e-4 ± 5.30e-5	< 0.001	2.36e-5

1265 observations; 261 groups. Autocorrelation parameter: $\Phi_1 = -0.50$.

Table A.3

Summary of the mixed-effects model (Eq. 2) explaining the growing period length (GP, in days). GDD for growing degree-days (in°C•days; see Eq. 1), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (9 levels) and is included as a numeric variable. Data cover the periods 2005-2007 and 2009-2012.

| | GP (response variable) | | |
| | Fixed effects | | Random effects |
Predictor variable	Estimate ± SE	P	SD
Intercept	129.95 ± 8.26	< 0.001	0.15
GDD	2.79e-2 ± 2.75e-3	< 0.001	3.16e-3
Elevation	-2.18e-2 ± 6.09e-3	< 0.001	1.01e-5
GDD:Elevation	0.00 ± 2.00e-6	0.049	1.65e-6

1264 observations; 261 groups. Autocorrelation parameter: $\Phi_1 = 0.09$.

Table A.4

Summary of the mixed-effects model (Eq. 2) explaining ring width (RW; in 1/100 mm). GDD for growing degree-days (in°C•days; see Eq. 1), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (8 levels) and is included as a numeric variable. Data cover the period from 2005 to 2013.

| | RW (response variable) | | |
| | Fixed effects | | Random effects |
Predictor variable	Estimate ± SE	P	SD
Intercept	365.12 ± 29.56	< 0.001	95.13
GDD	-6.24e-2 ± 9.64e-3	< 0.001	2.01e-3
Elevation	-0.24 ± 2.74e-2	< 0.001	6.07e-2
GDD:Elevation	1.00e-4 ± 1.00e-5	< 0.001	1.58e-5

1757 observations; 197 groups. Autocorrelation parameter: $\Phi_1 = 0.49$.

Table A.5

Summary of the mixed-effects model (Eq. 2) explaining ring-width index (RWI; spline detrending). GDD for growing degree-days (in°C•days; see Eq. 1), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (8 levels) and is included as a numeric variable. Data were collected from 2005 to 2013.

| | RWI (response variable) | | |
| | Fixed effects | | Random effects |
Predictor variable	Estimate ± SE	P	SD
Intercept	1.50 ± 0.12	< 0.001	2.01e-5
GDD	-1.96e-4 ± 4.19e-5	< 0.001	6.80e-11
Elevation	-4.96e-4 ± 9.45e-5	< 0.001	1.86e-9
GDD:Elevation	2.00e-7 ± 4.00e-8	< 0.001	8.82e-15

1757 observations; 197 groups. Autocorrelation parameter: $\Phi_1 = 0.37$.

Table A.6

Summary of the mixed-effects model (Eq. 2) explaining ring width (RW; in 1/100 mm). GP for growing period length (in days), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (8 levels) and is included as a numeric variable. Data cover the periods 2005-2007 and 2009-2012. The interaction GP:Elevation is not included in the model, because it was not significant. The random effect was omitted for GP because the model did not converge.

| | RW (response variable) | | |
| | Fixed effects | | Random effects |
Predictor variable	Estimate ± SE	P	SD
Intercept	177.08 ± 28.97	< 0.001	99.88
GP	0.10 ± 0.11	0.353	-
Elevation	-5.79e-2 ± 1.43e-2	< 0.001	5.94e-2

975 observations; 196 groups. Autocorrelation parameter: $\Phi_1 = 0.36$.

Table A.7

Summary of the mixed-effects model (Eq. 2) explaining ring-width index (RWI, spline detrending). GP for growing period length (in days), SE for standard error, P for P value and SD for standard deviation. Elevation ranges from 131 to 1630 m a.s.l. (8 levels) and is included as a numeric variable. Data cover the periods 2005-2007 and 2009-2012. The random effect was omitted for GP:Elevation because the model did not converge.

| | RWI (response variable) | | |
| | Fixed effects | | Random effects |
Predictor variable	Estimate ± SE	P	SD
Intercept	1.20 ± 0.20	< 0.001	1.65e-5
GP	-1.19e-3 ± 9.61e-4	0.213	1.51e-15
Elevation	-2.51e-4 ± 1.64e-4	0.127	1.26e-17
GP:Elevation	1.80e-6 ± 8.50e-7	0.031	-

975 observations; 196 groups. Autocorrelation parameter: $\Phi_1 = 0.21$.

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