

Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range

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Abstract With global warming, an advance in spring leaf phenology has been reported worldwide. However, it is difficult to forecast phenology for a given species, due to a lack of knowledge about chilling requirements. We quantified chilling and heat requirements for leaf unfolding in two European tree species and investigated their relative contributions to phenological variations between and within populations. We used an extensive database containing information about the leaf phenology of 14 oak and 10 beech populations monitored over elevation gradients since 2005. In parallel, we studied the various bud dormancy phases, in controlled conditions, by regularly sampling low- and high-elevation populations during fall and winter. Oak was 2.3 times more sensitive to temperature for leaf unfolding over the elevation gradient and had a lower chilling requirement for dormancy release than beech. We found that chilling is currently insufficient for the full release of dormancy, for both species, at the lowest elevations in the area studied. Genetic variation in leaf

unfolding timing between and within oak populations was probably due to differences in heat requirement rather than differences in chilling requirement. Our results demonstrate the importance of chilling for leaf unfolding in forest trees and indicate that the advance in leaf unfolding phenology with increasing temperature will probably be less pronounced than forecasted. This highlights the urgent need to determine experimentally the interactions between chilling and heat requirements in forest tree species, to improve our understanding and modeling of changes in phenological timing under global warming.

Keywords Climate change · Phenology · Cuttings · Heat/chilling requirement · Leaf unfolding · Sessile oak · European beech

Abbreviations

GDD Growing degree days

T_b Base temperature for chilling and heat accumulation

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Introduction

The timing of leaf unfolding is a key phenological event in temperate tree species because it affects their productivity (Myneni et al. 1997; Hasenauer et al. 1999; White et al. 1999; Zhou et al. 2001), distribution range (Chuine and Beaubien 2001; Chuine 2010), and, indirectly, the climate (Richardson et al. 2013). In most temperate trees, the timing of leaf unfolding depends mostly on temperature, with some species, including European beech, also sensitive to photoperiod (Polgar and Primack 2011; Basler and Körner 2012; Laube et al. 2013; Vitasse and Basler 2013). The recent increase in surface air temperature has led to strong phenological shifts in the timing of leaf unfolding in temperate trees

(Root et al. 2003; Menzel et al. 2006; Richardson et al. 2006). These shifts differ substantially between temperate tree species: An 1 °C increase in air temperature in spring advances leaf unfolding by 2 to 10 days, depending on the species (Chmielewski and Rotzer 2001; Penuelas et al. 2002; Karlsson et al. 2003; Vitasse et al. 2009b, 2011). Frost-sensitive active tissues in the buds are protected against frost damage in temperate trees by an endodormancy phase in winter (controlled by internal factors), generally induced and released by photoperiod and chilling temperatures, respectively (Coville 1920; Doorenbos 1953; Nienstaedt 1966; Heide 1993; Horvath et al. 2003; Campoy et al. 2012), followed by an ecodormancy phase of sensitivity to warm temperatures (reviewed in Lang 1987). However, there are complex relationships between chilling and heat requirements.

Warmer temperatures in early spring affect flushing by shortening the ecodormancy phase. By contrast, warmer temperatures during winter may lead to later endodormancy release or to insufficient chilling for the full release of endodormancy in temperate regions, increasing the heat required for leaf unfolding in a nonlinear manner (Wareing 1953; Sarvas 1972; Cannell and Smith 1986; Murray et al. 1989). Thus, the role of chilling may become more important with increasing air temperature, warmer temperatures therefore leading to a nonlinear advance in tree leaf unfolding phenology in the future (Chuine et al. 2010; Fu et al. 2012a; Laube et al. 2013). The relationship between heat and chilling requirements differs considerably between species (Murray et al. 1989; Cannell 1997; Vitasse and Basler 2013). In trees with a low chilling requirement, leaf unfolding will probably occur earlier in the next few decades under conditions of continued climate change, whereas species with a high chilling requirement may display unchanged or even delayed leaf unfolding date because chilling requirements are not satisfied or endodormancy release occurs later (Murray et al. 1989; Harrington et al. 2010; Morin et al. 2010; Vitasse et al. 2010; Polgar and Primack 2011; Fu et al. 2012a). However, the environmental mechanisms involved in bud dormancy processes are far from fully understood (Cooke et al. 2012).

The timing of leaf unfolding in temperate tree species is highly plastic with respect to temperature changes and also has a genetic determinism (Derory et al. 2006; Vitasse et al. 2010), with high heritability reported for both deciduous (Howe et al. 2000; Baliuckas et al. 2005; Alberto et al. 2011) and evergreen tree species (Billington and Pelham 1991). In particular, temperature requirements are under strong genetic control, essentially of two types (Rousi and Pusenius 2005; Sanz-Perez et al. 2009): the first acts on the duration of the chilling period and the “amount” of chilling required to overcome endodormancy (Bennett 1949; Nooden and Weber 1978; Perry and Wu 1960; Samish 1954; Sherman et al. 1977) and second acts on sensitivity to heat temperatures as demonstrated in several plantations of walnut trees (Mauget

and Germain 1980; Charrier et al. 2011). However, the threshold temperature to which buds are sensitive during the ecodormancy phase and the optimum chilling temperature for dormancy release are known accurately for only a few species, principally fruit trees (reviewed in Faust et al. 1997). Moreover, it has been shown that, within species, populations often have different chilling and heat requirements, depending on their climate of origin (Charrier et al. 2011; Polgar and Primack 2011). Clinal variations in the timing of leaf unfolding along gradients of elevation and latitude have been observed in *common garden* experiments (along elevation gradients: Vitasse et al. 2009a; Gomory and Paule 2011; along latitudinal gradients: Myking and Heide 1995), possibly due to genetically determined temperature requirements (Vitasse et al. 2010). Interestingly, these genetic clines may run in the same direction as the phenotypic in situ cline occurring along these biogeographical gradients (cogradient variation), as in *Quercus petraea*, *Fraxinus excelsior*, and *Acer pseudoplatanus*, for example, or they may run in the opposite direction (counter-gradient variation), as in *Fagus sylvatica* or *Pseudotsuga menziesii* (Chmura and Rozkowski 2002; Acevedo-Rodriguez et al. 2006; Vitasse et al. 2009a, 2013; Alberto et al. 2011; Gomory and Paule 2011), for example. This raises questions as to whether the genetic difference in leaf unfolding timing between populations growing in contrasting climates results from differences in chilling or heat requirements. The resolution of this issue would have important implications for improving phenological predictions for temperate forests under climate warming.

Renewed interest in predicting changes in temperate forest phenology in response to climate change has triggered the development of numerous phenological models, of various degrees of complexity, integrating the main drivers of leaf unfolding phenology: heat and chilling requirements, photoperiod, and their interactions. Most predictions to date have forecasted an advance in the timing of leaf unfolding in temperate tree species in the near future (Morin et al. 2009; Vitasse et al. 2011). However, in fruit tree, delayed leaf unfolding due to insufficient chilling has recently been demonstrated for pistachio trees in Tunisia (Elloumi et al. 2013), walnut trees in California and cherry trees in Germany (Luedeling and Gassner 2012; Luedeling et al. 2013), and apple trees in Japan (Honjo 2007). Legave et al. (2013) recently reported a delayed endodormancy release for apple trees in the south of France, but with no effect on leaf unfolding date. However, models including chilling are generally outperformed by classic models based on heat requirement only (such as the widely used thermal model; Fu et al. 2012b). This may be because they were calibrated over the whole distribution of a given species, such that only a very small number of populations located in the warmest part of the species distribution would lack chilling during warm winters, or in the central part of the distribution, in which chilling was

probably sufficient. Thus, predictions based on these data are likely to underestimate the role of chilling because the data used for calibration include too few years and/or populations undergoing insufficient chilling to constrain the models. There is an urgent need to understand the role and importance of chilling requirements in tree phenology because the frequency of winters with insufficient chilling is likely to increase, particularly in the southernmost parts of species ranges (Darbyshire et al. 2013b; Legave et al. 2013). A combination of in situ observations in the warmest part of the species distribution, together with warming and photoperiod experiments, is a useful approach likely to improve prediction of the phenological shift over the next few decades.

We used an extensive phenological database containing data acquired along two elevation gradients, to assess and compare the heat and chilling requirements of European beech and sessile oak in natural conditions. These two species are the predominant deciduous trees in Europe, with markedly different phenological sensitivities to temperature (Kramer 1995; Vitasse et al. 2009b; Čufar et al. 2012; Phillimore et al. 2013; Schieber et al. 2013; Vitasse and Basler 2013). Our study area is located at the warmest limit of the species distribution range, in which chilling requirements for the release of bud dormancy may remain unsatisfied in lowland forests. In parallel, we experimentally characterized the chilling (for endodormancy release) and heat (for ecodormancy release) requirements for leaf unfolding, in cuttings from low- and high-elevation populations, including early- and late-flushing individuals from the same population. For both species studied, we aimed (a) to determine the extent of change in heat requirements over a range of chilling durations, (b) to determine whether genetic variations in the timing of leaf unfolding between and within populations are driven by changes in heat and/or chilling requirements, and (c) to determine whether populations growing in the warmest area of the species distribution currently experience insufficient chilling for full dormancy release.

Materials and methods

Study area and species description

This study was conducted in two valleys of the Pyrenees mountains in southern France (from 43°15'N, 00°44'W to 42°53'N, 00°06'E). A first transect was set up in the Ossau valley (Pyrénées Atlantiques), and a second was established in the Gave valley (Hautes Pyrénées) (Table 1). These two valleys, located 30 km apart, are parallel and display an increase in elevation from north to south. This region is characterized by a temperate oceanic climate, with mean annual and winter (from January 1st to the end of March) temperatures of 12.4 and 7.0 °C, respectively (1931–2011), at low elevation (Lourdes—43°06'18"N; 00°03'42"W, Météo

France). Mean annual temperatures decreased linearly with elevation, by about 0.43 °C for every 100 m increase in elevation (mean from 2005 to 2011). We selected two common deciduous European tree species with different responses to spring temperature (Vitasse et al. 2009b): European beech (*Fagus sylvatica* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.). European beech occurs mostly in central and western Europe, in various habitats, ranging from mountainous regions in southern and eastern Europe to lowlands in central Europe (Bolte et al. 2007). Sessile oak occurs throughout most of Europe, from the Mediterranean to southern Scandinavia and from Ireland to the Ural Mountains in Russia. Thus, in the Pyrenees, both species are at the southern limit of their distribution range. For these two species and the two transects, 24 natural established populations were monitored for leaf unfolding phenology, from 131 to 1,630 m above sea level, in hill and mountain vegetation belts (Table 1). The range of elevation extended over 1,499 m for oak and 1,473 m for beech. For each population, we monitored 10 to 34 dominant, mature individuals of comparable height. Beech populations were located on north-facing slopes, and oak populations were located on south-facing slopes.

Phenological observations in situ

We monitored the timing of leaf unfolding along the two elevation gradients, for 7 years (2005–2007 and 2009–2012). Bud development was monitored at 10-day intervals in each population, from March to June, on the same selected individuals. Observations were made by two observers with binoculars (magnifying power 10), about 15 m away from the tree. We considered leaf unfolding date to have been reached for a bud when at least one of its leaves was fully unfolded (Biologische Bundesanstalt, Bundessortenamt, and Chemische Industrie (BBCH) scale, stages 10 to 19—see Meier 2001), and we visually evaluated the percentage of buds at this stage in the bulk of the foliage. At the tree level, leaf unfolding date was considered to have been reached when 50 % of the buds had reached this threshold. This date was estimated, for each selected tree, by linear regression between two measurement campaigns. Finally, for each population, leaf unfolding date was calculated as the mean of the estimated dates for the sampled individuals.

Meteorological measurements

Air temperature was recorded with data loggers (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, MA, USA) at each study site (24 sites). All sensors were intercalibrated in the laboratory before installation. At each site, sensors were installed 1.5 m above the ground, in an open area close to the study population (10 to 100 m away, at the same elevation). Sensors were protected by a white plastic shelter, to prevent exposure to rain or direct sunlight. Data were recorded at 15-

Table 1 Elevation (meters above sea level), coordinates, number of trees (n) for phenology monitoring, number of trees (n) for the bud dormancy experiment, mean spring temperature calculated from the February 1 to the May 31 of each year for the 2005–2007 and 2009–2012 periods (T_{mean} , in degree Celsius) and mean date of leaf unfolding for the all populations during the 2005–2007 and 2009–2012 periods (LU_{mean} , in Julian days) for each site in the two different valleys for the species *Fagus sylvatica* and *Q. petraea*

Species	Valley	Site	Elevation (m ASL)	Coordinates	PM (n)	BDE (n)	T_{mean} (°C)	LU_{mean} (JD)
<i>Fagus sylvatica</i>	Gave	Laveyron	131	43°45'N, 00°13'W	10–22	10	11.11	111
	Ossau	Josbaig	148	43°15'N, 00°44'W	10–21		9.68	116
	Ossau	Bager	422	43°07'N, 00°32'W	10–20		10.52	114
	Gave	Lourdes	488	43°05'N, 00°05'W	10–20		9.52	116
	Gave	Chèze	773	42°55'N, 00°02'W	10–28		8.03	129
	Ossau	Eaux-Bonnes	824	42°56'N, 00°22'W	10–20		7.71	121
	Gave	Haugarou	1,190	43°00'N, 00°12'W	10–21		4.29	127
	Ossau	Fabrèges	1,260	42°52'N, 00°24'W	10–24		4.41	124
	Ossau	Bious	1,551	42°51'N, 00°27'W	10–27		3.18	136
	Gave	Barèges	1,604	42°53'N, 00°06'E	10–25	10	3.77	134
<i>Quercus petraea</i>	Gave	Laveyron	131	43°45'N, 00°13'W	10–28		11.11	95
	Ossau	Josbaig	259	43°15'N, 00°44'W	10–26		11.27	92
	Gave	Ibos	387	43°07'N, 00°32'W	10–25	10	10.51	95
	Ossau	Bager	422	43°07'N, 00°32'W	18		11.69	97
	Gave	Adé	427	43°08'N, 00°00'W	10–34		10.37	102
	Gave	Pierrefitte	627	42°56'N, 00°03'W	10–22		9.68	111
	Gave	Chèze	803	42°55'N, 00°02'W	10–25		8.70	120
	Ossau	Le Hourcq	841	42°54'N, 00°26'W	10–22		7.03	119
	Gave	Bourdalats	1,082	42°54'N, 00°06'W	10–29		7.19	123
	Ossau	Gabas	1,194	42°53'N, 00°25'W	10–34		6.40	125
	Gave	Gèdre Bas	1,235	42°47'N, 00°01'E	10–28	10	7.08	128
	Gave	Gèdre Haut	1,349	42°47'N, 00°02'E	10–27		5.96	130
	Ossau	Artouste	1,614	42°53'N, 00°24'W	11–15		4.22	141
	Gave	Péguère	1,630	42°52'N, 00°07'E	10–27		4.69	143

PM phenology monitoring, BDE bud dormancy experiment

min intervals from 1 January 2005 to 15 June 2005 and hourly from 15 June 2005 to October 2012. Several weather stations suffered from technical faults over short periods. For most stations, the missing data were inferred by gap filling by linear interpolations from data from the most strongly correlated weather stations ($R^2 > 0.91$). However, in some years, the correlations were too weak for the estimation of missing temperature values at specific stations. We therefore did not calculate the heat and chilling requirements at these stations, for the years concerned. We compared the response of leaf unfolding timing to early spring temperature in situ between the two species studied, by averaging temperatures from February 1 to May 31, corresponding to about 2 months before the first date of leaf unfolding at low elevation and to the last date of leaf unfolding at high elevation, respectively.

Dormancy release in controlled conditions

The bud dormancy experiment was conducted on European beech and sessile oak populations from the Gave valley

transect. For each species, two populations were selected: one at low elevation (<387 m above sea level) and one at high elevation (>1,235 m above sea level, see Table 1). In each population, 10 trees were selected from among those used for phenology monitoring. For the low-elevation populations, in which a high level of phenological diversity for leaf unfolding was observed, we selected five early-flushing and five late-flushing trees. At intervals of about 2 weeks, from mid-October 2010 until mid-April 2011, twigs containing numerous buds were sampled from each selected tree in each population, at height of about 10 m, with a pole pruner (or from higher up, with a shotgun). The twigs were immediately placed in cooling boxes, in which they were transported to the laboratory. They were then placed in a growth chamber under long-day conditions (16 h, $230 \text{ mol}_{\text{photon}} \text{ m}^{-2} \text{ s}^{-1}$), at a warm temperature (25 °C) and a humidity of 70 %. Cuttings were shown to be a good proxy for adult trees, for the assessment of phenology (Vitasse and Basler 2014). For oak, twigs were cut in the laboratory into 5-cm-long pieces, each bearing a single bud (the classical “one-node cutting” method—e.g.,

Pouget 1963; Rageau 1978; Champagnat 1989; Balandier et al. 1993), and we studied five buds per individual. For non-apical buds, the top of the stem segments was covered with wax. No significant difference in timing of leaf unfolding was observed between non-apical and apical buds for these species (Marc Bonhomme, unpublished results). Segments were planted in rockwool and then in an aluminum tray filled with tap water and a piece of charcoal to purify the water. Because short-cuttings die rapidly in beech, we used 20-cm-long cuttings carrying about 10 buds. We studied a mean of 34 buds per individual. Shoot cuttings were placed in glass bottles with tap water and a piece of charcoal. Bud development was monitored at 2- to 3-day intervals until mid-May, and we recorded the time at which stage 9 occurred on the BBCH scale (i.e., buds opening), when reached (stages 10–19 are not observed on cuttings because the buds on cuttings generally dry out rapidly after this stage. By contrast, stage 9 is difficult to observe on mature trees). We then calculated a mean date of leaf unfolding per individual ($n=5$ and $n=34$ for oak and beech, respectively). We also calculated the leaf unfolding rate, corresponding to the number of buds from which leaves were produced by harvesting date over the total number of buds (as a percentage).

Assessment of chilling and heat requirements

Over the last four decades, numerous methods have been generated to assess chilling and heat requirement necessary for dormancy release and budburst, respectively. We selected two classical methods to compute chilling and heat accumulation, commonly used in alternating (Cannell and Smith 1983; Murray et al. 1989; Kramer 1994) and sequential models (Sarvas 1974; Hänninen 1987, 1990; Kramer 1994). For each method, we tested two base temperatures (T_b): 5 and 10 °C, with and without the inclusion of negative temperatures in chilling accumulation. We explored different start dates (t_1) for chilling and forcing units accumulation ranged, respectively, between September 1 and January 1 and between September 1 and March 1. We explored different end dates (t_2) for chilling accumulation between January 1 and the leaf unfolding date whereas the end date for heat accumulation was set by the leaf unfolding date. These different dates' combinations led us to compute chilling (C) and heat (H) accumulations alternatingly, sequentially or in parallel.

Computation 1

$$C = \sum_{t_1}^{t_2} y(T) \quad (1)$$

$$y(T) = \begin{cases} 0, & T > T_b \\ 1, & T \leq T_b \end{cases}$$

where T is the daily mean temperature.

$$H = \sum_{t_1}^{t_2} y(T) \quad (2)$$

$$y(T) = \begin{cases} 0, & T \leq T_b \\ T - T_b, & T > T_b \end{cases}$$

Computation 2

$$C = \sum_{t_1}^{t_2} y(T) \quad (3)$$

$$y(T) = \begin{cases} 0, & T \leq -3.4 \text{ or } T \geq 10.4 \\ \frac{T + 3.4}{T_b + 3.4}, & -3.4 < T \leq T_b \\ \frac{T - 10.4}{T_b - 10.4}, & T_b < T < 10.4 \end{cases}$$

$$H = \sum_{t_1}^{t_2} y(T) \quad (4)$$

$$y(T) = \begin{cases} 0, & T \leq 0 \\ \frac{28.4}{1 + e^{-0.185(T - 18.4)}}, & T > T_b \end{cases}$$

We assessed the relationship between heat and chilling accumulation by fitting several different equations (exponential, power, logarithmic, and linear). We selected the best fit on the basis of the coefficient of determination (R^2) and the coefficient of variation (CV; root mean square error divided by the mean of the values) for each base temperature (5 and 10 °C). All these tests were carried out on data from phenological observations in situ. We then applied the same method of computation with the same start and end dates to calculate chilling and heat accumulation for the growth chamber experiment.

Results

Phenological sensitivity to spring temperature

Significant linear trends were found for the relationship between the timing of leaf unfolding and spring temperatures for both species studied along the elevation gradients (Fig. 1, $P < 0.0001$). However, the slopes of the linear regressions differed considerably between the two species: Oak had a much stronger response to spring temperature (leaf unfolding advanced by 6.48 days °C⁻¹ increase in temperature) than

beech ($2.76 \text{ days } ^\circ\text{C}^{-1}$). These values remained stable over time, from 2005 to 2012, and oak also displayed higher levels of between-year variation than beech (Table S1).

Chilling and heat requirements

Assessment of chilling and heat requirements

For both species and each base temperature (5 and $10 \text{ }^\circ\text{C}$), the best fit was that obtained with (a) method of computation 1 (i.e., chilling days and growing degree days (GDD)), (b) chilling requirements calculated from the November 1 to the date of leaf unfolding and heat requirements from the January 1 to the date of leaf unfolding, and (c) a linear model for beech and a power model for oak. Better performances were obtained if negative temperatures were included in the chilling accumulation.

In situ monitoring

Irrespective of the threshold used for chilling and heat accumulation (i.e., $5 \text{ }^\circ\text{C}$ or $10 \text{ }^\circ\text{C}$), a clear trend toward a decrease in heat requirements was observed with increasing accumulation of chilling, for both species (Fig. 2, $P < 0.0001$). However, as the $5 \text{ }^\circ\text{C}$ threshold outperformed the $10 \text{ }^\circ\text{C}$ threshold for both species, we subsequently consider only the results obtained with this threshold (Fig. 2).

For oak, a power model fitted the data better than a linear model. Growing degree days tended to reach a plateau beyond 90 chilling days (the value at which the derivative of the power function fell below one). Populations at low elevations (below 500 m above sea level), which displayed low chilling values, had the highest heat requirements (steep increase in growing degree days); conversely, GDD requirements were the lowest for some high-elevation populations (above 1,000 m above sea level) with the highest levels of chilling. By contrast, for beech, the best relationship between heat and chilling requirements was achieved with a linear regression. For sites with low numbers of chilling days (at low elevation), heat requirement was higher for beech than for oak, whereas for sites with large numbers of chilling days (high-elevation populations), oak had the higher heat requirement.

Interestingly, the highest heat requirements by elevation for oak were observed in 2007 (Fig. 2), a year with an unusually warm winter (from the November 1 through the end of February, $3.17 \text{ }^\circ\text{C}$ warmer than the winters of 1931–2011 in Lourdes, southwest France ($43^\circ 06' 18'' \text{N}$; $00^\circ 03' 42'' \text{W}$), Météo France) (Fig. S1). For beech, only low-elevation populations displayed a higher heat requirement in this year.

Controlled experiment

The use of $10 \text{ }^\circ\text{C}$ as the threshold was more appropriate (Fig. 3) for estimating the chilling received in situ before sampling and for the heat requirement accumulating in the conditions of the test ($25 \text{ }^\circ\text{C}$, 16 h of light). We therefore consider only the results obtained with this threshold later in this section.

We observed the same patterns as in situ, with a plateau for oak and a linear decline for beech and with a higher heat requirement under conditions of low chilling for beech (Fig. 3). We observed differences in heat requirements for leaf unfolding between low- and high-elevation populations for oak, but not for beech. Indeed, for a given number of chilling days, high-elevation populations of oak required a larger number of growing degree days to reach the leaf unfolding stage in controlled conditions than did low-elevation populations. In addition, three phases of dormancy were clearly observed for the high-elevation oak population: entry into endodormancy, reflected by an increase in the number of growing degree days required for leaf unfolding to a maximum at 40 chilling days; endodormancy release, as demonstrated by a decrease in the number of growing degree days for leaf unfolding until a minimum at 90 days of chilling (endodormancy released) for 250 GDD; and, finally, the ecodormancy phase, in which an increase in chilling (up to 130 chilling days) had no significant effect on the number of growing degree days required for leaf unfolding at cooler locations, whereas a decrease was observed at warmer locations (low elevation). For beech, a markedly different pattern was observed: After reaching the endodormancy maximum, the number of growing degree days for leaf unfolding decreased linearly until the end of the experiment for the highest location and until 120 days of chilling for the lowest population, corresponding to 200 GDD. At the end, for both species (except for the high-elevation beech population), we observed a rapid decline due to bud growth in situ before sampling, permitted by temperature (above 90 and 140 chilling days for oak low- and high-elevation populations, respectively, and 120 chilling days for the beech low-elevation population).

Within populations (no difference in chilling between individuals), late-flushing oak required more degree days for leaf unfolding than early-flushing oak after entry into dormancy, whereas no differences were observed for beech (Fig. 4—the last sampling date for oak has been removed because leaf unfolding was still occurring in situ for early- and late-flushing individuals). For oak, the low-elevation population had a higher leaf unfolding rate (76 % on average) than the high-elevation population (37 % on average), throughout the experiment. A similar low rate of leaf unfolding was observed for both beech populations (26 %).

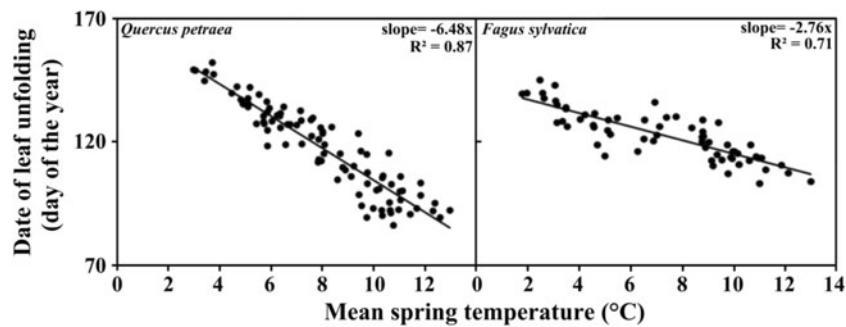


Fig. 1 Mean date of leaf unfolding against mean spring temperature (calculated from February 1 to May 31) for populations of *Q. petraea* and *Fagus sylvatica* monitored across two elevation gradients in the Pyrenees mountains during the 2005–2007 and 2009–2012 periods (R^2 , coefficient of determination— $P < 0.0001$). The studied sites covered 10

populations of *Fagus sylvatica* and 14 populations of *Q. petraea*, at elevations ranging from 131 to 1,630 m above sea level. Air temperature at a height of 1.5 m from the ground was recorded hourly at each site, and leaf unfolding was monitored every 10 days

Discussion

Phenological sensitivity to temperatures differed considerably between the two species studied. Sessile oak showed much greater phenological variation than European beech along the elevation gradients and between years, as previously reported (Vitasse et al. 2009b). This difference probably reflects a

complex interplay between winter and spring temperatures. A substantial change in forcing temperature requirement as a function of chilling duration was observed for both species, but beech displayed (a) a higher chilling requirement for full dormancy release and (b) a higher sensitivity to chilling temperature (i.e., a faster decrease in forcing requirement over the same gradient of chilling duration). Moreover, genetic

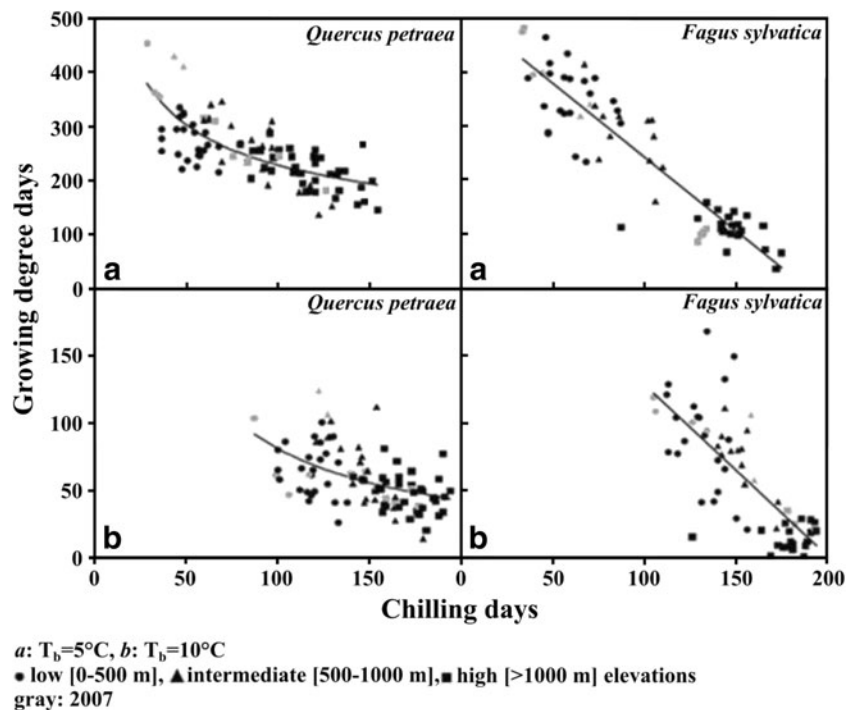
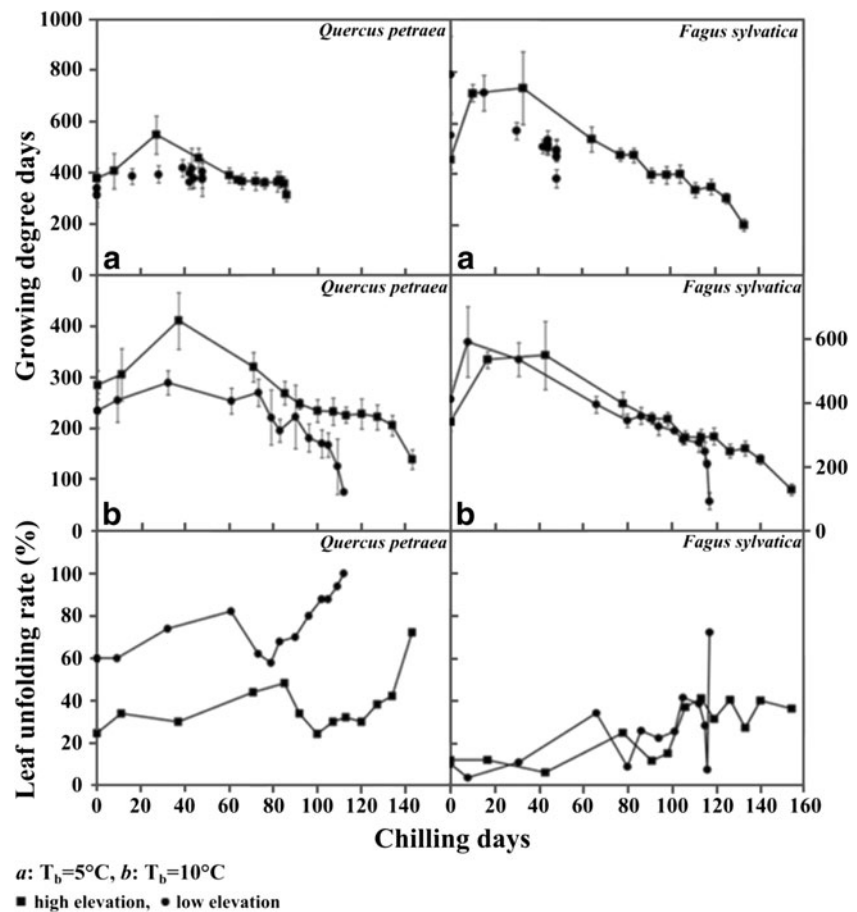


Fig. 2 Relationship between the heat requirement for leaf unfolding, calculated as the sum of growing degree days > 5 or 10°C from January 1 to the date of leaf unfolding, and the cumulative number of chilling days < 5 or 10°C from November 1 to the date of leaf unfolding (y), for populations of *Q. petraea* and *Fagus sylvatica* monitored across two elevation gradients in the Pyrenees mountains, during the 2005–2007 and 2009–2012 periods (R^2 and CV coefficients of determination, $P < 0.0001$). A linear regression model was fitted to the data for *Fagus sylvatica* (5°C : $y = -2.7382x + 514.9$, $R^2 = 0.84$, $\text{CV} = 0.21$; 10°C : $y =$

$-1.2723x + 255.62$, $R^2 = 0.59$, $\text{CV} = 0.48$), and a power model was fitted to the data for *Q. petraea* (5°C : $y = 1,437.7x^{-0.3997}$, $R^2 = 0.98$, $\text{CV} = 0.16$; 10°C : $y = 5679.4x^{-0.9234}$, $R^2 = 0.91$, $\text{CV} = 0.33$). The studied sites covered 10 populations of *Fagus sylvatica* and 14 populations of *Q. petraea*, at elevations ranging from 131 to 1,630 m above sea level. Air temperature at a height of 1.5 m above the ground was recorded hourly at each site, and leaf unfolding was monitored every 10 days. *a* $T_b = 5^\circ\text{C}$, *b* $T_b = 10^\circ\text{C}$; black circle low (0–500 m), black triangle intermediate (500–1,000 m), black square high ($> 1,000$ m) elevations; gray 2007

Fig. 3 Relationship between the heat requirement for leaf unfolding in the growth chamber, calculated as the sum of growing degree days >5 or 10°C from January 1 2011 to the date of leaf unfolding, and the cumulative number of chilling days <5 or 10°C from November 1 2010 to the date of leaf unfolding, for cuttings sampled on 13 different dates from mid-October 2010 until mid-April 2011, from 10 individuals from each population of *Q. petraea* (387 and 1,235 m above sea level) and *Fagus sylvatica* (131 and 1,604 m above sea level). Air temperature was recorded hourly, at a height of 1.5 m above ground level, at each site. *a* $T_b=5^{\circ}\text{C}$, *b* $T_b=10^{\circ}\text{C}$; *black square* high elevation, *black circle* low elevation



variation in the timing of leaf unfolding between and within oak populations is probably due to differences in heat requirements rather than differences in chilling requirements, whereas no differences in forcing requirement were found for a given amount of chilling in beech. Finally, in most beech populations, chilling requirements were not fully satisfied in

current conditions, whereas chilling was insufficient only in 2007 for oak populations, due to an unusually warm winter. This raises the possibility that the widely expected advance in the timing of leaf unfolding with increasing temperatures might be offset by a lack of chilling, particularly in the warmest areas of the distribution of the species concerned.

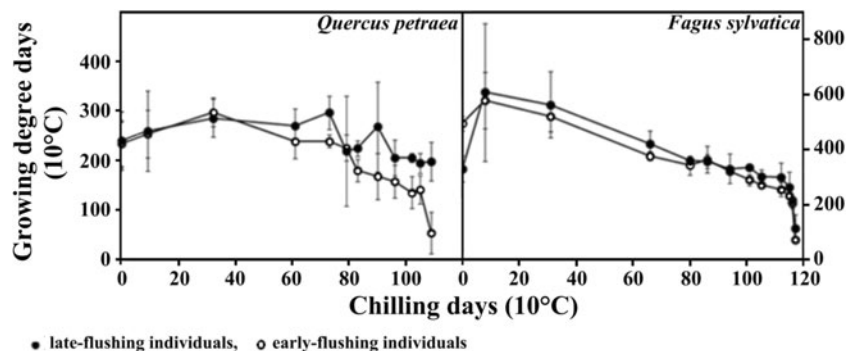


Fig. 4 Relationship between the heat requirement for leaf unfolding in the growth chamber, calculated as the sum of growing degree days $>10^{\circ}\text{C}$ from January 1 2011 to the date of leaf unfolding, and the cumulative number of chilling days $<10^{\circ}\text{C}$ from November 1 2010 to the date of leaf unfolding, for cuttings sampled at 12 and 13 different dates from mid-October 2010 until mid-April 2011 from five early-flushing and five late-flushing individuals from low-elevation

populations of *Q. petraea* (387 m above sea level) and *Fagus sylvatica* (131 m above sea level), respectively (the last sampling date was excluded for oak because leaf unfolding was still occurring in situ for early- and late-flushing individuals). Air temperature was recorded hourly, at a height of 1.5 m above the ground, at each site. *Black circle* late-flushing individuals, *white circle* early-flushing individuals

Relationship between heat and chilling requirements

The linear relationship between heat and chilling requirements found in both experimental and natural conditions confirmed the high chilling requirement for dormancy release in beech (Murray et al. 1989; Falusi and Calamassi 1990; Heide 1993; Caffarra and Donnelly 2011; Vitasse and Basler 2013). In this study, we found that sessile oak required a larger number of growing degree days (high heat requirement) for leaf unfolding than beech after long periods of chilling accumulation in natural conditions. However, for oak, this heat requirement reached a minimum after 90 chilling days ($T_b=5\text{ }^\circ\text{C}$), suggesting that chilling requirements were fulfilled at this point, whereas it continued to decrease until 175 chilling days in beech. For the latter species, heat requirements may likely reach a plateau beyond a certain threshold that cannot be determined with our current dataset. In conclusion, full chilling requirements were not satisfied in most of the beech populations studied, except, perhaps, for the populations at the highest elevations, which experienced about 150 chilling days over the winter. The lower sensitivity of beech to spring temperatures may reflect the lack of sufficient chilling for full dormancy release in the beech populations in our study area. These patterns obtained in situ took both population genetic differentiations and phenotypic plasticity into account, and a common garden experiment would be required to disentangle these effects.

Our results appear to indicate a higher full chilling requirement for dormancy release in beech (at least 120 vs. 90 chilling days) and, probably, higher heat requirements after dormancy release in oak (250 vs. 200 GDD) ($T_b=10\text{ }^\circ\text{C}$). Indeed, while full chilling requirements did not appear to be satisfied in beech populations at high elevation, the minimal beech chilling requirement at low elevation can be approximated to 120 chilling days, corresponding to a heat requirement of 200 GDD ($T_b=10\text{ }^\circ\text{C}$), values at the beginning of the final rapid decline (Fig. 3). For oak, chilling requirements were fulfilled for 90 chilling days, corresponding to the plateau of 250 GDD ($T_b=10\text{ }^\circ\text{C}$) at high elevation and to the final decline at low elevation. Chilling days, widely used in phenological studies to compare species, are a simple proxy to describe a very complex physiological process such as dormancy release, and the amount of chilling requirement should therefore be interpreted with caution. Moreover, the relationship between heat and chilling requirements could be altered by differences in photoperiod between sampling campaigns. However, as all populations were collected through the same day at each campaign, the comparison of chilling and heat requirements was robust and accurate in detecting genetic differentiation and species-specific differences.

Vitasse and Basler (2013) suggested that the date of leaf unfolding in beech is probably driven by both chilling and heat, with an interaction between photoperiod and heat

requirement. Laube et al. (2013) confirmed experimentally that this species was sensitive to photoperiod when chilling requirements are not satisfied. In our experiment, during the endodormancy phase, we observed no difference in temperature requirements between low- and high-elevation populations of beech. Cuttings were exposed to a longer photoperiod in the growth chamber than in situ. As long days have been shown to substitute partially for winter chilling in this species (Falusi and Calamassi 1996), this may have buffered the possible genetic differences in chilling requirements between low- and high-elevation populations.

Differences in requirements between and within populations

Our experiment under controlled conditions allowed us to compare heat and chilling requirements both between and within populations of the two tree species. For the same amount of chilling, oak high-elevation populations required more degree days for leaf unfolding than low-elevation populations, even during the endodormancy phase. Similarly, within populations at low elevation, late-flushing individuals required larger numbers of growing degree days for leaf unfolding than early-flushing individuals (after entry into endodormancy). All these populations seemed to have the similar full chilling requirement for dormancy release (90 chilling days, $T_b=10\text{ }^\circ\text{C}$). Thus, genetic differentiation between and within populations may be associated with a difference in heat requirement for oak. This may explain the cogradient variation found in *common gardens* for oak (Vitasse et al. 2009a; Alberto et al. 2011): Populations from high elevations may flush later due to higher heat requirements rather than chilling requirements. Charrier et al. (2011) and Mauget and Germain (1980) also observed a higher heat requirement after the same amount of chilling for late genotypes of walnut trees.

For beech, for the same amount of chilling, no differences in heat requirements for leaf unfolding were observed between low- and high-elevation populations and between early- and late-flushing individuals throughout most of the experiment. However, at the end of the experiment, we observed a rapid decline of growing degree days for the low-elevation population, but not for the high-elevation population. Thus, differences observed in situ and the counter-gradient pattern observed in *common gardens* (vonWuehlisch et al. 1995; Chmura and Rozkowski 2002; Vitasse et al. 2009a; Gomory and Paule 2011) between populations may be due to differences in chilling requirements for dormancy release rather than in heat requirements, which are clearly low for both populations.

However, differences between and within species may also be accounted for by differences in cumulative chilling thresholds. High-elevation populations may have a slightly lower threshold for heat accumulation, or may simply accumulate

growing degree days more efficiently (more sensitive). Furthermore, different populations may accumulate chilling in different ways, with different ranges of effective temperatures. A more detailed experiment, with variations of chilling and heat temperatures for different populations, would be required to improve characterization of the range of temperatures over which both chilling and heat are effective.

Implications for global warming

Many studies have reported an advance in the timing of leaf unfolding in temperate trees with current increases in air temperature (Root et al. 2003; Menzel et al. 2006; Richardson et al. 2006), but such advances may not necessarily occur at the southern limit of the species distribution range. In 2007, the winter in the Pyrénées was unusually warm until late February (Météo France, Lourdes, see Fig. S1) and followed by two typical months (March and April 2.08 °C warmer than 1931–2011 but only 0.38 °C warmer than our other years of study). There may therefore have been insufficient chilling in that year. Delpierre et al. (2009) reported a general trend toward earlier leaf unfolding in the forest trees of Europe in 2007. By contrast, we observed no change, or even a delay (7 days) in the timing of leaf unfolding for oak, at high and low elevations, respectively (versus the average for the whole study period), probably due to a lack of chilling. Oak populations thus seem to have required much more heat temperatures to achieve leaf unfolding in this year than in the other years, even if the date of leaf unfolding was not itself delayed (Fig. 2). By contrast, we did not observe this pattern for beech at low elevations in 2007 because full chilling requirements were not satisfied in most of the beech populations along the gradient in any of the years studied. Climatic events such as that in 2007 are likely to become increasingly frequent in the next few years. These results strongly suggest that populations growing in the warmest areas of the current species distribution will rapidly be faced with conditions of insufficient chilling for full dormancy release.

Looking into the black box

The role of chilling in the timing of leaf unfolding is well documented in temperate tree species, particularly for fruit trees (Ruiz et al. 2007; Luedeling 2012; Darbyshire et al. 2013a), but a large gap remains in our knowledge, concerning the range and optimum for chilling temperatures and the complex interplay between chilling and heat requirement (Shirazi 2003). No data are currently available for determining the optimum temperature for dormancy release in most forest tree species, including *Q. petraea* and *Fagus sylvatica*. Effective chilling temperatures are assumed to be below 10 °C, with an optimum range of 2–7 °C for most species (Coville 1920; Doorenbos 1953; Nienstaedt 1966; Cannell 1989; Battey

2000). The heat vs. chilling requirement relationship for in situ populations estimated with $T_b=10$ °C was unrealistic for beech, with several GDD values equal to 0 for high chilling days. Consistent with the R^2 values, we thus discarded this relationship and selected the one with $T_b=5$ °C. However, we did not find any pattern with $T_b=5$ °C for the experiment in climatic chamber, with unrealistic GDD and chilling days values at low elevation. This discrepancy between optimal temperature thresholds found in situ and for the climatic chamber experiments might be due to the interaction between photoperiod and chilling requirements (Vitasse and Basler 2013). Furthermore, chilling temperatures clearly overlap active growth temperatures, making it difficult to include this interplay in phenological models. Moreover, our experiment demonstrates that active growth temperatures could act in conditions in which dormancy was not totally released (i.e., leaf unfolding observed for buds sampled from October to January). This phenomenon therefore undoubtedly occurred in situ. Chilling and heat temperatures cannot be disentangled in situ, and chilling requirements are probably satisfied in most of the distribution area of temperate trees, masking their role and making them difficult to study. This study thus highlights the difficulties involved in unraveling the complex interplay between chilling and heat requirements for leaf unfolding and the relationships between genetics and environment. These results will be of great importance for the future modeling of budburst dates. Indeed, chilling requirements will increasingly need to be taken into account in models, together with the local adaptation of populations. This will require further experiments, with controlled chilling.

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