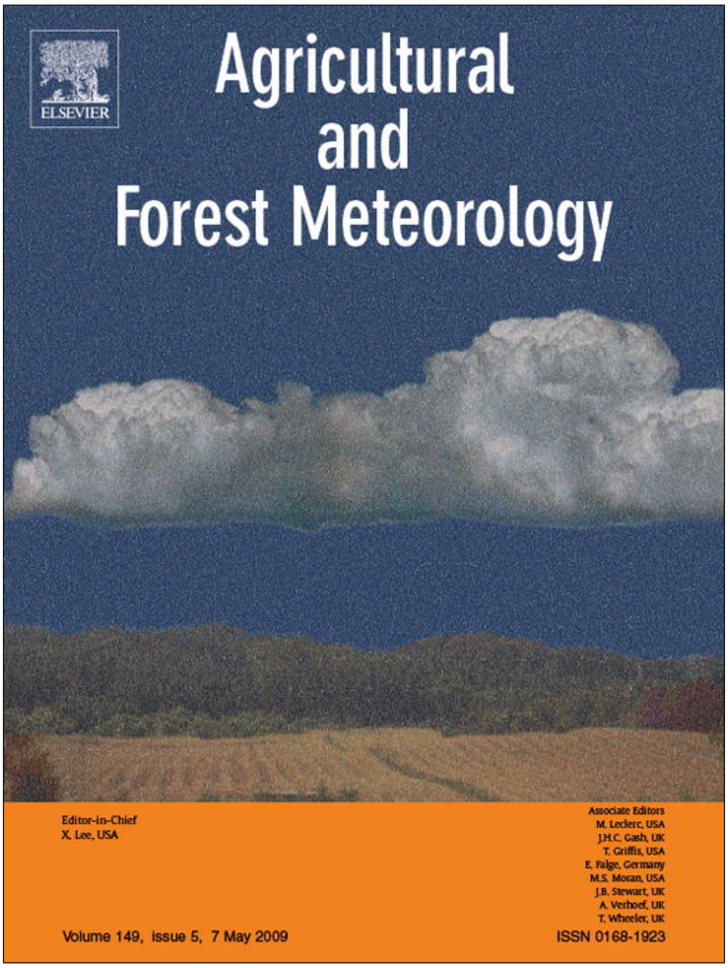

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Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses?

Yann Vitasse [a,b], *Sylvain Delzon* [a,b,*], *Eric Dufrêne* [c,d,e], *Jean-Yves Pontailler* [c,d,e], *Jean-Marc Louvet* [a,b], *Antoine Kremer* [a,b], *Richard Michalet* [a,b]

[a] *Université de Bordeaux, UMR BIOGECO, Av. des Facultés, 33405 Talence, France*
[b] *INRA, UMR BIOGECO, F-33610 Cestas, France*
[c] *CNRS, Laboratoire Ecologie Systématique et Evolution, F-91405 Orsay, France*
[d] *Univ Paris-Sud, UMR 8079, F-91405 Orsay, France*
[e] *AgroParisTech, F-75231 Paris, France*

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ABSTRACT

Consequences of climate warming on tree phenology are readily observable, but little is known about the differences in phenological sensitivity to temperature between species and between populations within a species. The aim of the present study is to compare phenological sensitivities to temperature of seven woody species between each other and within-species between two geographical areas using both altitudinal and temporal gradients (*Abies alba*, *Acer pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Ilex aquifolium* and *Quercus petraea*). The timing of leaf unfolding was monitored (i) over 2 years along two altitudinal gradients in the Pyrénées mountains (six species), and (ii) over 22 years in Fontainebleau forest (four species). Three species were present in both areas which allowed us to compare their phenological sensitivity to temperature over altitudinal and temporal gradients. Along altitudinal gradients, we observed for all species an advance in leaf unfolding with decreasing elevation, ranging from 11 to 34 days 1000 m^{-1} for beech and oak, respectively. Across the temporal gradient, we found significant advances in leaf unfolding for oak (−0.42 days $year^{-1}$) and ash (−0.78 days $year^{-1}$) since 1976, whereas no significant advance was observed for beech and hornbeam. For both gradients and for all species, significant correlations were found between leaf unfolding dates and temperature, except for beech in the temporal study. Moreover, we highlighted that phenological sensitivity to temperature was very similar between the two geographically separated populations (Pyrénées and Fontainebleau forests). Thus, oak had the strongest sensitivity (−7.48 and −7.26 days $°C^{-1}$ in altitudinal and temporal gradient, respectively) and beech had the lowest (−2.09 and −2.03 days $°C^{-1}$). Our results suggest that population sensitivity to global warming might be stable for a given species, in spite of its possible local adaptation.

1. Introduction

Tree phenology plays a crucial role in the carbon balance and productivity of terrestrial ecosystems (Keeling et al., 1996; Rotzer et al., 2004; Loustau et al., 2005) and in tree fitness (Rathcke and Lacey, 1985). To assess the possible impact of climate change on tree growth and species distribution, it is thus important to identify the climatic variables driving tree

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[*] *Corresponding author*. Tel.: +33 5 40 00 38 91; fax: +33 5 40 00 36 57.
E-mail address: sylvain.delzon@u-bordeaux1.fr (S. Delzon).

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phenology and the sensitivity of tree species to these variables. In mid and high latitudes, plant development is characterized by a rest period in winter and by an active growing period in spring and summer. Therefore, the impacts of climate warming on plant phenology are considered to be of major importance in the northern hemisphere where the growing season length closely depends on temperature (Zhang et al., 2004; Chen et al., 2005; Linderholm, 2006). Timing of tree phenological events is known to be tightly correlated to temperature and photoperiod (Wielgolaski, 1999; Rotzer and Chmielewski, 2001; Menzel, 2002; Doi and Katano, 2008). Indeed in temperate and boreal zones, models which predict most accurately tree leaf onset use temperature and daylength as parameters (*e.g.* Cannell and Smith, 1983; Chuine and Cour, 1999; Schaber and Badeck, 2003). Although it is assumed that spring temperatures play a crucial role in the triggering of bud burst, the roles of chilling and daylength in dormancy release still give rise to controversy. Several experimental studies highlighted that long days and chilling temperatures generally reduced the thermal time to budburst (Heide, 1993a; Falusi and Calamassi, 1990) but some species exhibited little or no sensitivity to these factors (Heide, 1993a; Schaber and Badeck, 2003). Adaptive responses of tree phenology to their local environment in temperate or boreal zones are either to avoid late frost damages and/or to increase their growing season length (Lockhart, 1983; Lechowicz, 1984). An earlier leaf unfolding provides a longer growing season but also induces a higher risk to late frost damage on leaves, resulting in reduction of leaf area and photosynthetic carbon gains (Leinonen and Hanninen, 2002). Timing of phenological events is therefore one of the processes through which temperature influences tree growth (Kramer et al., 2000) and constitutes a crucial trait driving survival responses to seasonal environmental changes (Orshan, 1989; Kikuzawa, 1995).

In Europe, there is a long history of phenological studies and these investigations concluded that climate warming induced advances in leaf unfolding and flowering events during the last decades (Menzel and Fabian, 1999; Ahas et al., 2002; Chmielewski and Rotzer, 2002; Root et al., 2003; Menzel et al., 2006) as well as in North America (Beaubien and Freeland, 2000; Schwartz and Reiter, 2000). However, most phenological studies were carried out along latitudinal gradients where temperature and photoperiod varied simultaneously and may influence plant phenology (Chmielewski and Rotzer, 2001; Ahas et al., 2002). To avoid photoperiod effects, phenological data monitored either along altitudinal gradients located within a short latitudinal range, or in wide areas along continental gradients or at a single location but over a long period, are necessary (Matsumoto et al., 2003; Richardson et al., 2006; Wesolowski and Rowinski, 2006). Species comparisons are crucial to evaluate the potential effects of climate warming on tree growth and species distribution. Indeed, since temperate forests are mostly mixed-species deciduous forests, differences in species-specific phenological responses to temperature could modify biotic interactions (Kramer et al., 2000) which is known to affect species distribution (Chuine and Beaubien, 2001).

Local adaptation of tree phenology could be a serious constraint on our ability to predict the general response of phenology to global climate changes. Indeed, the phenology of temperate woody plants is commonly assumed to be locally adapted to climate and a number of studies using provenance tests highlighted phenological differences between populations (von Wuehlisch et al., 1995; Ducousso et al., 1996; Chmura and Rozkowski, 2002; Chmura, 2006). Nevertheless, we do not know whether populations from different climatic zones will react in the same way to temperature increase (identical responses) in spite of their genetic differences. A modelling study has tested this hypothesis on flowering and concluded that local adaptation (genetic differences) will be of negligible impact when predicting the phenological responses of temperate lowland tree species (Chuine et al., 2000a). Very few studies have already compared leaf unfolding of several geographically distant tree populations to check whether the phenological sensitivity to temperature differs between populations of a given species (but see Karlsson et al., 2003; Chuine et al., 2000a). This question is crucial in determining the growing season length and for improving models and predicting the possible impacts of climate change on forests ecosystems.

The aim of our study was to assess spring leaf phenology of tree species growing in the temperate zone and to determine how temperature affects this event for various species. We first characterized the altitudinal trends in leaf unfolding timing of six woody temperate species along two altitudinal gradients in the Pyrénées mountains. Secondly, we analysed the timing of leaf unfolding of four tree species in a lowland forest monitored since 1976. Then phenological data were fitted to temperature in order to quantify leaf phenology sensitivities to temperature for the seven studied species. Finally, to investigate whether spring leaf phenology of different populations from the same species could respond differently to climate warming, we compared the temperature sensitivities of leaf phenology between populations for the three species occurring along both gradients.

2. Materials and methods

2.1. *Study areas and species*

The altitudinal study was conducted in two valleys of the Pyrénées mountains in southern France (from 42°53′N, 00°25′W to 43°45′N, 00°14′W). A first transect was set up in the Ossau valley (Pyrénées Atlantiques) and a second one in the Gave valley (Hautes Pyrénées). These two valleys, 30 km distant from each other are parallel and elevation increases from North to South. This region is characterized by a temperate oceanic climate, with a mean annual temperature of 12 °C and precipitation of 1079 mm (1946–2001) at low elevation (Tarbes, 43°11′N, 00°00′W, 360 m ASL, Météo France). There is a predictable gradient of temperature, precipitation and potential evapotranspiration along the two altitudinal transects. Average annual temperatures decreased linearly with elevation: temperature lapse rate is about 0.43 °C for every 100 m increase in elevation (average from 2005 to 2006).

We selected six common European woody species belonging to different taxa (conifers vs. broadleaved angiosperms), exhibiting different water transport characteristics (ring porous, diffuse porous and tracheid bearing), leaf lifespan (evergreen vs. deciduous) and nutrient use efficiency (conservative vs. exploitative). There were four deciduous species, sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), and two evergreen species, silver fir (*Abies alba* Millet) and holly (*Ilex aquifolium* L.). For each of the six species and in each transect, natural established populations were sampled at five altitudinal levels: 100, 400, 800, 1200 and 1600 m ASL (±50 m), i.e. at the hill and mountain vegetation belts. We used a GPS receiver (GPS Pathfinder ProXR, Trimble) to determine the precise altitude of each population. The range of the altitudinal gradient averaged 1367 m but varied according to the species due to their natural distribution area, ranging from 1164 to 1499 m for sycamore and oak, respectively (Table 1). For each population, we sampled 10 dominant and mature individuals of comparable height except for holly, always selected under forest canopy. All populations were located on a North-facing slope, except sessile oak which only naturally occurred in South-facing slopes.

The temporal study was located 650 km north of the altitudinal study in the Fontainebleau forest, (South-east of Paris, France, 48°25′N, 02°40′E). This large mixed deciduous forest extends over 17 000 ha on a flat terrain at an average elevation of 120 m. Climate is temperate with an average annual temperature of 10.2 °C and an average annual precipitation of 720 mm. The dominant species are oaks (*Q. petraea* (Matt.) Liebl. and *Quercus robur* (Matt.) Liebl.), European beech and Scots pine (*Pinus sylvestris*). The main understorey species are hornbeam (*Carpinus betulus* L.) and beech. Two plots, located 3 km north-west of the city of Fontainebleau, were selected. Both were ‘‘integral biological reserves’’ having experienced no notable forest exploitation for at least four centuries (Pontailler et al., 1997). The first one, ‘‘La Tillaie’’ (area 33 ha), is dominated by beech with scattered ash at the pole stage. The second one, ‘‘Le Gros Fouteau’’ (area 24 ha) is an oak-dominated stand with a heterogeneous understorey of hornbeam. Since 1976, phenology was monitored annually on four tree species: beech and ash in La Tillaie, and oak and hornbeam in Le Gros Fouteau. For each species observations were made on dominant trees (except for hornbeam in understorey position) and the number of target tree individuals varied between 30 and 100.

2.2. *Phenological observations*

Along the altitudinal gradient, timing of leaf unfolding (leaf unfolding, LU) was monitored during two consecutive years (2005 and 2006). We visited each population every 10 days from March to June to carry out phenological observations on the 10 selected individuals. Observations were made using binoculars (magnifying power: 10×) always by the same observer, at approximately 15 m distance from the tree. We recorded the development stage from bud dormancy to leaf unfolding, using a two to five intermediate stage scale according to the species (Table 2), and we visually evaluated the percentage of buds that were at the final stage. We considered that LU was reached for a bud when at least one of its leaves was fully unfolded. At the tree level, leaf unfolding date (LUD) was determined 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, LUD was calculated as the average of the estimated dates for the 10 sampled individuals.

For the temporal gradient, phenological observations were carried out from 1976 to 1984 and from 1992 to 2006 (over 22 years). However, depending on plot and species, some years were lacking (see Table 1 for details). Using binoculars, observations were made twice a week from March to

Table 1 – Altitudinal ranges (maximum amplitude of elevation) encompassed by each species along the altitudinal gradients studied in the French Pyrénées mountains and time period studied for each species in the Fontainebleau forest (temporal study). For the altitudinal study, n is the number of populations in both transects, Δ*a* is the altitudinal range (m), low and high representing the elevation (m) of the lowest and highest sites studied, respectively. ΔT2005 and ΔT2006 are the temperature lapse rates for each studied species (air temperature averaged from January to May) in 2005 and 2006, respectively. For the temporal study, n is the number of observations per species (number of years). Δ*T* is the temperature lapse rate (air temperature averaged from January to May) between the warmest and coldest years.

Species	Altitudinal ranges (Δ*a* [low–high]) (m)	*n*	ΔT2005 (°C)	ΔT2006 (°C)
Altitudinal study (Pyrénées)				
Abies alba	1182 [422–1604]	7	7.6	6.6
Acer pseudoplatanus	1164 [450–1614]	8	5.6	4.9
Fagus sylvatica	1473 [131–1604]	10	8.4	6.9
Fraxinus excelsior	1403 [130–1533]	9	7.0	6.1
Ilex aquifolium	1483 [131–1614]	9	7.0	5.8
Quercus petraea	1499 [131–1630]	10	6.9	6.3

Species	Time period	*n*	Δ*T*
Temporal study (Fontainebleau)			
Carpinus betulus	1976–83; 1992–97; 1999; 2001–02; 2004–06	20	3.3
F. sylvatica	1976–84; 1992–06	24	
F. excelsior	1976–84; 1992–06	24	
Q. petraea	1976–79; 1982; 1993; 1995–06	19	

Table 2 – Phenological meaning of bud development codes used in the field. The date of leaf unfolding for one tree individual was reached when 50% of its buds had reached the stage indicated here in bold type.

Code	*A. alba*	*A. pseudoplatanus*	*C. betulus*	*F. sylvatica*	*F. excelsior*	*I. aquifolium*	*Q. petraea*
0	Dormant winterbud	Dormant winterbud	Dormant winterbud	Dormant winterbud	Dormant winterbud	Dormant winterbud	Dormant winterbud
1	Buds expanding and are new green behind a transparent cupule	Bud-swollen (a whitish down is visible)	Bud-swollen	Bud-swollen	Bud-swollen and green	Bud-opening	Bud-swollen
2	**Needles unfolding, cupule coming off**	Buds expanding and green	Bud-burst	Bud-burst	Bud-burst	**At least one leaf unfolding**	Buds expanding and are new green
3		Bud-burst	**At least one leaf unfolding**	**At least one leaf unfolding**	**At least one leaf unfolding**		Bud-burst
4		**At least one leaf unfolding**					**At least one leaf unfolding**

mid-May along transects, on dominant trees of the relevant species. Observations and calculation of LUD were conducted using the same protocol as for the altitudinal study (Table 2) but the number of observed trees was different, ranging between 30 (hornbeam, ash) and 100 (beech, oak).

2.3. *Meteorological measurements*

For the altitudinal study, air temperature was measured using data loggers (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, MA) located at each site along the altitudinal gradients (31 sites). At each site, sensors were installed 1.5 m-high above the ground using a pole located in an open area near to the studied population (from 10 to 100 m distance to the plot, at the same elevation). Sensors were protected by a white plastic shelter to prevent any exposure to rain or to direct sunlight. Data were recorded every 15 min from 1 January 2005 to 15 June 2005 and hourly from 15 June 2005 to 31 December 2006. During 2 weeks in February 2005, several weather stations suffered from a technical fault and the missing data were gap-filled by linear interpolation using data from the most correlated functional weather stations ($R^2 > 0.91$). All sensors were inter-calibrated in the laboratory before installation. For the temporal gradient, we used data from the meteorological station of Melun-Villaroche located 20 km-north of the studied plots (Melun, 48°39′N, 02°38′W, 91 m ASL, Météo France). In both gradients, mean spring temperature was calculated as the mean daily temperature from 1 January to 31 May.

2.4. *Statistical analysis*

Phenological data from the altitudinal study were analysed per year using a split-plot analysis of variance (ANOVA), with valley as block, altitude as main plot effect and species as subplot effect. For each species and each gradient, LUD variations according to altitude (days 1000 m^{-1}), time (days $year^{-1}$) and temperature of the first 5 months (days $°C^{-1}$) were tested by linear regression analyses. A covariance analysis (ANCOVA) was used to compare within-species regression lines on the relationship between LUD and temperature between the two studied gradients (Pyrénées vs. Fontainebleau). We thus tested whether any differences in phenological sensitivity to temperature exists between populations. All the analyses were performed with the SAS software (SAS, version 9.1, SAS Institute, Cary, NC, USA).

3. Results

3.1. *Altitudinal gradients*

Average spring temperatures (January–May) decreased linearly with elevation by 0.51 and 0.44 °C for every 100 m increase in elevation, in 2005 and 2006, respectively ($p < 0.0001$) (Fig. 1a). Temperature differences between populations of low and high elevations were 8.4 and 7.4 °C in 2005 and 2006, respectively (Fig. 1a). Mean spring temperatures were warmer in 2006 than in 2005, for all sites. The lapse rate of mean spring

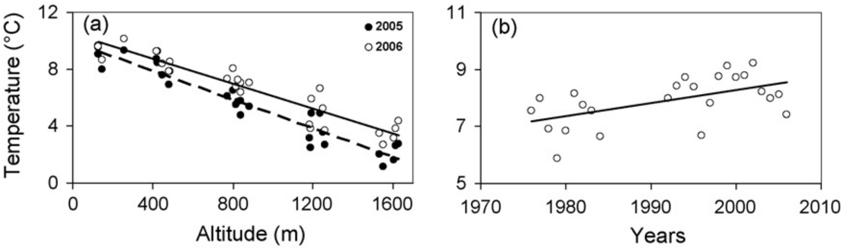

Fig. 1 – (a) Relationship between air temperature averaged from January to May (2005: full circles and dashed line; 2006: open circles and solid line) and elevation. Slopes indicate a 0.51 and 0.44 °C 100 m^{-1} decreases for 2005 and 2006, respectively ($p < 0.0001$). (b) Mean air temperature from January to May *vs.* years during monitoring phenology (1976–1984 and 1992–2006) at Melun. Slope indicates an increase of 0.46 °C $decade^{-1}$ ($p < 0.0063$).

Table 3 – Split-plot analysis of 2005 and 2006 leaf unfolding dates, with transect as block, altitude as main plot and species as subplot.

	Leaf unfolding 2005				Leaf unfolding 2006			
	DF	MS	F	p	DF	MS	F	p
Transect	1	9.5	0.05	ns	1	1.19	0.01	ns
Altitude	4	20763	113.1	***	4	13319	74.5	***
Species	5	4943	202.3	***	5	6597.5	264.4	***
Species × altitude	18	722	29.5	***	18	712.8	28.6	***

DF: degree of freedom; MS: mean square; F: Fisher's F value; ns: non-significant.
*** $p < 0.001$.

temperatures between sites occupied by a species varied from 4.9 °C in 2006 for sycamore to 8.4 °C in 2005 for beech, as a result of differences in species distribution range across the elevation gradient (Table 1). In addition, temperature lapse rates were lower in 2006 than in 2005 for all species.

LUD were not significantly different between the two transects (Table 3), independently of the year. Consequently, data of LUD from the two transects were pooled in the following analyses for each altitude. Overall, we found similar altitudinal patterns in spring phenology from year to year whatever the species (similar shape between curves, Fig. 2). However, LU occurred earlier in 2006 than in 2005 and interannual differences of LUD increased with elevation except for ash (Fig. 2). Variations in LUD along altitudinal gradients (amplitudes) in 2005 were always higher than those of 2006, except for ash (Fig. 2). These differences were due to higher spring temperatures in 2006, especially at the high elevation sites, resulting in a lower temperature gradient in 2006 (Fig. 1a). Table 3 reports significant effects of altitude, species and their interaction on LUD, showing that altitudinal variations in phenology differed according to species. For all species, populations at higher altitudes showed later spring phenology: LUD was delayed with increasing elevation (Fig. 2 and Table 4). Moreover, we found large differences in the amplitude of LUD between species, ranging from 11 days to 34 days for every 1000 m increase in elevation, for beech and oak respectively on average for 2005 and 2006 (Table 4). Fir also exhibited a strong amplitude in LUD along the gradient with, on average, 32 days 1000 m^{-1}. Ash, sycamore and holly had intermediate amplitudes of LUD. LUD also differed according to species at a given altitude (Fig. 2); at low elevation (100 and 400 m ASL), fir, sycamore and oak always leafed out before late April (DOY 115) whereas beech, ash and holly leafed out later or around this date, oak and holly being the earliest and the latest, respectively (24 March and 8 May, DOY 91 and 129). At the highest elevations (1200 and 1600 m), species ranking

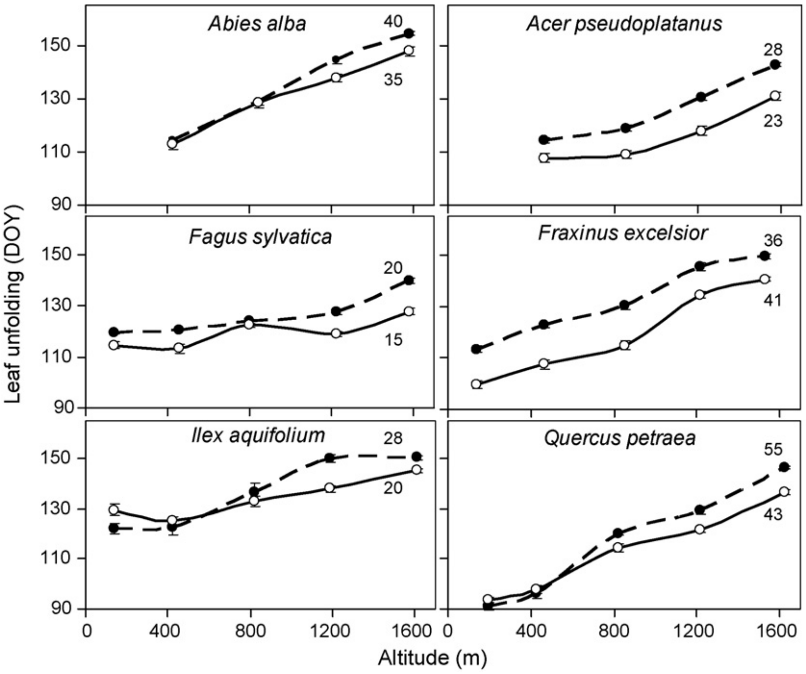

Fig. 2 – Leaf unfolding dates (DOY, day of the year) vs. elevation for the studied species in 2005 (full circles, dashed line) and 2006 (open circles, solid line) in the Pyrénées mountains. Each point represents the mean value of all individuals growing at the same elevation in both transects (two populations, *n* = 20 individuals) and bars are standard errors. The numbers above and below the curves represent the amplitudes of LUD across the gradient in 2005 and 2006, respectively.

Table 4 – Slopes of the linear regressions between LUD and altitude for every 1000 m increase in elevation in the Pyrénées in 2005 ($\delta_{LU2005}/\delta_{1000\ m}$, days 1000 m^{-1}) and 2006 ($\delta_{LU2006}/\delta_{1000\ m}$, days 1000 m^{-1}) and mean spring temperatures in both studies (Pyrénées and Fontainebleau) (δ_{LU}/δ_{Ts}, days °C^{-1}) for each species. R^2 indicates the determination coefficient of these last regressions. An analysis of covariance (ANCOVA) evaluated for a given species the location effect (Pyrénées or Fontainebleau, covariate) on the δ_{LU}/δ_{Ts} relationship. If slopes are not significantly different, the relationship between LUD and temperature are not moderated by location which means that the shift in LU per degree was similar for the two gradients (temporal and altitudinal).

Species	Pyrénées				Fontainebleau			ANCOVA (*p*)
	$\delta_{LU2005}/\delta_{1000\ m}$	$\delta_{LU2006}/\delta_{1000\ m}$	δ_{LU}/δ_{Ts}	R^2	δ_{LU}/δ_{Yr}	δ_{LU}/δ_{Ts}	R^2	
A. alba	$+35.5^{**}$	$+29.8^{**}$	-5.25^{***}	0.92	–	–	–	–
A. pseudoplatanus	$+26.2^{*}$	$+21.4^{ns}$	-5.37^{***}	0.84	–	–	–	–
I. aquifolium	$+22.7^{*}$	$+12.4^{*}$	-3.73^{***}	0.79	–	–	–	–
F. sylvatica	$+13.1^{*}$	$+8.7^{ns}$	$\mathbf{-2.09}^{***}$	0.63	-0.03^{ns}	$\mathbf{-2.03}^{ns}$	0.15	ns
F. excelsior	$+26.9^{**}$	$+30.8^{**}$	$\mathbf{-6.82}^{***}$	0.93	-0.78^{***}	$\mathbf{-6.66}^{**}$	0.34	ns
Q. petraea	$+39.7^{***}$	$+30.1^{***}$	$\mathbf{-7.48}^{***}$	0.91	-0.42^{*}	$\mathbf{-7.26}^{**}$	0.39	ns
C. betulus	–	–	–	–	-0.18^{ns}	-4.58^{*}	0.27	–

ns: non-significant ($p > 0.05$).
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

changed: the three earlier species were sycamore, beech and oak (LUD occurred before 24 May, DOY 144) as opposed to holly, ash and fir. It is worthwhile noting that LUD for oak at 100 m ASL occurred 25 days earlier than beech whereas at 1600 m ASL, LUD of oak occurred 8 days later than beech.

3.2. *Temporal gradient*

In Fontainebleau forest, spring temperatures rose at a rate of 0.046 °C year^{-1} ($p < 0.006$) during the study period (1976–2006, Fig. 1b) and contrasting results have been observed across species for phenology. Indeed, there were no significant differences in LUD over years for beech and hornbeam. LU of beech occurred around day 115 (25 April) and LU of hornbeam occurred around day 93 (3 April). In contrast, we observed a significant temporal shift of LUD for both oak and ash, of 0.42 and 0.78 days year^{-1}, respectively (Fig. 3 and Table 4). From 1976 to 1984, LU of oak occurred around 26 April against around 16 April from 1992 to 2006. For ash, LU occurred around 14 May during the former period and around 27 April during the latter. Over the whole study period, amplitude in LUD differed strongly between species, with the highest amplitude for oak and ash (42 and 36 days of advance between 1979 – cool year – and 2003/1997 – warm years – respectively) and the lowest for hornbeam and beech (24 and 16 days of advance between 1979 – cool year – and 1994/1997 – warm years – respectively). 1979 was the coolest year within the whole period (−1.9 °C below the average) and for all four species it corresponded to the latest LUD.

3.3. *Phenological sensitivity to temperature*

Along the altitudinal gradient, highly significant correlations were found between spring temperatures and LUD for all species (Fig. 4a). However, the slopes of the regressions were highly species-dependent (Fig. 4a and Table 4). The strongest sensitivity to temperature was found for oak and ash (−7.5 and −6.8 days of advance in LUD °C^{-1}, respectively); the lowest for holly and beech (−3.7 and −2.1 days °C^{-1}, respectively); and

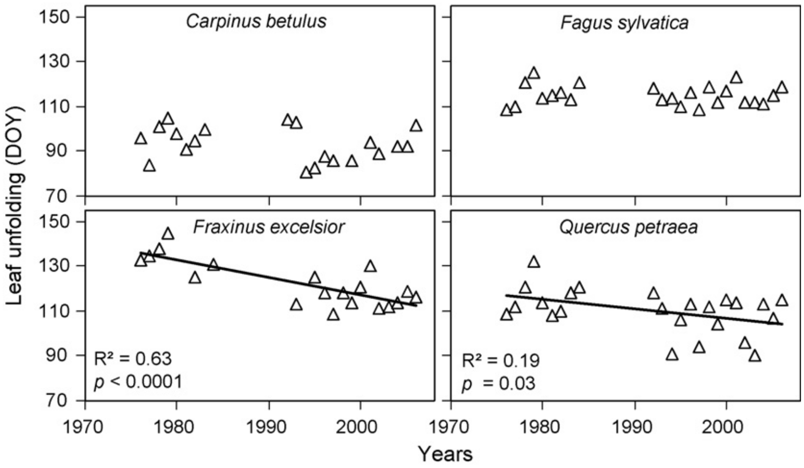

Fig. 3 – Trends in leaf unfolding dates (DOY, day of the year) since 1976 for the four studied species in the Fontainebleau forest.

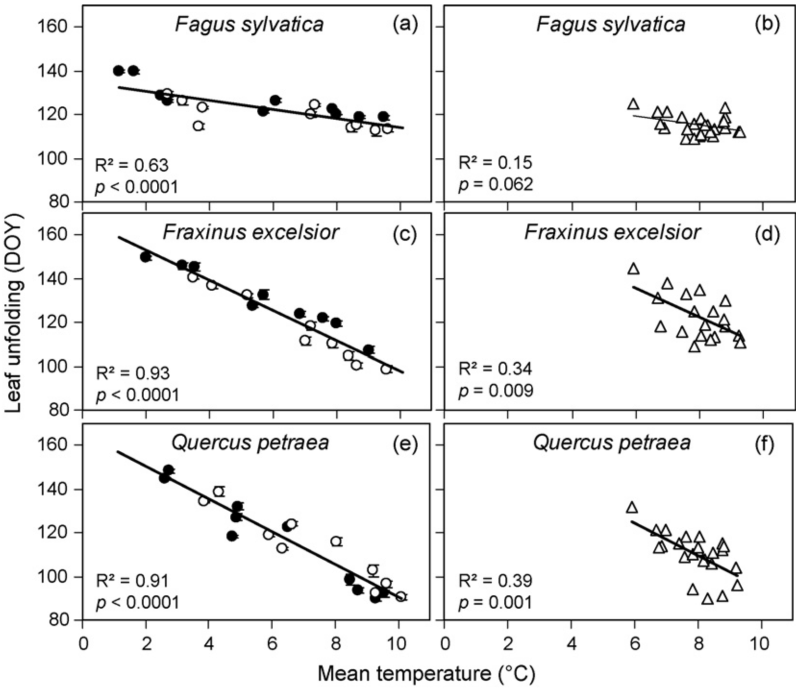

Fig. 4 – Relationships between LUD (leaf unfolding dates) and mean spring temperatures per species (a–c) along the altitudinal gradient (2005: full circles; 2006: open circles), and (d–f) across the temporal gradient (Fontainebleau forest). See Table 4 for the R^2 and p-values.

intermediate ones for fir and sycamore (−5.3 and −5.4 day-°C^{-1}, respectively).

Along the temporal gradient, we observed significant correlations between LUD and spring temperature for oak, ash and hornbeam but not for beech ($p = 0.061$) (Fig. 4b and Table 4). In agreement with the results of the altitudinal study, temporal data showed that phenological sensitivity to temperature strongly differed between species. Beech exhibited the lowest sensitivity (−2.0 days °C^{-1}) and oak the highest (−7.3 days °C^{-1}); ash also had a strong sensitivity (−6.7 day-days °C^{-1}) and hornbeam an intermediate one (−4.6 day-days °C^{-1}). These values were very close to those found along the altitudinal gradient. Indeed, we did not find any significant slope differences among the two studies for a given species (ANCOVA, Table 4). This means that LUD sensitivity to temperature was similar for each species through the two gradients (temporal and altitudinal gradients) (Table 4, bold characters).

4. Discussion

This study allowed us to characterize trends in spring phenology of tree species along altitudinal and temporal gradients and to quantify their phenological sensitivity to temperature. We found high correlations between LUD and temperature for all species and gradients, except for beech in the temporal gradient (only marginal). However, we observed that temperature sensitivity of leaf phenology was highly species-dependent. In particular, the two dominant species of European temperate forests, oak and beech, exhibited very contrasting responses. Then, we showed that temperature sensitivity of leaf phenology were identical within-species populations for the three studied species (oak, beech and ash).

4.1. *Altitudinal and temporal trends*

Our study showed that there were strong altitudinal trends in leaf phenology with a delay of 1.1–3.4 days for every 100 m increase in elevation. However, these trends strongly varied among species. Our results are not in accordance with Hopkin's Law, stating that a 3.3 days delay in the onset of spring occurs for every 100 m increase in elevation (Fitzjarrald et al., 2001) whatever the species. Indeed, this law cannot be applied to all species, as beech and holly for instance. Few data sets are available along altitudinal gradients but several studies found similar results, with a delay of 2–4 days 100 m^{-1} (Rotzer and Chmielewski, 2001; Dittmar and Elling, 2006; Richardson et al., 2006). For example, Dittmar and Elling (2006) found a delay of 2 days 100 m^{-1} for beech and Rotzer and Chmielewski (2001) showed a delay of 2.8 days 100 m^{-1} for downy birch.

In the temporal gradient, we found an advance in LUD during recent decades for two species, ash and oak (7.8 and 4.2 days decade^{-1}, respectively), whereas no significant trend was found for beech and hornbeam. Tree phenology was widely monitored in low elevation forests or in International Phenological Gardens (IPG) in Europe during recent decades. In general, all these studies showed an advance in spring phenological events such as flowering or flushing in relation to climate warming (Menzel and Fabian, 1999; Beaubien and Freeland, 2000; Schwartz and Reiter, 2000; Ahas et al., 2002; Chmielewski and Rotzer, 2002; Schaber and Badeck, 2005; Menzel et al., 2006). In Europe, Menzel (2000) used IPG data to show that spring phenological events were advanced by 6.3 days between 1951 and 1996 (2.3 days decade^{-1}). Another study considered this rate to vary between 1.4 and 3.1 days decade^{-1} for European trees during the past 30–48 years (Walther et al., 2002). Finally, the advance in spring/summer phenology of more than 125 000 observational series of plants and animals was reported to average 2.5 days decade^{-1} in 21 European countries over the period 1971–2000 and it was strongly correlated to an increase in temperature in the study area (Menzel et al., 2006). Phenological advances observed in our study for oak and ash were higher than those found in previous studies (Scheifinger et al., 2002; Schaber and Badeck, 2005) but could be explained by the strong temperature increase in spring which occurred between 1976 and 2006 in the studied area (0.46 °C decade^{-1}, $R^2 = 31\%$, $p < 0.006$, Fig. 1b).

4.2. *Phenological sensitivity to temperature*

We found highly significant relationships between LUD and spring temperature for all species in both locations, except for beech in the temporal gradient. These results support the hypothesis that in temperate climates, the timing of tree flushing is mainly sensitive to the temperature of the previous months (Saxe et al., 2001; Badeck et al., 2004). Moreover, studies based on phenological models showed that effective temperatures after dormancy release are sufficient predictive variables; temperatures at the end of winter and beginning of spring explained the strongest percentages of variance for timing of flushing (Hunter and Lechowicz, 1992; Chuine and Cour, 1999; Linkosalo et al., 2006). Penuelas et al. (2002) also showed that these events were correlated to the increase in temperature during the winter/spring period, especially temperatures from January to April which correspond to the period of tree bud quiescence. In a recent study, Menzel et al. (2006) showed that the best correlation was found between LUD and mean monthly temperatures of the month of leaf onset and of the two previous months. Focusing on a linear response function (averaging over spring time temperatures) is very useful in order to compare between-species differences, although it does not allow the dual role of temperature (chilling versus forcing temperatures) to be taken into account. Indeed, according to prevailing theory, prolonged exposure to chilling during bud dormancy accelerates rest completion whereas afterwards, prolonged exposure to warm conditions causes ontogenetic development leading to budburst (Saxe et al., 2001). In further studies, our data set will be used to fit models to investigate the species sensitivity to chilling and forcing temperatures as well as daylength (*e.g.* Chuine, 2000; Schaber and Badeck, 2003; Hanninen and Kramer, 2007).

At both sites (Fontainebleau forest and Pyrénées mountains), beech had the lowest amplitude of LUD, suggesting that, for this species, temperature is not the only factor triggering leaf flushing. This confirms the results of other studies which observed that beech reacted less to changes in winter and spring temperatures than most tree species (Kramer, 1995b; Menzel et al., 2001). In our study, the lack of a significant trend in LUD for beech in Fontainebleau with time or temperature suggests that other factors than temperature, such as photoperiod, triggers LU for this species. It has been shown in controlled conditions that photoperiod could trigger beech spring phenological phases (Heide, 1993b). However, the exact role of photoperiod in natural conditions is still highly controversial (Kramer, 1994; Schaber and Badeck, 2003). Several studies concluded that long days are required to start bud development even in the case of fully chilled beech trees (Wareing, 1953; Lavarenne-Allary, 1965; Falusi and Calamassi, 1990; Heide, 1993b; Schaber and Badeck, 2003). On the contrary, other studies showed that chilling temperatures and spring warming temperatures were sufficient to explain timing of LU (Hunter and Lechowicz, 1992; Kramer, 1994). Finally, although phenology of beech was abundantly documented, there is no agreement about the factors driving bud development.

Along both the altitudinal and temporal gradients we found that phenological sensitivity to temperature dramatically differed among species, but not between within-species populations (for each of the three common species studied here). Specifically, we showed that some species, such as oak and ash, highly reacted to temperature (more −6.6 days °C^{-1}), as opposed to others, such as beech or holly (less −3.7 days °C^{-1}). Few studies showed the existence of interspecific differences of LUD sensitivity to temperature (Kramer, 1995a; Chuine and Cour, 1999; Wielgolaski, 1999; Chuine et al., 2000b; Wesolowski and Rowinski, 2006) and compared LUD sensitivity to temperature between populations growing at different locations (Chuine et al., 2000a,b; Karlsson et al., 2003). In our study, along both gradients, different populations of the same species exhibited an advance of about 2.1, 6.7 and 7.4 days °C^{-1} for beech, ash and oak, respectively, (i.e. similar phenological responses for natural populations of a given species growing at distant locations). Phenology appears to be a very heritable trait and a lot of studies have shown, using provenance trials, strong local adaptations (Chmura and Rozkowski, 2002; Hannerz et al., 2003; Chmura, 2006). However, our study suggests that population sensitivity to temperature is stable for a given species, in spite of its possible local adaptation. Along latitudinal and temporal gradients, Kramer (1995b) showed for beech that the phenotypic responses of LUD to temperature in clones varied by a similar magnitude than the responses of genetically different trees (−2.0 and −2.4 days °C^{-1} for genetically different trees and clones, respectively). We found equivalent values for this species in our study, strengthening the conclusion that temperature sensitivities of leaf phenology do not differ between populations of a given species. LU sensitivity to temperature fluctuations was also studied by Matsumoto et al. (2003) on 64 populations of *Ginkgo biloba* from 1953 to 2000. A reanalysis of their dataset (Table 1 in Matsumoto et al., 2003) showed a weak variability between populations (mean = -−2.9 days °C^{-1} ± 0.1 with values ranging from −1.19 to −4.95 days °C^{-1}). Furthermore, Chuine et al. (2000a) showed through modelling that, for most species, genetic variations between populations were an insignificant factor to predict flowering events. They also demonstrated that phenological responses to temperature were constant within most species, although populations were geographically distant. However, in our study, we only compared populations growing at two different latitudes; therefore, more experiments will be necessary to confirm these results and we recommend conducting studies or analysing existing data in order to compare population sensitivities to temperature within species.

5. Conclusions

Our results suggest that population sensitivity to global warming might be stable for a given species, in spite of its possible local adaptation. However, this result needs to be confirmed by other data from populations located on a wider latitudinal range. If so, models that are parameterized according to data obtained for a particular population of a given species might be used to predict the response of this species to global climate change. Species having a strong phenological sensitivity to temperature are expected to quickly react to climate change. These species will increase their growing season length in a larger extent but could be more affected by late frost damage (Hanninen, 1991). Consequently, according to species, growth is expected to be differently affected by a rise in temperature, and this could affect their competitive abilities and therefore their distribution range. To predict tree response to global climate change, we recommend considering each species separately when parameterizing phenological models.

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