

Assessing the effects of climate change on the phenology of European temperate trees

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ABSTRACT

Modelling phenology is crucial to assess the impact of climate change on the length of the canopy duration and the productivity of terrestrial ecosystems. Focusing on six dominant European tree species, the aims of this study were (i) to examine the accuracy of different leaf phenology models to simulate the onset and ending of the leafy season, with particular emphasis on the putative role of chilling to release winter bud dormancy and (ii) to predict seasonal shifts for the 21st century in response to climate warming.

Models testing and validation were done for each species considering 2 or 3 years of phenological observations acquired over a large elevational gradient (1500 m range, 57 populations). Flushing models were either based solely on forcing temperatures (1-phase models) or both on chilling and forcing temperatures (2-phases models). Leaf senescence models were based on both temperature and photoperiod.

We show that most flushing models are able to predict accurately the observed flushing dates. The 1-phase models are as efficient as 2-phases models for most species suggesting that chilling temperatures are currently sufficient to fully release bud dormancy. However, our predictions for the 21st century highlight that chilling temperature could be insufficient for some species at low elevation. Overall, flushing is expected to advance in the next decades but this trend substantially differed between species (from 0 to 2.4 days per decade). The prediction of leaf senescence appears more challenging, as the proposed models work properly for only two out of four deciduous species, for which senescence is expected to be delayed in the future (from 1.4 to 2.3 days per decade). These trends to earlier spring leafing and later autumn senescence are likely to affect the competitive balance between species. For instance, simulations over the 21st century predict a stronger lengthening of the canopy duration for *Quercus petraea* than for *Fagus sylvatica*, suggesting that shifts in the elevational distributions of these species might occur.

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1. Introduction

The timing of phenological events is a major determinant of plant productivity and species distribution (Chuine and Beaubien, 2001; Rathcke and Lacey, 1985). In temperate climates, plant phenology appears mostly driven by temperature (Chuine and Cour, 1999; Murray et al., 1989). As a result of the recent increase in surface temperature, strong phenological shifts have been observed in the northern hemisphere from temperate to boreal latitudes (Linderholm, 2006; Menzel et al., 2001; Menzel and Fabian, 1999; Parmesan, 2006; Schwartz and Reiter, 2000). In some cases these

shifts have been associated to modifications of the species distribution ranges, e.g. migrations toward higher elevation and latitude (Bertin, 2008). For tree species, an average lengthening of the growing season of about 11 days has been detected in Europe from the early 1960s to the end of the 20th century (Menzel and Fabian, 1999), mostly due to earlier leaf emergence and to a lesser extent to later leaf senescence (Linderholm, 2006; Menzel et al., 2006). Simultaneously, an increase in plant productivity has been detected in the northern high latitudes from remote-sensing data, with the underlying hypothesis that the extension of the growing season may enhance net carbon uptake period (Churkina et al., 2005; Myneni et al., 1997; Zhou et al., 2001). Indeed, earlier leaf emergence and later leaf senescence allow an increase in the length of the photosynthetically active period. A longer growing season length is linked to a better gross primary production (Kramer, 1995a; White

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et al., 1999) especially when bud burst occurs earlier (Delpierre et al., 2009b; Richardson et al., 2009). To this respect, an accurate prediction of leaf flushing in spring is needed to improve the prediction of primary productivity in the next decades (Chiang and Brown, 2007; Kramer et al., 2000; Leinonen and Kramer, 2002; Rotzer et al., 2004). One of the challenges in the modelling of phenological phases is that phenological models are species-dependent (Chuine, 2000; Hunter and Lechowicz, 1992) models for a number of common and emblematic tree species regarding biodiversity conservation or timber industry is still missing. The prediction of the future response of the length of the growing season to an increase in temperature may constitute a first step in our ability to evaluate the influence of climate change on the distribution of temperate tree species (Chuine, 2010; Chuine and Beaubien, 2001; Morin and Lechowicz, 2008).

Two classes of process-based models have been developed for the simulation of spring phenological phases. Models belonging to the first class, called hereafter the “1-phase models”, are the simplest models and are used in agronomy since the 18th century (Réaumur, 1735). These models assume that bud burst occurs after a fixed sum of forcing units has been reached. Forcing units are a dimensionless unit of bud development function of temperature. This kind of model implicitly assumes that bud dormancy is fully released before the starting date of forcing units accumulation. The second class of models, called hereafter the “2-phases models”, considers the action of both chilling temperatures during the endodormancy phase (winter deep dormancy caused by plant endogenous factors), and forcing temperatures during the ecodormancy phase (dormancy induced by environmental factors) (Lang et al., 1987). These models assume that the accumulation of forcing units starts and/or evolves according to the state of bud development during endodormancy (Chuine et al., 2000; Hanninen and Kramer, 2007), and that the critical sum of forcing units may be related to the amount of chilling units previously accumulated (Cannell and Smith, 1983). The 2-phases models are of more recent development, and conceptually based on experimental studies which highlighted that chilling was the major factor responsible for dormancy release (Falusi and Calamassi, 1990; Faust et al., 1997; Heide, 1993b; Murray et al., 1989; Sarvas, 1974).

Some studies have shown that the simpler 1-phase models do perform as well as the 2-phases models, and in some cases outperformed them (Linkosalo et al., 2006, 2008). The analogous performance of 1-phase and 2-phases models when applied to actual phenological time series suggests that under current conditions, the accumulation of chilling seems to have an insignificant role in the timing of tree flushing. In other words, the amount of chilling may currently be sufficient to systematically allow for a full release of tree dormancy. However, the relative importance of chilling in the timing of tree flushing may increase in the next decades with winter temperatures rising and could alter the performance of 1-phase models (Linkosalo et al., 2008; Thompson and Clark, 2008). This could be especially true for species having a high chilling requirement or for populations located at the current low-latitude or elevation margins of the species' distribution area. Therefore the characterization of species sensitivities to chilling appears crucial for predicting the likely impact of climatic warming on tree phenology.

Conversely to bud burst, the environmental factors which drive autumn phenological events of deciduous trees, such as leaf colouration or leaf fall, are less understood, probably due to the difficulty to accurately acquire leaf senescence observations (Estrella and Menzel, 2006), and paucity of the literature regarding the involved environmental processes (Lim et al., 2007; Nooden et al., 1997). Very few phenological models addressing the simulation of autumn phases have been published to date and therefore little has been made to investigate how canopy duration will be modified

by climate change. In spite of the multitude of factors which could play a role on the onset and on the regulation of leaf senescence (Lers, 2007), it is generally assumed that for temperate trees under favourable conditions (i.e. no water or nutrient stress), the leaf senescence process is affected by two main environmental factors: photoperiod and temperature (Estrella and Menzel, 2006; Koike, 1990). Leaf senescence models published in the literature were shaped on these two environmental cues (Delpierre et al., 2009a; Jolly et al., 2005; White et al., 1997). These models have so far been tested and validated on very few species, and generally over small datasets.

In this paper we took advantage of a phenological database acquired along an elevational gradient to fit, test and compare different models of leaf flushing and senescence for common tree species. Elevational gradients are particularly interesting because they provide a wide temperature range on a very short distance reducing therefore photoperiod influence. The first aim of this study was to assess through a comparison of phenological models for six dominant tree species in Europe (including four deciduous and two evergreen species) (i) the accuracy of leaf phenology estimation (flushing and senescence events) using temperature and photoperiod as variables and (ii) the present role of chilling and forcing temperatures on leaf flushing. The study area is located at the warmest part of the distribution range for all the studied species where the chilling requirements could become insufficient to release bud dormancy at lower elevations. The second objective was to predict seasonal shifts over the 21st century along the elevational gradient, and therefore to assess under climate warming potential changes in competitive balance of co-existent species.

2. Materials and methods

2.1. Study areas and species description

Phenological data were recorded in two valleys of the Pyrenees Mountains in south western France (latitude 42°47'N to 43°45'N; longitude 00°44'W to 00°06'E, see Fig. 1). A first transect was set up in the Ossau valley (Pyrénées Atlantiques) and a second one in the Gave valley (Hautes Pyrénées). These valleys run parallel to each other but are separated by 30 km. Their elevation increases from North to South. The study area is characterized by an oceanic climate. At low elevation, the mean annual temperature is about 12.6 °C and the mean annual precipitation is about 946 mm (Tarbes, 2004–2007, 43°11'N, 00°00'W, 360 m asl., Météo France); at high elevation the mean annual temperature is about 7.4 °C and the mean annual precipitation is 1317 mm (Gavarnie, 2004–2007, 42°44'N, 00°00'W, 1380 m asl., Météo France).

We selected six tree species (4 deciduous and 2 evergreen) having a wide range of natural distribution over Europe and which are widely used for timber industry. Species included fir (*Abies alba* Mill.), sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.), holly (*Ilex aquifolium* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). All these species were located in the southern limits of their distribution range, which confers a particular interest to the study of their response to climate change. For each species and in each transect, naturally established populations were sampled along two elevational transects from 100 m to 1600 m and 10 individuals were selected in each population for phenological observations. The elevational gradient exceeded 1400 m for all species except for *Acer pseudoplatanus* ($\Delta = 1164$ m). The populations were sampled on North-facing slopes, except for *Quercus petraea* that only grew on South-facing slopes. More information about the characteristics of the sites is available in Vitasse et al. (2009b).

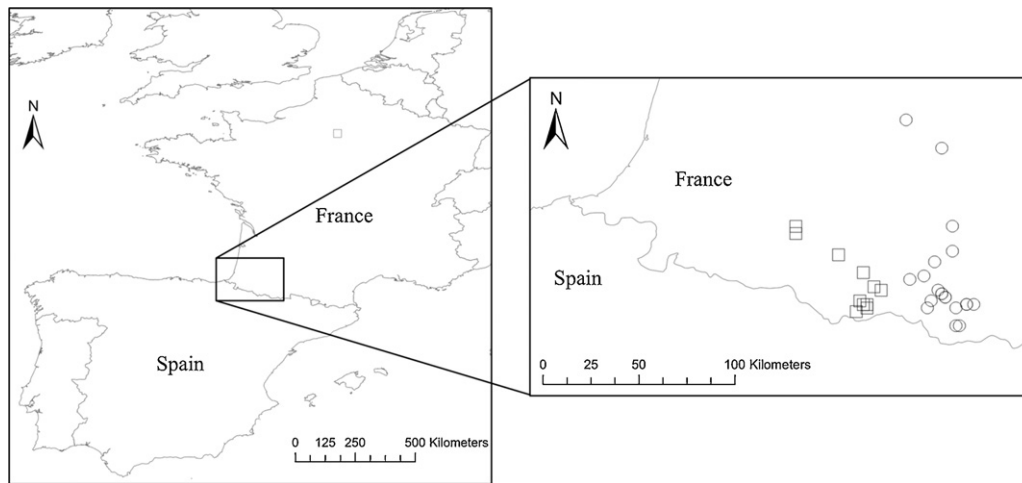


Fig. 1. Location of the study sites in Pyrenees Mountains: squares = phenological stations within Ossau valley; circles = phenological stations within Gave valley.

2.2. Phenology monitoring

Leaf flushing and senescence for deciduous species only were monitored every 10 days from March to June and September to December, respectively, on all the sampled trees during 2 or 3 years (2005–2006 for *Fraxinus*, *Acer*, *Abies* and *Ilex*; 2005–2007 for *Quercus* and *Fagus*). We used the dataset published in Vitasse et al. (2009a, 2009b) for both phenological events. For each tree, the flushing date was assumed to correspond to the date when 50% of the buds had fulfilled the criterion “at least one leaf unfolding” (see methods in Vitasse et al., 2009a). In autumn, we combined assessment of coloration and leaf fall to more accurately estimate the end of growing season of deciduous species. Percentages of missing leaves, as well as percentages of coloured leaves on the totality of the remaining leaves in the canopy were assessed visually. We considered that senescence date was reached in one tree when 50% of its leaves were either coloured or fallen according to the following equation (1):

$$x_t = \frac{\alpha_t \times (100 - \beta_t)}{100} + \beta_t \quad (1)$$

where x_t is the percentage of coloured or fallen leaves in the selected tree at date t , α_t is the percentage of coloured leaves at date t and β_t is the percentage of missing leaves at date t .

Then, the dates of flushing and senescence were estimated by linear interpolation between two consecutive field observations, further providing a daily resolution for the observations. Then, canopy duration was defined at individual scale as the period between flushing and senescence dates, corresponding to the leafy season. At the population scale, flushing, senescence and canopy duration values corresponded to the mean of the 10 sampled individuals.

2.3. Meteorological measurements

Air temperature was measured using data loggers (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, MA 02532) located in each population (31 sites). In each site, sensors were settled at 1.5 m above the ground on a pole located in an open area nearby the studied population (distant from 10 to 100 m, at the same elevation). To prevent any exposure to rain or direct sunlight, sensors were protected by a shelter constituted with three layers of white plastic, spaced from each other to allow good air circulation. Data were recorded every hour from 1 January 2005 to 31 December 2007. 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 working weather stations (minimum $R^2 > 0.91$). All sensors were inter-calibrated in the laboratory before installation. Average annual temperatures decreased linearly with increasing elevation, of about 0.43°C for every 100 m increase in elevation (average from 2005 to 2007). For both flushing and senescence models, we used daily temperature calculated as the average of the 24 hourly values recorded daily at each site.

2.4. Models used, method of fitting and validation

All phenological models were fitted over the whole dataset (2–3 observation years, along both elevational gradients) for each species. During this process of model fitting, models' parameters were derived by using either a simulated annealing algorithm (Chuine et al., 1998; Chuine et al., 1999) for Spring Warming (SW) and Sigmoid models, or a full exploration of the parameters space for Cannel & Smith Spring Warming 4 (CS-SW4) and senescence models.

To assess the robustness of the models, a leave-one-out cross-validation approach has been performed: a single observation from the original sample (of size n) was used as the validation datum using parameters fitted on the remaining observations (of size $n-1$). Each observation in the whole data set of each species was iteratively used as the validation datum. In order to assess the uncertainty of prediction over the past century, we calculated 95% confidence intervals using the predictions obtained with all parameter sets derived with the leave-one-out cross-validation. We compared the models' accuracies on the basis of the root mean square error (RMSE) and model efficiency (ME) metrics, calculated for both the fit on the whole data set and the leave-one-out cross-validation (Table 1) following these equations:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (O_i - P_i)^2}{n}} \quad (2)$$

$$\text{ME} = 1 - \frac{\sum_{i=1}^n (O_i - P_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2} \quad (3)$$

where O_i represents an elementary observation in the observed dataset (n observations) and P_i represents an elementary prediction in the modelled dataset (n predictions).

2.4.1. Flushing phenological models

For flushing timing, we compared and tested five 1-phase models existing in the literature (Chuine, 2000; Chuine et al., 1999;

Table 1

Performance of the selected flushing and senescence models fitted on the whole data set and on the leave-one-out cross-validation.

Models	Abies						Acer						
	Whole dataset ($n = 14$)			Cross-validation ($n - 1$)			Whole dataset ($n = 16$)			Cross-validation ($n - 1$)			
Flushing	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	
1-Phase models													
SW	4.1		0.92	−0.2	4.9	0.87	−0.0	3.6	0.91	−0.1	4.2	0.87	0.1
Sigmoid	4.0		0.91	0.3	5.4	0.84	0.2	3.9	0.89	−0.0	7.5	0.59	1.3
2-Phases model													
CS-SW4	3.7		0.93	0.6	4.4	0.90	0.15	3.9	0.90	0.9	4.2	0.88	0.0
Senescence													
Delpierre			−			−		5.6	0.82	0.8	5.9	0.80	0.6
Models	Fagus						Fraxinus						
	Whole dataset ($n = 30$)			Cross-validation ($n - 1$)			Whole dataset ($n = 18$)			Cross-validation ($n - 1$)			
Flushing	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	
1-Phase models													
SW	4.6	0.62	0.8	5.1	0.53	1.0	2.6	0.97	−0.1	3.1		0.96	−0.2
Sigmoid	3.9	0.72	0.0	4.5	0.62	−0.0	2.7	0.97	−0.0	4.3		0.92	−0.3
2-Phases models													
CS-SW4	3.6	0.77	1.0	3.9	0.73	0.8	2.6	0.97	1.1	3.1		0.96	1.4
Senescence													
Delpierre	6.4	0.86	−0.1	7.7	0.80	0.5	9.4	0.02	2.2	10.0		−0.10	2.3
Models	Ilex						Quercus						
	Whole dataset ($n = 18$)			Cross-validation ($n - 1$)			Whole dataset ($n = 42$)			Cross-validation ($n - 1$)			
Flushing	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	RMSE	ME	Bias	
1-Phase models													
SW	4.0		0.85	2.4	7.3	0.53	1.0	5.0	0.91	0.1	5.4	0.90	−0.7
Sigmoid	4.8		0.79	0.1	6.3	0.65	0.3	4.5	0.93	0.3	4.8	0.92	0.3
2-Phases model													
CS-SW4	3.9		0.87	0.95	5.1	0.78	1.12	4.7	0.92	1.4	5.5	0.90	1.9
Senescence													
Delpierre			−			−		4.5	0.87	−0.5	4.8	0.85	−0.5

RMSE, root mean square error; ME, model efficiency; Bias, mean difference between the observed and the predicted dates.

Wang and Engel, 1998) and three 2-phases models (Cannell and Smith, 1983; Chuine, 2000) differing by their response function to forcing and chilling temperatures.

Most of 1-phase models accurately predicted leaf unfolding dates for all species but the best results (lowest RMSE, bias and highest ME) were obtained with the Sigmoid and the SW models. As these two latter models also have low number of parameters reducing risks of over-parametrization, they were used in the prospective modelling simulations. These two models are characterized by two common parameters: t_0 , which is the date when the accumulation of forcing units (R_f) starts and F^* which is the critical sum of forcing units required to bud burst at the date t_f . These models are described as following:

The model Spring Warming SW (Chuine et al., 2003) has three parameters and uses a linear sum of degree days with a threshold temperature T_b . Thus, bud burst occurs at t_f following Eqs. (4) and (5):

$$\sum_{t_0}^{t_f} R_f(T_{(d)}) \geq F^* \quad (4)$$

with $T_{(d)}$ the daily temperature, R_f the rate of forcing according to Eq. (5):

$$R_{f(T_{(d)})} = \begin{cases} 0 & \text{if } T_{(d)} < T_b \\ T_{(d)} - T_b & \text{if } T_{(d)} \geq T_b \end{cases} \quad (5)$$

with T_b the temperature threshold required to accumulate forcing temperatures.

The model Sigmoid (Chuine and Cour, 1999) has four parameters and uses a sigmoid response to temperature with parameter β corresponding to the temperature of mid-response and parameter α corresponding to the slope at the inflection point following Eq. (6):

$$R_f(T_{(d)}) = \frac{1}{1 + e^{\alpha(T_{(d)} - \beta)}} \quad (6)$$

For 2-phases models, the CS-SW4 model appeared as the most efficient during the external validation for all species and has lower number of parameters (six) compared to the other ones, reducing the risk of over-parametrization. This model was therefore selected to represent 2-phases models in prospective simulations for all species.

The CS-SW4 model is a generalisation of SW-type models, based on the model of Cannell and Smith (1983) where the critical sum of forcing F^* is not a constant anymore but depends on the number of chilling days (C_{tot}). C_{tot} is computed between two dates t_{cstart} and t_{cend} as follows:

$$C_{tot} = \sum_{t_{cstart}}^{t_{cend}} R_c(T_{(d)}) \quad (7)$$

where the rate of chilling (R_c) is a number of chilling days (Cannell and Smith, 1983) following these equations:

$$R_c(T_{(d)}) = \begin{cases} 1 & \text{if } T_{(d)} < T_c \\ 0 & \text{if } T_{(d)} \geq T_c \end{cases} \quad (8)$$

with T_c the temperature threshold required to accumulate chilling days.

A fit is then performed to obtain the critical sum of forcing F^* as a negative linear function of the sum of chilling days (C_{tot}):

$$F^* = \max(gC_{tot} + h) \quad (9)$$

Note that g is negative. Therefore, in case of very high values for C_{tot} (i.e. a significantly higher number of chilling days than observed in our database), F^* may potentially be negative. In practice this has never been observed: F^* always remains positive for all observed and predicted C_{tot} values.

Then the model follows a SW-type scheme where the rate of forcing R_f is similar to the sigmoid approach, following a linear sum of forcing units (number between 0 and 1) when temperatures are between a minimum threshold (T_a) and a base temperature (T_b):

$$R_f(T_{(d)}) = \begin{cases} 0 & \text{if } T_{(d)} < T_a \\ (T_{(d)} - T_a)/(T_b - T_a) & \text{if } T_a \leq T_{(d)} < T_b \\ 1 & \text{if } T_{(d)} \geq T_b \end{cases} \quad (10)$$

2.4.2. Senescence models

We compared the performances of three models of leaf senescence namely: the continental phenology model (White et al., 1997), the growing season index (GSI) (Jolly et al., 2005) and the cold-degree day photoperiod-dependent model (Delpierre et al., 2009a). Following Jolly et al. (2005), who suggest that phenology is not constrained by the vapour pressure deficit (VPD) at temperate latitude, we fixed the daily VPD modifier ($iVPD(d)$) to 1 in GSI model. All of these models are based on the same environmental cues, considering photoperiod and temperatures as driving forces of senescence in temperate trees. However, their effects are accounted for in different ways for each model. After assessing the performance of all three models, we selected the cold-degree day photoperiod-dependent model, which showed the best results in the external validation for all species (not shown, but see Delpierre et al., 2009a for a comparative assessment of all three model types on a companion dataset). This model defines a colouring state (S_{sen} , arbitrary units) for each day (d) following D_{start} (the date at which a critical photoperiod P_{start} is reached), representing the progress of the senescence processes. Leaf colouring is achieved when S_{sen} reaches a threshold value (Y_{crit} , arbitrary units). In this model, the time derivative of the state of colouring (R_{sen} , arbitrary units) on a daily basis is formulated as:

$$\text{If } P_{(d)} < P_{start} \begin{cases} \text{if } T_{(d)} < T_b & R_{sen}(d) = [T_b - T_{(d)}]^x \times f[P_{(d)}]^y \\ \text{if } T_{(d)} \geq T_b & R_{sen}(d) = 0 \end{cases} \quad (11)$$

$$\text{If } P_{(d)} \geq P_{start} \quad S_{sen}(d) = 0 \quad (12)$$

$$\text{If } P_{(d)} < P_{start} \text{ and } T_{(d)} < T_b \quad S_{sen}(d) = S_{sen}(d-1) + R_{sen}(d) \quad (13)$$

where $P_{(d)}$ is the photoperiod expressed in hours on the day of year d ; $T_{(d)}$, the daily mean temperature ($^{\circ}\text{C}$); T_b , the maximum temperature at which senescence process is effective ($^{\circ}\text{C}$); $f[P_{(d)}]$, a photoperiod function that can be expressed as follows:

$$f[P_{(d)}] = \frac{P_{(d)}}{P_{start}} \quad (14)$$

or

$$f[P_{(d)}] = 1 - \frac{P_{(d)}}{P_{start}} \quad (15)$$

The complete model therefore includes five parameters (P_{start} , T_b , x , y , Y_{crit}). The dummy parameters x and y (Eq. (11)) may take any of the $\{0,1,2\}$ discrete values, to allow for any absent/proportional/more than proportional effects of temperature and photoperiod to be included. The photoperiod was calculated for all the senescence models following (Guyot, 1997).

2.5. Climate change impact on canopy duration

Prospective simulations of the leaf phenological events were performed using temperature simulated by a General Circulation model developed by Météo France and called ARPEGE (Déqué et al., 1998) under the A1b IPCC scenario (IPCC, 2007). The original ARPEGE grid has a 60-km spatial step and a 1-day time resolution. A statistical downscaling method provided temperature data on a 8-km grid (Boé et al., 2006). For a given phenological station, we selected the ARPEGE grid points located less than 5 km from the station. A lapse rate of $0.43^{\circ}\text{C}/100\text{ m}$ of elevation was applied to correct temperature for elevational differences between the ARPEGE points and the observations stands, based on the measured thermal gradient across the elevational gradient (Vitasse et al., 2009b). Reconstructed minimum and maximum temperature time series were computed as the mean of the daily data over all retained ARPEGE points, weighted by the inverse of the distance to the phenological stand (Delpierre et al., 2009a).

We used the best models (see Section 2.4 above) for each species to predict flushing and senescence over the 21st century at five elevations in the two valleys (10 sites) corresponding to the beech stands sampled: at 100, 400, 800, 1200 and 1600 m asl. $\pm 50\text{ m}$ (see methods in Vitasse et al., 2009b for the exact elevation of the sites), as these elevations were common to most species. We calculated from 2000 to 2100 the canopy duration in these stations for *Fagus* and *Quercus* only because we were not enough confident in senescence predictions for the two other deciduous species (see Section 3.2). The use of ARPEGE temperatures resulted in biased predictions of observed actual canopy duration mainly due to the difference between predicted and recorded temperatures. Leaf flushing and senescence dates predicted were corrected for these biases before further analyses about the predicted evolution of canopy duration of *Fagus* and *Quercus* (average biases amounted -0.2 days on *Fagus* and $+12.4$ days on *Quercus* for the leafing phase, and $+15.5$ days on *Fagus* and $+8.1$ on *Quercus* for the senescence phase).

3. Results

3.1. Flushing models

Fitted on the whole data set, the best models provided high values of model efficiencies (ME), from 0.77 to 0.97 and low values of root mean square errors (RMSE) from 3.6 to 2.6 days, for *Fagus* and *Fraxinus*, respectively (Table 1). Overall, the 2-phases model CS-SW4 performed better than the 1-phase models for *Abies*, *Fagus* and *Ilex*, and as efficiently for the other species (Table 1, with Annex 1 documenting parameters' values).

For the best models, cross-validation yielded ME spanning 0.73–0.96 (for *Fagus* and *Fraxinus*, respectively) with RMSE values in the range of 3.1–5.1 days (for *Fraxinus* and *Ilex*, respectively). The 2-phases model CS-SW4 outperformed the 1-phase models in cross-validation for *Abies*, *Fagus* and *Ilex* whereas it yielded similar accuracies of predictions than the 1 phase-models for *Acer*, *Fraxinus* and *Quercus* (Table 1 and Fig. 2). In summary the cross-validation RMSE is around 3 days for *Fraxinus*, 4 days for *Abies*, *Acer* and *Fagus*, and 5 days for *Ilex* and *Quercus*. These are fair results if we keep in mind that the observation accuracy is about 3 days (considered that the time-span between two observation campaigns is of 10 days and that observation errors are uniformly distributed within this time-span).

3.2. Leaf senescence models

Fitted on the whole data set, ME of the Delpierre model was above 0.86 for *Quercus* and *Fagus*, yielding RMSE of 4.5 and 6.4

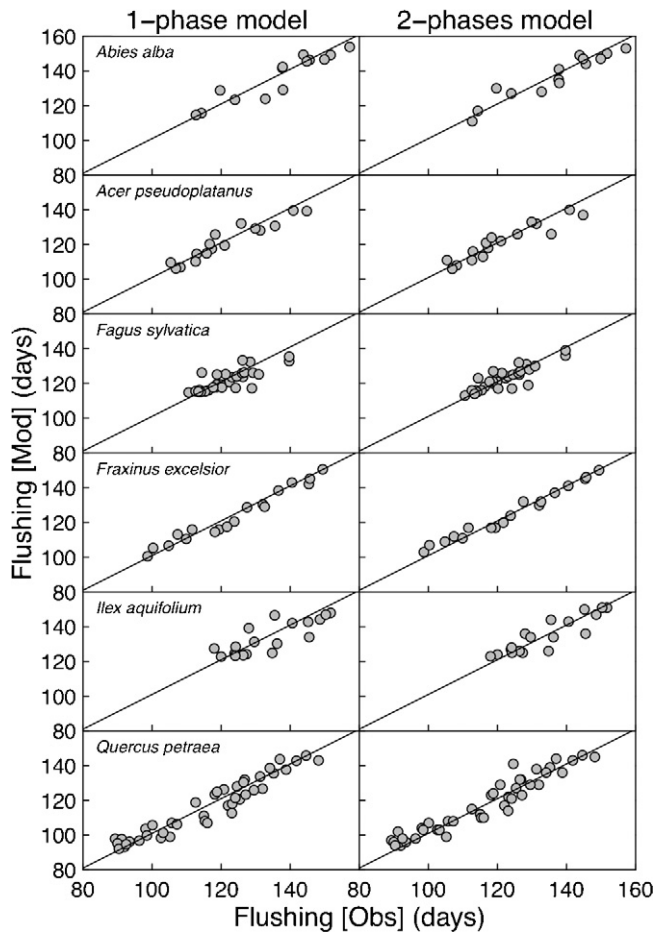


Fig. 2. Comparison of predicted flushing dates using one-leave-out cross-validation versus observed flushing dates with the best of 1 and 2-phases models. The best models were used for each species: 1-phase models: “sigmoid” for Fagus, Ilex, Quercus and “SW” for Abies, Acer and Fraxinus; 2-phases models: “CS-SW4” for all species. The identity line is reported.

days, respectively (Table 1, with Annex 2 documenting parameters' values). For Acer, although the Delpierre model provided high ME, the model fits were strongly driven by a group of senescence observations from the lowest elevation populations (at 400 m asl.) that exhibited a significant delay in comparison to all the higher populations (Fig. 3). This should be therefore interpreted with caution. Hence, we are not confident enough in the predictions of leaf senescence for this species and we have chosen not to use the model prediction in the prospective analysis under climate warming scenario. For Fraxinus, none of the bioclimatic senescence models outperformed the null model. Consequently, the evolution of the canopy duration over the 21st century was not presented for these two latter species.

The Delpierre model selected for prospective simulations over the 21st century provided more accurate predictions for Quercus than for Fagus in cross-validation yielding RMSE of 4.8 and 7.7 days, respectively (Table 1). The predicted ranges of senescence dates properly matched the observed ones for the two species (Fagus, observed range: 61 days, predicted range: 58 days; Quercus, observed range: 53 days predicted range: 46 days, Fig. 3).

3.3. Simulation of flushing and senescence dates over the 21st century

3.3.1. Flushing

Except for Ilex at low elevation, both 1 or 2-phases models predicted significantly earlier leaf unfolding dates over the 21st

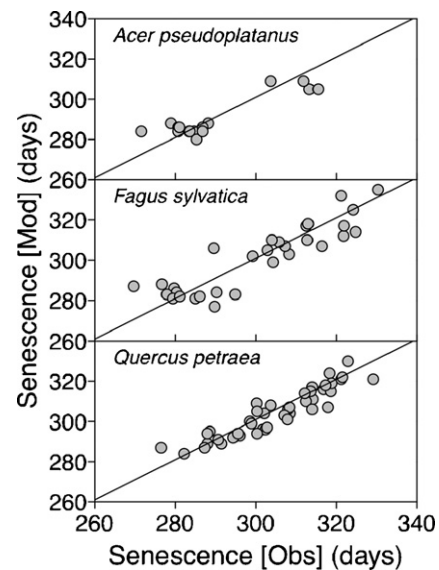


Fig. 3. Comparison of predicted senescence dates using one-leave-out cross-validation versus observed senescence dates for Fagus, Quercus and Acer. The “Delpierre” model was used for the three species: the graph of Fraxinus is not plotted here because we found no senescence models better than the null model. The identity line is reported.

century from -0.2 to -3.0 days per decade depending on elevation (Table 2, Fig. 4). Irrespective of elevation, the greatest expected changes in flushing dates was found for Quercus and Fraxinus with a similar advance of about 2.4 days per decade; the lowest changes for Fagus (average -0.5 days per decade) and Ilex (-1.1 days per decade or no trend according to the 2 phases-models) and intermediate ones for Abies and Acer (from -0.9 to -1.6 days per decade). Interestingly, for Ilex, the 1-phase model predicted an advance of leaf unfolding all along the elevational gradient whereas the 2-phases model predicted an advance at high elevations but a delay at low elevations.

For some species, there was a substantial divergence in the predictions of flushing timing with climate warming between the two types of flushing models. The 2-phases model predicted similar phenological changes than 1-phase model for Fagus, Fraxinus, Quercus and Acer, while it predicted lower shifts for Abies and Ilex especially at low elevation (Table 2 and Fig. 4). In addition, our results showed that phenological shifts predicted using the 1-phase models increased with increasing elevations for all species (Table 2 and Fig. 4).

3.3.2. Senescence

Across the 21st century, simulations showed that senescence dates are expected to be delayed both for Fagus and Quercus. However, the predicted shift in senescence was greater for Fagus than for Quercus with a delay of about 2.3 and 1.4 days per decade, respectively. These trends varied according to elevation with higher predicted delay at low elevations for both species (Fig. 5 and Table 3).

3.4. Canopy duration of Fagus and Quercus

3.4.1. Simulations

Across the 21st century, simulations showed a significant lengthening of canopy duration for both species (Fig. 6). Quercus exhibited greater phenological variability from year to year and stronger shifts in canopy duration than Fagus: predicted changes over the century were about 3.7 and 2.8 days per decade, for Quercus and Fagus, respectively (Table 3 and Fig. 6). For Fagus

Table 2

Flushing trends (slope in days per decade) predicted for each species along the elevation gradient from 2000 to 2100. Phenological trends correspond to the slope of the linear regression between predicted dates by the best flushing models and years from 2000 to 2100. All trends were significant ($p < 0.05$). Negative values correspond to an advance in flushing dates and positive values to a delay. ΔT corresponds to the mean annual temperature increase from 2000 to 2100, calculating as the slope of the linear regression between predicted temperatures by the ARPEGE model and years from 2000 to 2100.

	Abies		Acer		Fagus		Fraxinus		Ilex		Quercus		$\Delta T (^{\circ}\text{C})$
	1-Phase	2-Phases	1-Phase	2-Phases	1-Phase	2-Phases	1-Phase	2-Phases	1-Phase	2-Phases	1-Phase	2-Phases	
Elevation (m)													
100	−1.0	−0.4	−0.7	−1.0	−0.2	−0.5	−1.4	−1.7	−0.9	+0.7	−1.6	−1.8	+2.90
400	−1.2	−0.5	−0.8	−1.2	−0.3	−0.6	−1.7	−2.2	−1.0	+0.6	−2.2	−2.3	+2.94
800	−1.4	−0.8	−1.2	−1.4	−0.4	−0.6	−2.1	−2.5	−1.1	+0.4	−2.4	−2.5	+2.95
1200	−1.9	−1.1	−1.6	−1.6	−0.5	−0.6	−2.6	−2.6	−1.2	−0.4	−2.6	−2.7	+2.98
1600	−2.3	−1.8	−2.2	−1.9	−0.8	−0.6	−3.0	−2.7	−1.3	−1.4	−2.6	−2.2	+3.01
Mean	−1.6	−0.9	−1.3	−1.4	−0.4	−0.6	−2.2	−2.4	−1.1	−0.0	−2.3	−2.3	+2.96

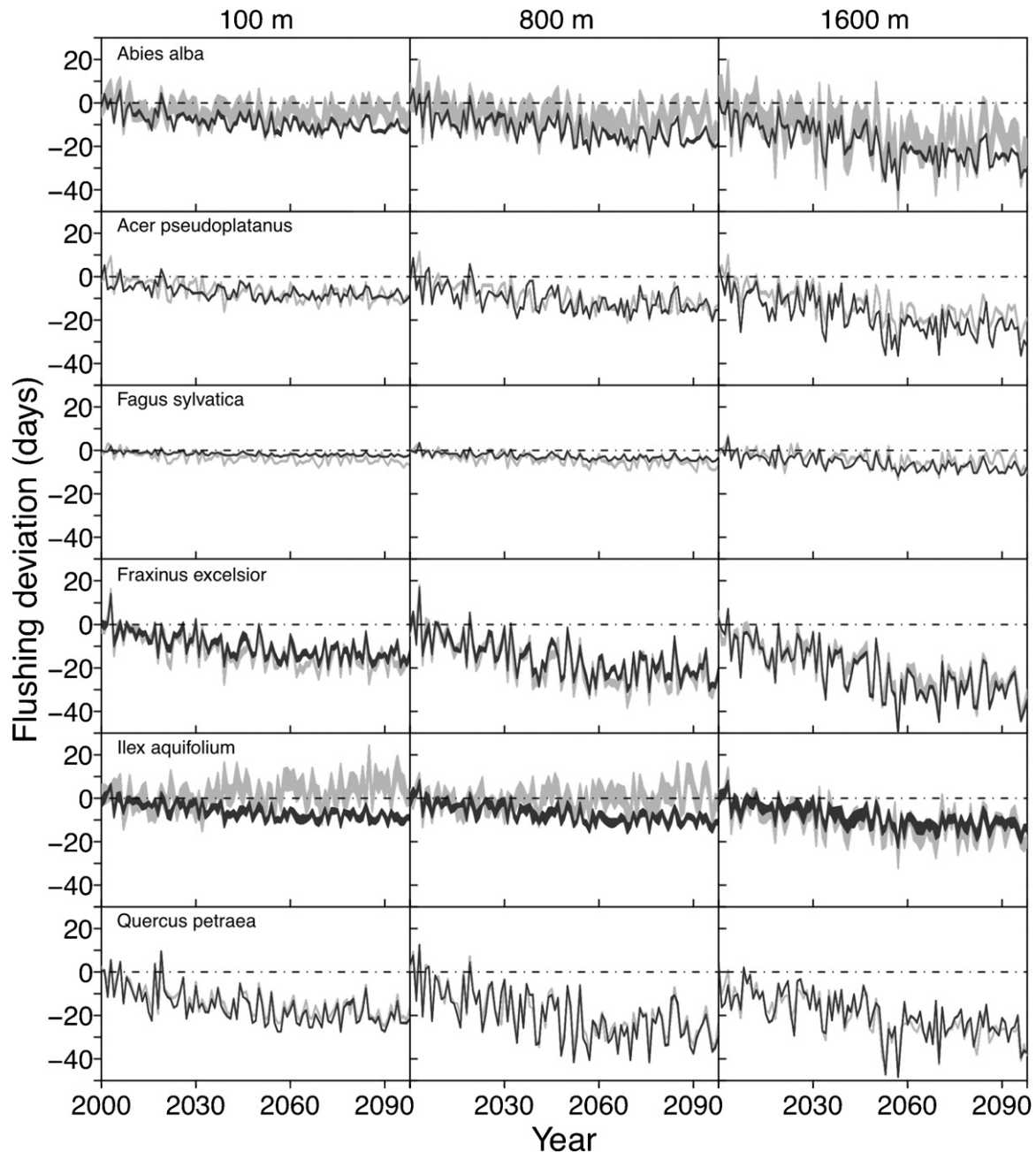


Fig. 4. Predicted flushing dates over the 21st century related to 1950–1999 at three elevations (100, 800 and 1600 m asl.) for the six studied species: dark grey area = prediction based on 1-phase models (“sigmoid” for Fagus, Ilex, Quercus and “SW” for Abies, Acer and Fraxinus) ± 95 confidence intervals obtained with all parameter sets derived with the leave-one-out cross-validation; light grey area = prediction based on 2-phases models (“CS-SW4” for all species) ± 95 confidence intervals obtained with all parameter sets derived with the leave-one-out cross-validation.

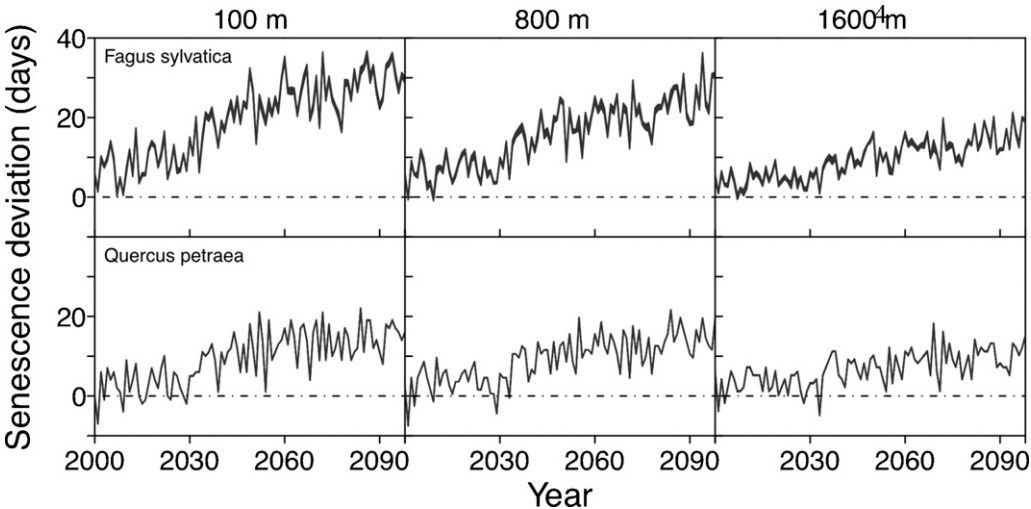


Fig. 5. Predicted senescence dates over the 21st century related to 1950–1999 for three elevations (100, 800 and 1600 m asl.) for *Fagus* and *Quercus*: dark grey area represents simulations were obtained for these two species by the “Delpierre” model, ± 95 confidence intervals obtained with all parameter sets derived with the leave-one-out cross-validation.

the lengthening of canopy duration is expected to decrease with increasing elevation while for *Quercus* the greatest shift is expected at intermediate elevation (Table 3). Furthermore, no significant difference was detected in canopy duration trends using the two types of flushing models (1 and 2-phases models, Fig. 6). The lengthening of canopy duration in response to temperature increase over the 21st century is mainly the consequence of leaf senescence delay on *Fagus* while it is mainly due to advance of flushing date on *Quercus*.

3.4.2. Species comparison

At present, canopy durations of *Fagus* and *Quercus* are similar at approximately 700 m of elevation corresponding in average to 190 days (Fig. 7). Above this elevation, the canopy duration of *Fagus* is longer than the *Quercus*’ one, whereas the opposite pattern occurs under this elevation (Fig. 7). Simulations of canopy duration over the next decades showed that the elevation where the canopy duration is identical for the two species (*i.e.* the intersection between the two curves) is expected to dramatically increase from the end of the 20th to the end of the 21st century (Fig. 8).

Table 3

Senescence and canopy duration trends (slope in days per decade) predicted for *Quercus* and *Fagus* along the elevation gradient from 2000 to 2100. Senescence trends correspond to the slope of the linear regression between predicted dates by the best senescence models and years from 2000 to 2100, canopy duration trends to the slope of the linear regression between predicted canopy duration (either using 1 or 2-phases of flushing models) and years. All trends were significant ($p < 0.05$). Positive values correspond to a delay in senescence dates or a lengthening of canopy duration. ΔT corresponds to the mean annual temperature increase from 2000 to 2100, calculating as the slope of the linear regression between predicted temperatures by the ARPEGE model and years from 2000 to 2100.

	Senescence		Canopy duration				ΔT (°C)
	<i>Fagus</i>	<i>Quercus</i>	<i>Fagus</i>		<i>Quercus</i>		
			1-Phase	2-Phases	1-Phase	2-Phases	
Elevation (m)							
100	+2.9	+1.7	+3.1	+3.3	+3.3	+3.4	+2.90
400	+2.7	+1.5	+3.0	+3.3	+3.8	+3.9	+2.94
800	+2.4	+1.5	+2.8	+3.0	+3.9	+4.0	+2.95
1200	+2.0	+1.3	+2.5	+2.6	+3.9	+4.0	+2.98
1600	+1.4	+1.0	+2.2	+2.0	+3.5	+3.2	+3.01
Mean	+2.3	+1.4	+2.7	+2.7	+3.7	+3.7	+2.96

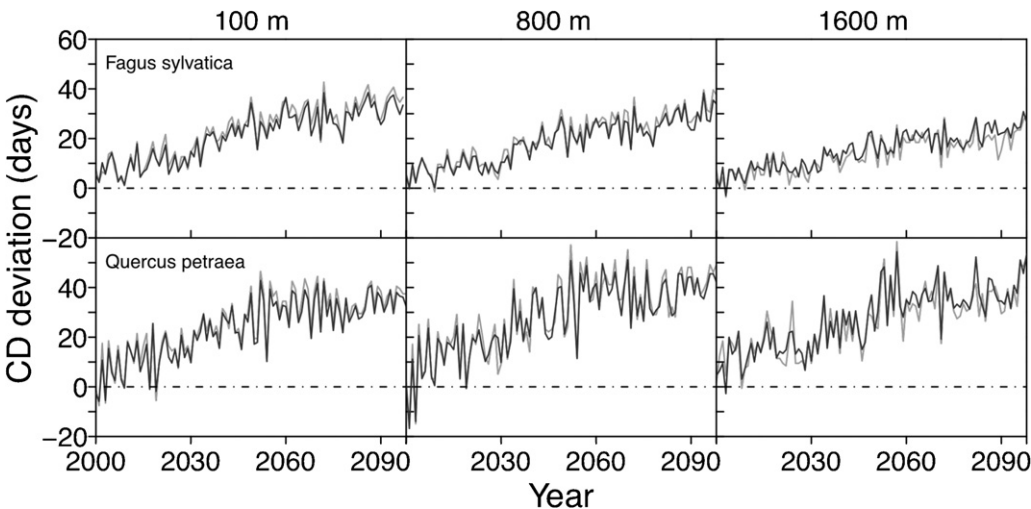


Fig. 6. Predicted canopy duration (CD) over the 21st century related to 1950–1999 for three elevations (100, 800 and 1600 m asl.) for *Fagus* and *Quercus*: light grey line = prediction based on 2-phases models; dark grey line = prediction based on 1-phase models.

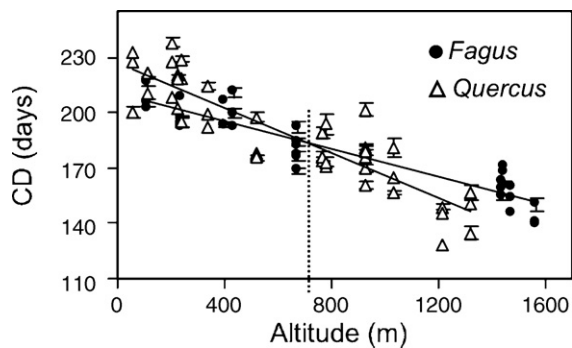


Fig. 7. Elevational variations of observed canopy duration (CD) for *Fagus* and *Quercus* for the 2005–2007 period. Due to slope effect, elevation of *Quercus* was adjusted to correspond to the elevation of *Fagus* stand using slope of linear regression between elevation and mean annual temperature of *Fagus* stations ($R^2 > 0.91$, $P < 0.0001$): discs = *Fagus*; triangles = *Quercus*.

4. Discussion

4.1. Relative merits of 1- and 2-phase models to predict flushing time

The effect of chilling temperature has been demonstrated in experimental conditions on several tree species, especially *Fagus*

sylvatica (Heide, 1993a,b; Murray et al., 1989) but we still do not know whether under temperate climate the current chilling requirements of the species are far-exceeded or not. For 1-phase models, it is implicitly assumed that buds have been sufficiently chilled previously to bud quiescent period, so that dormancy release is related solely to one environment cue that can be modelled with a fixed starting date. This assumption seems justified at high elevation where the chilling requirement for dormancy release is likely fully reached. However, this assumption may not be valid in the future warmer climate, especially at low elevation (Linkosalo et al., 2008). Hence, the performance of spring phenological models which do not consider the amount of chilling in their formulation may be challenged when attempting to predict the occurrence of budbreak for the next decades, especially at the southern limit of the species distribution. Overall, in this study, 1-phase and 2-phases models yielded comparable accuracies of prediction for most species, suggesting that under current climate conditions, chilling temperatures does not seem to have a major effect on the flushing time, probably because they are always sufficient to fully release bud dormancy. This result is in agreement with previous study (Chuine and Cour, 1999; Hunter and Lechowicz, 1992; Linkosalo et al., 2006, 2008). However, some recent studies pointed out a better performance of the 2-phases models, especially for late-leaving species (Morin et al., 2009; Thompson and Clark, 2008). These 2-phases models have a larger number of

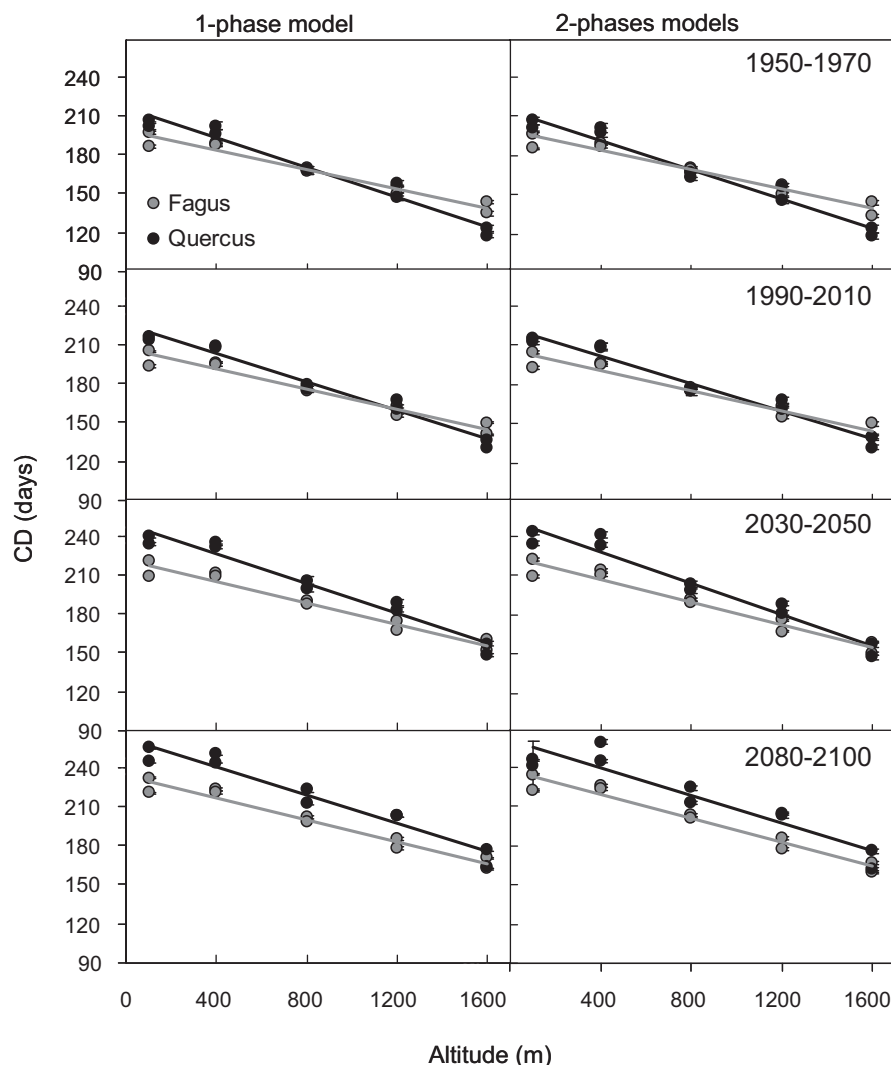


Fig. 8. Predicted canopy duration (CD) for *Fagus* and *Quercus* at different periods from 1950 to 2099. Predicted values of flushing and senescence dates have been previously corrected on observations basis monitored at the same elevation during 2005–2007 (for further details, see Section 2).

parameters that may not be robustly adjusted with small datasets (over-parameterization). Yet, in the present paper, the CS-SW4 model with six independent parameters is a relevant model to test the effect of chilling temperatures and provided accurate fits on the overall dataset and satisfying predictions when assessed for cross-validation, for most species. However, as most observations in our dataset were acquired over populations living in cold climate, due to their location along the elevational transect, more observations at low elevations may be needed to accurately quantify the chilling requirement of these species. For *Quercus* and *Fraxinus*, the starting date of the forcing temperatures accumulation, marking the onset of quiescence period, converged among the different 1-phase models which suggest that this date seems to be accurately predicted (Annex 1). For all models, this date was fitted between day 50 and 60 for *Quercus* and before day 31 for *Fraxinus*. Now, one of the major issue to confirm and improve these predictions will be to accurately characterise the date of dormancy release to climate variation using experiments in condition of cold deprivation in greenhouse (Arora et al., 2003; Granhus et al., 2009; Heide, 1993a). This would be helpful to predict phenological trends of these species in other part of the continent, especially at the southern limit of the species' distribution.

4.2. Evolution of leaf flushing dates over the 21st century

Predicted phenological changes over the next decades were highly variable among species. Our study predicted strongest shifts in leaf unfolding for *Fraxinus* and *Quercus* and lowest for *Fagus* which are in line with phenological trends observed for these species over the last decades (Kramer, 1995b; Lebourgeois et al., 2010; Studer et al., 2005; Vitasse et al., 2009a). We found that flushing simulations over the 21st century were similar between 1 and 2-phases models for four out of the six studied species, strengthening the previous observation of a very modest/absent implication of chilling as considered in our models for the leafing of considered species under current climate conditions. However, we found different patterns for *Abies* and particularly for *Ilex*, in which flushing is expected to be delayed in the next decades at low elevation with the 2-phases model due to a lack of chilling requirement. These results highlight that dormancy could not be fully released for these two species in a warmer climate, suggesting that the relative role of chilling temperatures could increase for the future and should be considered when predicting flushing time. For these species, the impact of climate warming will likely depend on their capability to maintain a low critical sum of forcing units with decreasing chilling period (Murray et al., 1989; Thompson and Clark, 2008). Nevertheless, these projections should be taken with caution, especially for lower elevations, since they were based on temperature range that is outside from the one used to fit the models.

4.3. Evolution of leaf senescence dates over the 21st century

Photoperiod has frequently been reported as the main driver of leaf senescence (Keskitalo et al., 2005; Lee et al., 2003). However, when tested over extensive datasets, autumnal temperature, considered as an independent variable of correlative models (Matsumoto et al., 2003) or incorporated in bioclimatic thermal time models (Delpierre et al., 2009a; Migliavacca et al., 2008) appears to explain a higher proportion of observed variance in the timing of senescence (reminding that considering photoperiod as the sole senescence trigger is equivalent to considering the occurrence of senescence to vary only with latitude). Our result showed that a model based on cold-degree day summation procedure allows to explain most of the variability of leaf senescence of *Fagus* and *Quercus* ($ME > 0.86$). *Quercus* and *Fagus* exhibited a large variability of senescence timing along the elevational gradi-

ent despite the latitudinal proximity of monitored stand stations, discarding photoperiod as a crucial driver of the senescence variability over the considered dataset. The analysis of the estimated parameters confirmed that photoperiod had no modulation effect on cold-degree sum on *Quercus* and only a slight effect on *Fagus*. These results are in agreement with those previously reported, showing a modulation of the cold-degree influence on senescence by photoperiod for *Fagus sylvatica* whereas no effect was detected for *Quercus petraea* (Delpierre et al., 2009a). For *Fraxinus*, the null model was better than the bioclimatic models, which leads us to retain the null hypothesis: namely that for the given dataset, photoperiod may likely trigger senescence process in *Fraxinus*. However, consistent phenological differences occurred between the two studied years stressing out that senescence timing might be regulated by factors other than photoperiod alone. Finally for *Acer*, although the efficiency of the combined photoperiod/temperature-dependent models reached up to 0.82 when fitted over the whole dataset and 0.80 in cross-validation, our analyses underlined that a combination of photoperiod and temperature as drivers to trigger senescence timing do not constitute a satisfactory hypothesis to explain phenological variability of this species. Indeed, no gradual shifts in senescence timing occurred along the elevational gradient; only the two lowest populations (at 400 m asl.) exhibited a significant delay of senescence timing both in 2005 and 2006. More phenological data are therefore needed to clearly determine environmental factors which regulate leaf senescence timing of *Acer*.

For *Fagus* and *Quercus*, our simulations showed that senescence timing is expected to occur significantly later under a warmer climate with a higher shift for *Fagus*, especially at low elevation (up to 2.9 days per decade). Other studies have reported a significant delay of leaf senescence for temperate tree species in the last decades (Defila and Clot, 2001; Matsumoto et al., 2003; Menzel, 2000), which might continue over the 21st century (Delpierre et al., 2009a). However, senescence timing could be affected by drought that would trigger an earlier leaf fall (Bréda et al., 2006; Vitasse et al., 2010) and. The occurrence and severity of drought and heat waves will likely increase during the summer period in Europe (Schär et al., 2004), leading to a decrease in soil water availability and an increase in evaporative demand during the months preceding senescence. Such events could interplay with the general trend to later senescence attributed to warmer autumn, possibly counterbalancing the lengthening of canopy duration especially at low elevation (Angert et al., 2005; Hu et al., 2010; White and Nemani, 2003).

4.4. Increase in canopy duration under climate change

Our results predicted a lengthening of the canopy duration in response to warmer climate both for *Quercus* and *Fagus* in the next decades, as previously reported over the last decades (Linderholm, 2006; Menzel and Fabian, 1999). Our results suggest that climate change will lengthen the tree life cycle and consequently could enhance tree growth and productivity (Kramer et al., 2000; Myneni et al., 1997; Piao et al., 2007; White et al., 1999). However, at low elevation, summer drought may likely increase due to an earlier soil water depletion caused by an earlier beginning of the growing season (Davi et al., 2006) and this effect could offset the carbon gain resulting from the lengthening of canopy duration. In addition, at the ecosystem scale, the carbon uptake does not necessary increase with increasing growing season length. It has been shown that the ecosystem carbon storage might decrease in response to autumn warming due to changes in the carbon budgets of other ecosystem compartments such as soil organic matter (Piao et al., 2008).

Finally, this study pointed out that shifts in life cycle will likely differ between species, e.g. here being more pronounced for *Quercus* than for *Fagus* (3.7 and 2.8 days per decade, respectively). Compared to *Quercus*, canopy duration of *Fagus* is currently longer

at high elevation (above approximately 700 m) and shorter at low elevation. The prospective analysis predicted for the 2000–2020 period an equivalence of canopy durations of these two species at slightly higher elevations than nowadays. Interestingly, the models predicted that the elevational equivalence of canopy duration will likely increase in the next decades. In addition, the lengthening of canopy duration in response to temperature increase is mainly due to an advance of flushing for *Quercus*, whereas it is mainly the result of a delay in leaf senescence for *Fagus*. As the photosynthetic capacities of leaves and day length are more favourable at the beginning of the growing season than at the end (Morecroft et al., 2003), these phenological differences in the species response to temperature may enhance growth of *Quercus* to a larger extent than for *Fagus*, assuming no concomitant increase in drought frequency. Consequently, our results suggest that the competitive balance between species could be modified under climate warming to favour *Quercus* over *Fagus* over the elevational gradient, leading to possible shifts in their distributions range (Penuelas and Boada, 2003).

5. Conclusion

Although the phenological observations were carried during a short period (3 years), the considered elevational gradient explores a temperature range about 7 °C which often exceeds the interannual variations of temperatures obtained in one site during several decades (Vitasse et al., 2009a). This gradient is therefore particularly reliable to fit different phenological models. Bioclimatic models were able to explain and predict accurately the leaf unfolding date for all the species considered, whereas they failed to predict senescence date for two out of the four species. Strong differences in phenological sensitivities were detected among species and therefore the predicted trends over the 21st century consistently varied among species. Although the current chilling temperatures are likely sufficient to fully release bud dormancy for most species, they seem to be already insufficient for *Abies* and *Ilex*. In addition, the lack of chilling temperatures may increase in the coming decades with winter temperatures rising and could alter the predictions of 1-phase models. We therefore recommend to use 2-phases models for the future. Finally, the simulations showed species differences in lengthening of canopy duration and consequently suggested changes in the competitive balance between species over the current century.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2011.03.003.

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