

Simulating phenological shifts in French temperate forests under two climatic change scenarios and four driving global circulation models

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Abstract After modeling the large-scale climate response patterns of leaf unfolding, leaf coloring and growing season length of evergreen and deciduous French temperate trees, we predicted the effects of eight future climate scenarios on phenological events. We used the ground observations from 103 temperate forests (10 species and 3,708 trees) from the French Renecofor Network and for the period 1997–2006. We applied RandomForest algorithms to predict phenological events from climatic and ecological variables. With the resulting models, we drew maps of phenological events throughout France under present climate and under two climatic change scenarios (A2, B2) and four global circulation models (HadCM3, CGCM2, CSIRO2 and PCM). We compared current observations and predicted values for the periods 2041–2070 and 2071–2100. On average, spring development of oaks precedes that of beech, which precedes that of conifers. Annual cycles in budburst and leaf coloring are highly correlated with January, March–April and October–

November weather conditions through temperature, global solar radiation or potential evapotranspiration depending on species. At the end of the twenty-first century, each model predicts earlier budburst (mean: 7 days) and later leaf coloring (mean: 13 days) leading to an average increase in the growing season of about 20 days (for oaks and beech stands). The A2-HadCM3 hypothesis leads to an increase of up to 30 days in many areas. As a consequence of higher predicted warming during autumn than during winter or spring, shifts in leaf coloring dates appear greater than trends in leaf unfolding. At a regional scale, highly differing climatic response patterns were observed.

Keywords Phenology · Leaf unfolding · Leaf coloring · Spatial variation · Climate change · Global circulation model

Introduction

Since the emergence of phenology as a major focus for ecological research, multispecies studies have highlighted large differences in responses within various communities of plants and animals and across the whole of Europe (Kramer et al. 2000; Menzel et al. 2006a; Parmesan 2007; van Asch et al. 2007). Although under strong genetic control, plant phenological traits are also under strong environmental control. This environmental control is now well-documented even if the conceptual mechanisms are still under discussion and the underlying biochemical processes are not well understood. Temperature appears to be the main governing factor of leaf development of tree species (Chuine 2000; Schaber and Badeck 2003), although

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the effects of photoperiod (Falusi and Calamassi 1997; Heide 1993; Kramer 1995; Partanen et al. 1998; Sanz-Perez et al. 2009) and soil moisture availability (Penuelas et al. 2004) are sometimes evoked. Because of this strong environmental control, phenological traits have also been clearly identified as the main fingerprints of climate change in living organisms. Thus, the response to warming by phenological change across the Northern Hemisphere is especially well documented (Chmielewski and Rötzer 2001; Linderholm 2006; Menzel and Fabian 1999; Menzel et al. 2006a; Schwartz et al. 2006; Thompson and Clark 2008). These studies showed that spring phenological events now occur earlier, while autumn phenological events occur later, leading to an extension of the length of the growing season of between 7 and 15 days since the 1960s.

Because climate will continue to change, a clear insight into future phenological shifts appears crucial for accurate assessment of processes related to start and duration of the growing season. Changing phenological events can force adjustments in the functioning of forest ecosystems. An increased risk of frost damage associated with earlier budburst or later leaf coloring cannot be ruled out, which poses a challenge for many forest species (Kramer et al. 2000). Leaf phenology being a major determinant of water and CO₂ fluxes, recent studies have clearly shown that growing season length controls net ecosystem primary productivity and that phenological shifts have already modified the annual carbon cycle of terrestrial ecosystems (Berthelot et al. 2005; Churkina et al. 2005; Davi et al. 2006; Delpierre et al. 2009b; Duursma et al. 2009; Richardson et al. 2009; Saito et al. 2009; Yuan et al. 2008). An earlier onset of the growing season generally leads to an upward trend in carbon absorbed by forests because warming increases photosynthesis more than respiration in spring. For European temperate forests, Churkina et al. (2005) showed that the annual net ecosystem exchange (NEE) of carbon increased linearly according to the length of the carbon uptake period (CUP being controlled mainly by the growing season length) and was significantly different between vegetation types. Thus, for a range of CUP between about 100 and 300 days, the increased annual NEE rate of each additional CUP day averages about 5.8 g C m⁻² for deciduous broadleaf forests and about 3.4 g C m⁻² for conifers. In New England forests dominated by Eastern hemlock, red maple, paper birch and American beech, a 1-day advance in spring onset increased springtime net ecosystem productivity (NEP) by 2–4 g C m⁻² day⁻¹ (Richardson et al. 2009). In two French deciduous forests (dominated by *Fagus sylvatica* and *Quercus petraea*) growing under oceanic and continental climates, Davi et al. (2006) showed that the lengthening of the growing season by 38 days predicted from 1960 to 2100 will stimulate the NEP by about 150–220 g C m⁻² year⁻¹. As a consequence of

different phenological cycles, *Quercus petraea* will benefit more of this phenology effect than *Fagus sylvatica*. Most of these studies indicate that improving future spatial predictions of net terrestrial carbon fluxes requires reliable prediction of budburst at large scale and for different plant functional types.

In situ historical observations are crucial for monitoring the seasonality of phenological events of various species (Menzel et al. 2006a). Unfortunately, France has thus far not taken part in the International Phenological Gardens network founded at the end of the 1950s. Thus, at present, the main large-scale source of ground based phenological data for France lies with the observations initiated in 1997 in the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR). This network was created in 1992 to complement existing French forest health monitoring activities. It consists of 102 deciduous and evergreen permanent stands representing ten different forest species (26,000 trees). It covers a wide range of bioclimatic conditions, from oceanic to continental and Mediterranean contexts. It aims mostly to monitor long-term changes in the state of health, growth and biochemical cycles of carbon and minerals nutrients of French forest ecosystems. After 10 years of monitoring, this French database provides a unique source of data allowing a broad-scale analysis of the variability of phenological events in forest trees. Until now, phenological data collected by the network have been used mainly to configure an ecophysiological water balance model (Lebourgeois et al. 2005). More recently, a subset of the observations was used to validate the onset of green-up in deciduous broadleaved forests derived from moderate resolution imaging spectroradiometer data (Soudani et al. 2008) and to study the annual timing of temperate forest leaf coloring (Delpierre et al. 2009a).

The first focus of this study was to describe and model the spatial variability of spring leaf unfolding (LU) at national and regional scales. As most soil–vegetation–atmosphere schemes used on such geographic scales are parameterized according to plant functional type (i.e., temperate evergreen or deciduous forests), we first computed phenological models for coniferous (silver fir, spruce, pines, Douglas-fir and larch) and broadleaved (oak and beech) forests only. Afterward, we also computed species-specific models for oak and beech as a recent study showed that rising temperatures should affect oak and beech spring phases differently and thus differentially modify their annual carbon dioxide cycles (Davi et al. 2006). This specific modeling was possible because these species presented the largest amount of available data and had a broad spatial distribution. Modeling of leaf senescence is only just beginning to emerge and just a few studies have highlighted the broad-scale response to leaf coloring of deciduous temperate

trees (Delpierre et al. 2009a; Estrella and Menzel 2006; Jolly et al. 2005; Vitasse et al. 2009b). Thus, for each broadleaved species, dates of autumn leaf coloring (LC) and length of the growing season (LGS) were also modeled.

For each plant functional type (evergreen forests and broadleaved trees) or species (oak and beech trees) the resulting regression models were used to draw phenological maps at the French scale under present climate conditions. Most published papers dealing with such large-scale spatial analyses have demonstrated the usefulness of including many topographic and geographical parameters to explain phenological phases among broad taxonomic/functional groups (Dittmar and Elling 2006; Menzel et al. 2006b; Parmesan 2007; Rötzer and Chmielewski 2001; Vitasse et al. 2009a). Thus, we first ran the model by taking into account not only climate data but also elevation, latitude, longitude, distance from the Atlantic Ocean and from the Mediterranean sea. But, as these geographical variables are stable over time, they must be excluded as driving variables for an accurate and reliable predictive modeling including various climate change hypotheses. Finally, we compared the results of both methods to evaluate the role of non-climatic parameters in the predictions. As we seek phenology models that are general enough to be applied at large scale, and robust enough to perform acceptably for both current and future climatic conditions, only bioclimatic models have been considered in the second part of this work, which intended to evaluate phenological shifts under climatic change. Because the intensity of climate change will be heterogeneous throughout France (Déqué 2007; Planton et al. 2008), there is a clear expectation of strong different sub-regional phenological responses. However, the strength and the range of response between species and locations are still largely unknown. Although the reality of climatic warming is now largely acknowledged, great uncertainties still exist regarding future climate scenarios (Mitchell et al. 2004). Thus, to better highlight the range of phenological shifts, we tested the effects of various SRES scenarios (A2, B2) and global circulation models (GCMs, i.e., HadCM3, CGCM2, CSIRO2 and PCM) for each phenological stage and plant functional type and compared current observations and predicted values for the periods 2041–2070 and 2071–2100

Materials and methods

Phenology database

Phenological observations are available for 101 of the 102 permanent plots of the French network RENECOFOR. We also took into account data from two stands of the

Luxembourg network that are located near the French border. Long-term monitoring protocols in Luxembourg are similar to those in France. The total of 103 sampled forests are composed of mature pure stands and correspond to managed high forests (see Appendix S1 in the electronic supplementary material), and cover all bioclimatic contexts: oceanic along the west coast and in the north, continental in the interior of the country, Mediterranean in the south and mountain at high elevations (Fig. 1).

Ten species are represented (51 broadleaved stands and 52 coniferous forests). *Quercus petraea* ($n=21$ stands) and *Q. robur* ($n=8$) stands were sampled mainly in northern France, with a homogeneous distribution from west to east (20–370 m a.s.l.). *Fagus sylvatica* ($n=22$) stands are located in northeastern plains (250–570 m) and in mountain contexts in southern and south-eastern France (400–1,400 m). *Picea abies* ($n=11$), *Abies alba* ($n=11$) and *Larix decidua* (1) stands correspond mainly to mountain forests in eastern France (400–1,850 m). For *Pinus* (23) and *Pseudotsuga menziesii* (6) stands, geographical locations and ecological conditions are more diverse. Beech, oak, silver fir, larch and some spruce stands are of local origin and correspond to long-term naturally regenerated stands. Pine and Douglas-fir stands derived mostly from plantations. Even if no precise information is available for these stands, the common afforestation practice is to select well-adapted climatic

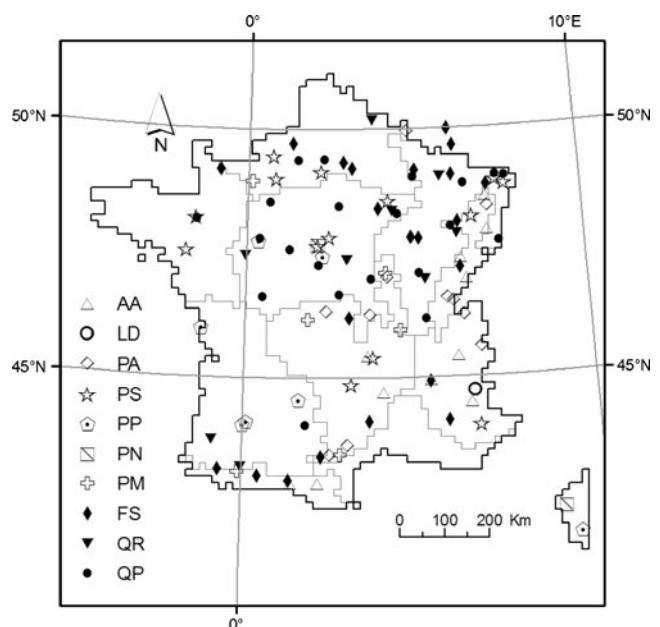


Fig. 1 Location of the 103 forest stands (51 broadleaved stands and 52 coniferous forests) investigated in this study. AA *Abies alba* (11 stands), LD *Larix decidua* (1), PA *Picea abies* (11), PS *Pinus sylvestris* (14), PP *Pinus pinaster* (7), PN *Pinus nigra* ssp. *laricio* var. *Corsica* (2), PM *Pseudotsuga menziesii* (6), FS *Fagus sylvatica* (22), QR *Quercus robur* (8), QP *Quercus petraea* (21)

seeds. Thus, the studied trees are probably well adapted to prevailing climatic conditions.

LU and LC (only for broadleaved trees) have been monitored annually for 36 trees per plot ($n=3,672$ trees) since 1997. Phenological phases were observed weekly by local foresters with binoculars between March and June for LU and September and November for LC (broadleaved trees and larch). Two dates, in Julian days, hereafter termed LU1 and LU9, were defined as the dates when at least 20% of buds are open in 10% and 90% of the 36 trees, respectively. The same principle has been used for leaf coloring (LC1 and LC9). Because in situ observations were carried out on a weekly basis, we estimate a theoretical precision of 7 days and 3–4 days on average (Soudani et al. 2008). Between 1997 and 2006, 78 stands were monitored for at least 8 years, and 42 stands during the whole period (10 years). Thus, from 1997 to 2006, a total of 838 and 449 annual observations for LU and LC, respectively, are available. For oak, beech and larch stands, LGS was evaluated in four different ways according to the phase of development taken into account.

Climate data set

Meteorological data were gathered from the Renecofor meteorological sub-network (20 stations) and from the French National Climatic Network “Météo-France” (123 stations). For the latter stations, the locations were screened carefully to avoid urban effects and to be as representative as possible of stand weather conditions. The distance between phenological and meteorological stations averaged 11.1 km. The altitudinal difference was 172 m and less than 100 m in 55% of cases (mean difference=23 m). Monthly means of mean temperature (T) and precipitation (P) were calculated for each year for the period 1997–2006. These data have been completed by monthly global solar radiation (Rg; Piedallu and Gégout 2007) and potential evapotranspiration (PET in millimeters according to the Turc formula) to quantify the water balance ($WB = P - PET$). This formula was chosen because it requires simple monthly climatic parameters (only T and Rg) and has proved to be one of the simplest accurate formulas for ecology (Lebourgeois and Piedallu 2005). Finally, a pool of 48 regressors was defined. For the period 1997–2006, the correlation (r^2) between PET and Rg and PET and T averaged 0.44 and 0.64, respectively. An increase of Rg or T led to an increase of PET. The link between PET and Rg was minimum during winter months ($r^2 < 0.20$ for January and February) and increased during summer months ($r^2 = 0.68$ and 0.78 for June and July). Thus, during winter, PET values were linked mostly to temperature ($r^2 > 0.75$ from November to March). The link between T and Rg was weak and significant only during summer (data not shown).

Statistical modeling

RandomForest (RF) techniques were used to predict phenological dates. Within the last 10 years, there has been increasing interest in the use of such methods in ecological studies (Prasad et al. 2006; Vayssières et al. 2000) because they gave good predictive accuracy without overfitting the data (Breiman 2001). RF is a non-parametric procedure that does not require the specification of a functional form (Vayssières et al. 2000). This eliminates the need to make simplifying assumptions about the data. Moreover, unlike parametric models, which are intended to uncover a single dominant structure in data, RF is designed to work with data that might have multiple structures (Vayssières et al. 2000). Rather than identify a “single good model” (i.e., a single regression tree between the data and the explanatory variables), RF is a collection (10,000) of regression trees, the final model being an average of multiple good models. RF also incorporates automatically the possibility of interactions among the predictors and is able to handle non-linear relationships between parameters. Naturally, this method also has some disadvantages (Vayssières et al. 2000). Because RF represents a continuous factor by a series of distinct subranges, parametric methods are better at capturing a simple relationship between the response variable and a continuous factor. As a result, linear and simple curvilinear structures of the data of each parameter may be obscured by the decision tree. Furthermore, the influence (positive or negative) of each explanatory variable (monthly climatic variables in our study) cannot be evaluated in a straightforward manner by a simple obvious indicator.

The RF approach consists of a large number of random trees—a bootstrap sample (n_{tree}) of the training set being used to construct each tree. (Breiman 2001). At each node, “mtry” predictors (a subset of the total predictors) is chosen randomly and the best predictors (the best split) are selected. By growing each tree to maximum size without pruning, RF tries to maintain some prediction strength while inducing diversity among trees (Breiman 2001; Prasad et al. 2006). Random predictor selection diminishes correlation among unpruned trees and keeps the bias low; by taking an ensemble of unpruned trees, variance is also reduced. In a final step, annual predicted data are computed by averaging the predictions of the n_{tree} trees. To estimate the accuracy of the test set, the remaining training set samples that are not in the bootstrap for a particular tree (= the out-of-bag samples) can be run down through the tree [cross-validation to estimate an out-of-bag (oob) error]. Similarly, to measure the importance of the variable m , its values are permuted randomly in all cases of oob samples. These cases are then run down the current tree, their values noted and finally a new value of oob-error computed. This

increased oob error is an indication of the importance of that variable (Breiman 2001).

Two parameters (the number of aggregating trees n_{tree} and the number of predictors at each node, $mtry$) are defined by the user and must be optimized to minimize the oob error. In our study, n_{tree} was 10,000 and the optimal values for $mtry$ was 4. The selection of the final regressors was based on the percent increase in error (%IncMSE). For the final model, the ten best variables were selected. For each model, the RMSE of adjusted and predicted values and the percentage of predicted variance are given. For modeling, we used the RF package within the statistical software R 2.2.1. RF equations can be used to predict year-to-year variability in phenological dates. However, as the main objective of our study was to highlight phenological trends, only average predicted dates from different periods are presented in this paper.

Climatic change scenarios

We used RF models to generate maps of phenological dates throughout France. We used large-scale spatial monthly climate information available in France to calculate bioclimatic indices. For the period 1991–2000, we extracted data from the high-resolution grids ($10' \times 10'$) of observed monthly climate for Europe of the Climate Research Unit (CRU TS 1.2) at www.cru.uea.ac.uk (New et al. 2002). For the period 2001 to 2100, we used four general circulation model (GCM) projections (HadCM3, CSIRO2, CGCM2 and PCM) and two climate change scenarios (A2 and B2) available at the Tyndall Centre for Climate Change Research (TYN SC 1.0 – $10' \times 10'$; Mitchell et al. 2004). The A2 scenario represents high human population growth and slow technological advancement, while the B2 scenario has moderate population growth with more environmental protection. Future global solar radiations were calculated by the program Helios by integrating the variations of nebulosity predicted by the different scenarios (Piedallu and Gégout 2007). According to the GCM resolution, the phenological model was implemented for France with a 15×15 km spaced grid (2,460 points for the entire French territory). Timing of phenological events was projected for the periods 2041–2070 and 2071–2100 and compared to the reference period 1991–2000.

The two scenarios and the four models predict a significant warming. However, the upward shift is less pronounced with the PCM model. Thus, at the end of the century, the differences between this model and the other range between 1°C and more than 2°C according to the month taken into account (data not shown). For each GCM, warming is also less pronounced with the B2 scenario (about 1 to 1.5°C). Table 1 presents the predicted changes according to the more pessimist A2-HadCM3 scenario for the period 2071–2100 for each French climatic division.

Results

Species patterns and spatial variability

For the period 1997–2006, budburst started on average before mid-April for both oak species (Table 2). Within each stand, the interannual variability of LU1 averaged 4–6 days, the extreme differences varying between 11 and 36 days (not shown). Leaf coloring (LC) occurred in mid-October and the variation between years appeared greater than for LU. Thus, the interannual onset of LC and maximum differences averaged 15 and 29 days, respectively (not shown). Along the longitudinal gradient, the onset of spring phase was delayed by about 2.6 days for every 100 km, leading to a later LU by between 10 and 20 days for eastern stands (Lebourgeois et al. 2008). Finally, the growing season tended to be shorter for eastern stands (<200 days) as a consequence of both earlier LC and later LU.

The onset for beech stands occurred later, from the 3rd week of April onwards (Table 2). As observed for oak, the interannual LU variations ranged mostly between 4 and 8 days, and the extreme differences averaged 21 days (not shown). Since LC occurred in early October, a shorter duration of about 20 days can be observed in beech stands comparison to oak forests. As beech stands were sampled mostly in eastern France, the effect of longitude appeared less significant. Moreover, high elevation stands ($>1,300$ m) came into leaf later than low-elevation forests (~ 15 days; not shown).

Budburst occurred later for conifers (Table 2). The latest onset of spring is observed in high altitude silver fir, Norway spruce and larch forests. For these stands, budburst started from mid-May onwards. The extreme differences in the dates of the onset of LU were similar to those observed for broadleaved stands. Budburst appeared highly altitude-dependent, with a mean vertical gradient of 1.5 days per 100 m altitudinal increase (Lebourgeois et al. 2008).

RandomForest modeling

In each case, the best models were obtained with LU1, LC9 and LGS19 (LC9–LU1). The overall model singled out plant functional types (PFT), the five geographical variables and four climatic parameters (PET and T in March, T in February and April) as being the most important to predict the date of LU1. The model predicted 75.6% of the observed variance. The adjusted root mean squares error (RMSE) and the oob errors were 4.5 days and 8.4 days, respectively (not shown; Lebourgeois et al. 2008). RF based on climatic data appeared slightly less accurate. In each model, a decrease in predicted variance and an increase of both adjustment and oob errors were observed

Table 1 Average (SD) climatic changes for the period 2071–2100 according to the A2-HadCM3 scenario (reference period 1991–2000). The 11 areas correspond to the large-scale French climatic divisions. The climatic parameters correspond to the most important predictive factors for leaf unfolding (LU) and leaf coloring (LC, see Fig. 2). *PET* Potential evapotranspiration, *Rg* global solar radiation; absolute and relative (in %) changes are presented

French climatic divisions ^a	Δ Mean temperature (°C)						Δ PET (mm)						Δ Rg (MJ/m ²)										
	January		March		May		October		January		March		October		January		October		November				
	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD			
North-west (282)	3.1	(0.6)	2.8	(0.5)	2.5	(0.6)	4.2	(0.8)	3.2	(0.8)	+24%	5.4	(1.2)	+13%	-231	(185)	-4.8%	1,559	(598)	7.5%	817	(204)	8.5%
Center (399)	2.4	(0.2)	2.0	(0.2)	2.7	(0.1)	4.4	(0.2)	3.4	(0.3)	+31%	4.7	(0.7)	+11%	-570	(132)	-6.4%	2,227	(211)	10.7%	852	(226)	8.8%
North (276)	2.7	(0.2)	2.6	(0.1)	2.6	(0.1)	3.5	(0.1)	3.6	(0.2)	+40%	5.7	(0.3)	+17%	-368	(102)	-2.8%	1,680	(460)	9.3%	666	(129)	8.5%
North-east (267)	2.6	(0.4)	1.8	(0.4)	2.8	(0.2)	4.1	(0.2)	4.7	(0.9)	+88%	5.6	(1.0)	+16%	-670	(95)	-4.4%	2,344	(252)	12.5%	573	(269)	6.6%
Vosges-Jura Mountains(79)	2.3	(0.3)	1.5	(0.2)	3.2	(0.2)	3.6	(0.1)	6.3	(0.9)	+330%	7.3	(1.6)	+26%	-744	(106)	-1.3%	1,972	(341)	9.9%	153	(206)	1.7%
Alps (200)	2.7	(0.4)	2.2	(0.5)	3.3	(0.6)	4.4	(0.3)	5.9	(2.4)	+341%	10.8	(4.8)	+67%	-631	(125)	-5.2%	1,596	(346)	6.3%	555	(263)	4.1%
Massif Central (347)	2.8	(0.1)	2.4	(0.1)	2.7	(0.3)	3.9	(0.3)	5.2	(1.1)	+70%	5.3	(1.4)	+14%	-487	(176)	-8.3%	1,781	(589)	7.5%	1,168	(426)	10.6%
Pyrenees (69)	2.5	(0.2)	1.9	(0.3)	1.9	(0.5)	3.8	(0.3)	5.7	(1.8)	+131%	7.8	(3.1)	+70%	-237	(185)	-2.6%	1,010	(410)	3.6%	626	(137)	4.2%
South-west (371)	2.3	(0.1)	1.6	(0.1)	2.5	(0.2)	3.9	(0.2)	3.4	(0.5)	+20%	3.9	(0.8)	+7%	-680	(140)	-1.7%	1,821	(335)	7.2%	1,362	(300)	11.8%
Mediterranean area (133)	2.5	(0.2)	1.8	(0.3)	1.8	(0.5)	4.4	(0.3)	3.9	(0.4)	+19%	3.5	(0.9)	+6%	-193	(161)	-5.7%	528	(310)	1.8%	568	(87)	3.6%
Corsica (37)	3.1	(0.3)	2.7	(0.1)	2.1	(0.2)	3.7	(0.3)	5.0	(1.3)	+25%	8.7	(2.2)	+19%	-472	(622)	-8.6%	734	(902)	2.4%	712	(642)	4.1%
Mean	2.6		2.1		2.6		4.0		4.2		+69%	5.6		+18%	-503		-4.8%	1770		8.1%	848		8.1%

^a Numbers in parenthesis correspond to the number of predicted values in each area (grid 15×15 km; 2,460 values for the entire French territory)

Table 2 Mean (SD) [minimum–maximum] dates of LU and LC for each species (period 1997–2006; number of days after the beginning of the year=Julian day). LU1 and LU9 correspond to the dates (in Julian days) when at least 20% of buds are open in 10% and 90% of

the 36 trees, respectively. The same principle was used for LC. *n* Number of observations, *LLU* number of days (SD) between LU1 and LU9, *LLC* number of days (SD) between LC1 and LC9

Leaf unfolding

Species	<i>n</i>	LU1	LU9	LLU	
Broadleaves					
<i>Fagus sylvatica</i>	178	112 (12.3) [71–181]	121 (10.0) [98–188]	9.0 (5.4)	
<i>Quercus petraea</i>	182	100 (10.2) [78–124]	111 (12.3) [88–195]	11.1 (6.8)	
<i>Quercus robur</i>	71	100 (13.0) [71–125]	112 (14.7) [78–137]	12.9 (9.7)	
Conifers					
<i>Abies alba</i>	98	133 (12) [102–172]	141 (11.9) [116–179]	9.0 (4.2)	
<i>Larix decidua</i>	10	130 (5)[122–138]	141 (6.2) [129–146]	10.5 (4.9)	
<i>Picea abies</i>	83	132 (11.5) [97–166]	142 (11.3) [114–173]	10.8 (6.3)	
<i>Pinus nigra</i> ssp. <i>Laricio</i>	14	121 (14.9) [104–159]	131 (14.7) [114–166]	10.2 (4.1)	
<i>Pinus pinaster</i>	46	115 (17.8) [80–156]	126 (16.4) [97–163]	11.6 (6.6)	
<i>Pinus sylvestris</i>	108	125 (12) [90–159]	135 (12.3) [104–166]	10.9 (5.8)	
<i>Pseudotsuga menziesii</i>	48	124 (11.9) [97–142]	136 (11.6) [111–161]	12.1 (6.2)	
Leaf coloring					
Species	<i>n</i>	LC1	LC9	LLC (days)	Length of growing season (LC9-LU1) (days)
Broadleaves					
<i>Fagus sylvatica</i>	179	275 (16.5) [223–318]	292 (16) [244–332]	16.8 (10.3)	180 (22) [112–245]
<i>Quercus petraea</i>	188	284 (14.2) [247–323]	300 (11.3) [264–334]	15.8 (9.1)	200 (15.5) [154–245]
<i>Quercus robur</i>	72	283 (15.8) [251–332]	300 (14.6) [272–345]	16.6 (8.4)	200 (25.4) [161–266]
Conifers					
<i>Larix decidua</i>	10	273 (4.7) [264–282]	288 (5.0) [278–293]	14.7 (2.2)	158 (7.6) [147–168]

when geographical parameters were excluded from the analysis. The variation ranged between 10% and 25% for predicted variance and between 1 and 4 days for adjustment and oob errors. Geographical variables were replaced by winter temperatures (Jan–Feb), global solar radiations in winter (January), spring (May and June) and summer (July).

The ten best bioclimatic models are shown in Fig. 2. According to the phase and the PFT taken into account, the predicted variance ranged from 34.7% to 54.1%, with oob errors from 7.8 to 15.8 days. Global solar radiation, temperature and potential evapotranspiration were the most important variables, with 11, 10 and 7 different months, respectively, in the models. Precipitation and water balance (P-PET) played a minor role with only 1 and 2 observations. Global solar radiation in January entered in each model, and March PET in 7 out of 10. Winter and early spring conditions (mainly through January, March to May temperatures or PET) govern the onset of the growing season for broadleaves, whereas in conifers budburst depends mainly on spring and early summer conditions (mainly through global solar radiation; Fig. 2). For each broadleaved species, RF still indicated the important role of

January but the first position of this period for the beech models suggests a greater role for this month in this species. Afterwards the key periods focused mainly on March–April for oaks and April–May for beech.

For LC, predicted variances were lower than for LU and global solar radiations appeared to play a more important role than for LU. Temperature or global radiation in early autumn (mainly October) appeared as important predictors for both species. For the growing season length, six variables were common between both species but summer (July–August), and late autumn conditions (November) appeared more important in beech. RF also indicated less accurate models for beech than for oak trees.

Average phenological dates throughout France for the period 1991–2000 can be seen in Fig. 3. The large-scale maps highlight not only the overall differences between oaks, beech and conifers in phenological cycles but also spatial variation in the response patterns. The more precocious onset of the growing season is observed for broadleaved trees in southwestern France, and budburst is delayed between 10 and 20 days from west to east. Autumn leaf coloring occurs from the beginning of October (mainly in

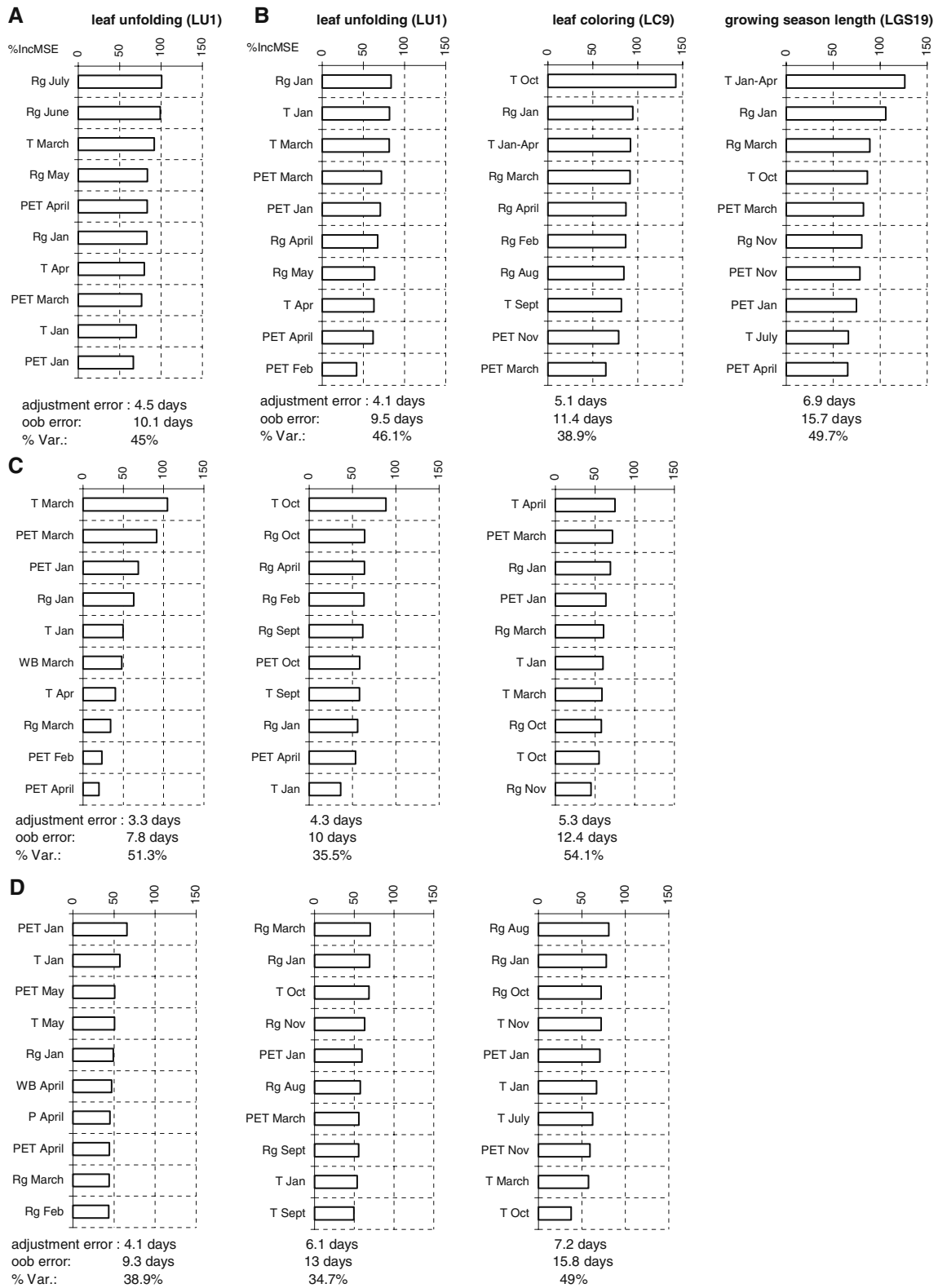


Fig. 2 Variable importance plot generated by RandomForest (RF) algorithm for leaf unfolding (LU1), leaf coloring (LC9) and growing season length (LGS19). The plots show the importance of the variable measured as increased mean square error (%IncMSE). Variables were sorted according to decreasing degree of importance in the modeling.

A Coniferous trees ($n=416$ observations), *B* broadleaved trees (oaks and beech; $n=410$), *C* oaks ($n=241$), *D* beech ($n=169$). *T* Temperature, *P* precipitation, *PET* potential evapotranspiration, *Rg* solar global radiation, *WB* P-PET. Only climatic variables were taken into account

mountain contexts) to late November (southwestern France, Mediterranean area). Finally, the length of the growing season ranges from less than 170 days to more than 230 days.

To gain insight into the respective influence of the most important climatic factors governing the phenological dates for broadleaved trees, and to partly highlight their interactions, we modified their values successively according to the A2-HadCM3 scenario (see Table 1). We used these new values to predict phenological dates and hence to perform the changes linked to the specific variation of each climatic parameter (all other parameters are also taken into account but their values are unchanged). The results presented in the Table 3 show that, for both species, a warming in January hastens LU in most cases, particularly for beech. On the other hand, contrasting effects are observed for the global solar radiation in January. For March, warmer temperatures hasten oaks leaf unfolding in more than 90% of cases. For beech, warmer temperatures in May tend to delay leaf unfolding. For both species, a simultaneous change of the three climatic factors leads to a mean advance of LU of 3.7 and 2.5 days for oaks and beech, respectively. At the end of the growing season, warmer October temperatures highly delay leaf coloring for both species, particularly for oaks. As observed for LU, more contrasting effects appear for autumnal Rg.

Predicted changes for the periods 2041–2070 and 2071–2100

For the period 2041–2070, the impact of the A2 scenario appears similar to the B2 hypothesis (Table 4). Analysis of the differences between the GCMs reveals that the HadCM3 and CSIRO models show the largest, and the PCM model the smallest, effects on predicted shifts. The overall trend corresponds to a more precocious date of budburst (mean: 3.3 days for conifers and broadleaved trees), a delay in leaf coloring (9.1 days) and a lengthening of the growing season of 14.7 days. At the regional scale, trends are less often significant in mountain contexts (Jura, Vosges, Pyrenees) for conifers and appear more consistent within areas for broadleaved trees.

At the end of the century, for the deciduous species, the lengthening of the growing season averages 20.7 days. Early budburst contributes about 30% to this change (mean advance of 6.8 days) and delayed leaf coloring about 70% (mean delay of 12.7 days). Moreover, the eight hypotheses produce widely different results (Table 4, Fig. 4). Whatever the global circulation model used, the impact of the A2 scenario appears higher than that of the B2 hypothesis. The average difference ranges from 1 to 9 days depending on the phenological phase or GCM model considered (Table 4). CSIRO and HadCM3 models predict the most important shifts. Considering broadleaved trees, the greater changes are observed at the end of the growing season with an

average delay of 19.4 days with the A2-HadCM3 model. Thus, the lengthening of 28.4 days for the growing season appears to be linked mainly to a delay in LC.

At the regional scale, the average lengthening of the growing season (>30 days with the A2-HadCM3 model) observed in a large part of western France is a consequence mainly of a significant delay in LC (>25) instead of a hastened date of budburst (5–15 days; Fig. 4). Trends are different in northeastern and eastern France. The advance of LU is more consistent throughout areas (5–15 days). The delay in LC is less (10–25 days) and leads to fewer changes in LGS (10–30 days). For conifer stands, the beginning of the growing season advances by between 10 and 20 days except in a broad part of northern France (<10 days).

For oak and beech, the A2-HadCM3 model predicts significant shifts, also larger at the end of the growing season, particularly for oak trees (Table 5, Fig. 4). Significant spatial shifts are observed for both oak and beech stands but the differences between areas appear more marked for the latter species. Thus, in northwestern beech stands, the increase in LGS (>30 days) is a consequence mainly of a marked delay in LC (>20 days). In southwestern areas, the lengthening is linked mainly to a hastened leaf unfolding (>15 days; Fig. 4). In northeastern beech stands, changes are less marked and often below 10 days. For oak stands, a growing season that is longer by between 20 and 40 days is observed in a broad part of northern and southwestern France. In western areas, this increase is mainly the consequence of a delayed autumnal phase (>25–30 days). In other areas, this lengthening is linked to a delay in LC (15–25 days) and to an advance in budburst (10–15 days).

Discussion

This study presents the first published French maps showing the annual cycles of phenological phases for common European evergreen and deciduous genera under current and future climate conditions. Our results also agree with findings of previous European studies on difference between species and the key periods for annual development cycles (Delpierre et al. 2009a; Vitasse et al. 2009a, b). On average, spring development of oak precedes that of beech, which precedes that of conifer stands.

Our results clearly showed that the geographical parameters commonly used in previous studies can be efficiently replaced by climatic parameters. In our bioclimatic models, annual cycles in budburst and leaf coloring are highly correlated with winter, spring and autumn weather conditions, the key months being January, March–April and October–November. As expected, tree phenology is essentially affected by temperature, which is in agreement with the general pattern for temperate trees

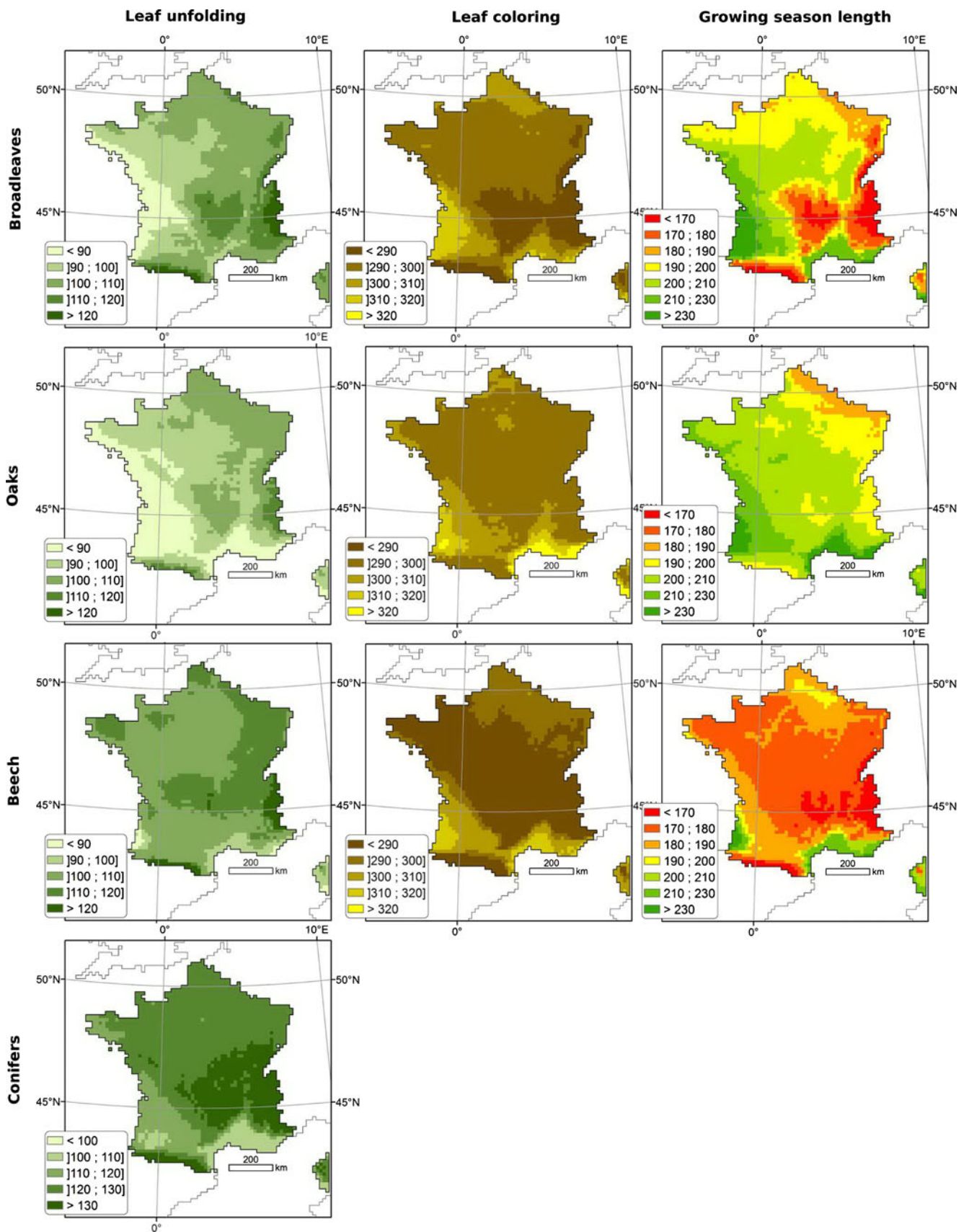


Fig. 3 Average spring leaf unfolding (LU1), autumn leaf coloring (LC9) and length of the growing season (LGS19) in France for the period 1991–2000. LU1 and LC9 are expressed in Julian days and LGS19 represents number of days. The mapping is based on RF models taking only the climatic variables into account (see Fig. 2 for details)

observed in mid-latitude Europe (Rötzer and Chmielewski 2001). The effects of winter and early spring months on budburst are coherent with the physiological approach of bud development based on the rate of degree-days accumulation (Chuine 2000; Kramer 1995). The greater sensitivity to winter temperature of beech in comparison to oak agrees with the more sophisticated modeling approach led by Kramer (1995) and with results obtained in comparative greenhouse-controlled experiments on different broadleaved species (Falusi and Calamassi 1997; Murray et al. 1989). Thus, in the study of Kramer (1995), the variance between LU and winter temperature explained by a simple linear model is less than 10% for oak and between 30 and 40% for beech, and warmer winter temperatures hasten leaf unfolding.

In our models, global solar radiation (R_g) also plays an important role in determining phenological dates. This is particularly apparent for conifers. For broadleaved trees, R_g tends to be more important in modeling for LC than for LU. As the relationships between R_g and T are weak, the effects of R_g on phenological dates cannot proceed from simple correlations between both variables. Thus, R_g effects are not “hidden” temperature effects. By combining numerous variables relating to earth–sun geometry and light characteristics, R_g is closely linked to light intensity and duration as well as day length (Piedallu and Gégout 2007; Vitasse et al. 2009b). Even if the underlying ecophysiological mechanisms are still largely unknown, many studies suggest the role of photoperiod on budburst for temperate trees. For example, in his study leads on *Fagus sylvatica*, Heide (1993) showed that for shoots chilled until March and then grown under long days, budburst was >93% for all ecotypes. Similar results were observed by Falusi and Calamassi (1997). These authors showed that winter chilling was the principal factor in the removal of dormancy in all the

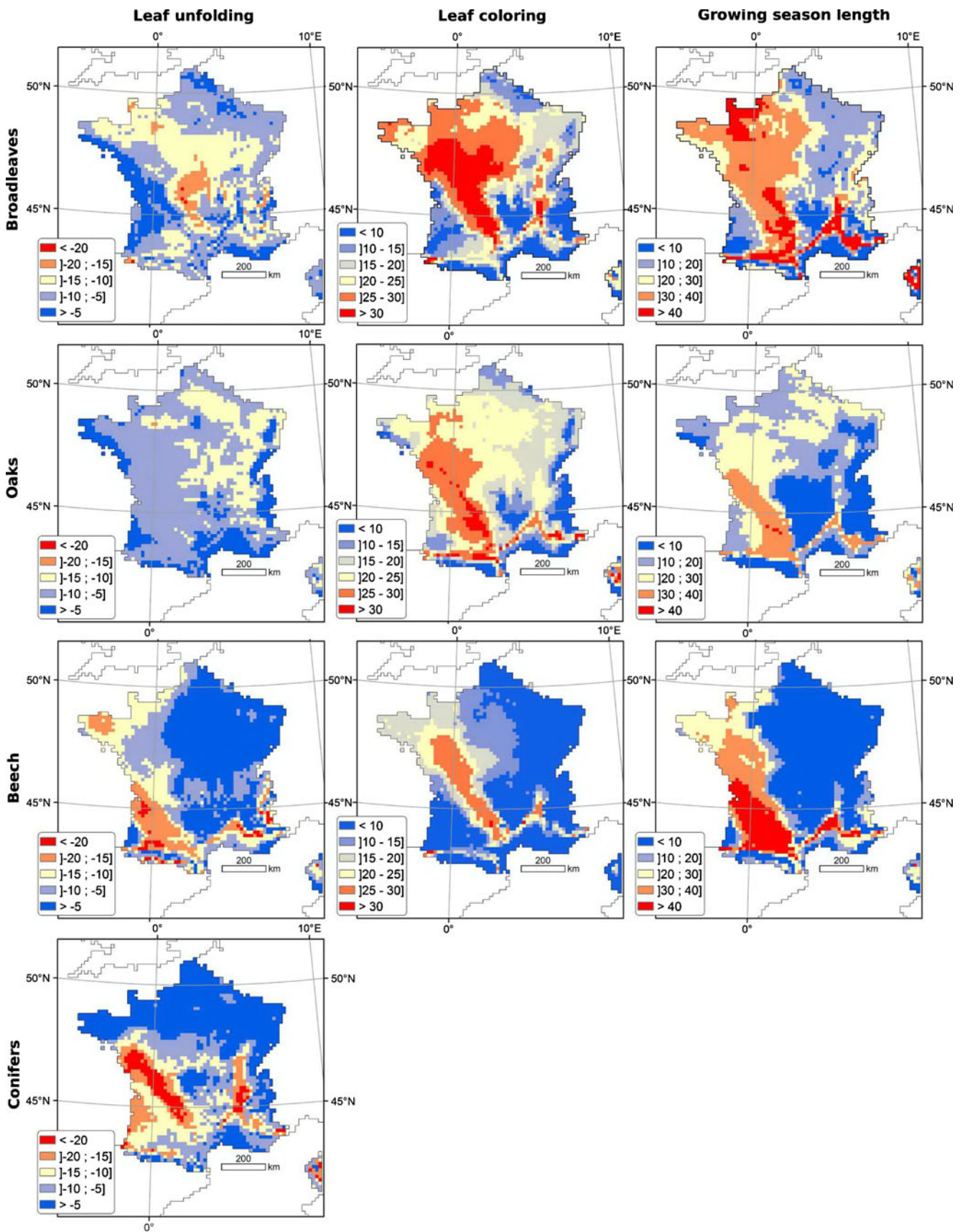
Table 3 Average predicted changes in LU and LC dates for oaks and beech according to the specific variations (Δ) in climatic parameters predicted by the A2-HadCM3 scenario (values in parenthesis, see Table 1). Annual predictions were performed according to the RandomForest (RF) models presented in Fig. 2 and only with the most important climatic driving factors. Annual changes were compared to the annual dates predicted for the period 1997–2006 ($N = 241$ and 169 phenological observations available for oaks and beech, respectively). For each case, the number of observations with

a delay (Nd) or an advance (Na) is presented and the corresponding shift was calculated. For example, for oaks, a single increase in 3°C in January leads to an advance in LU in 83% (203/241) of the cases (mean: -1.4 days). A simultaneous change in temperature and solar global radiation (a+b+c) hastens LU by about 4.6 days in 85% of the cases (204/241) but delays LU by about 1.4 days in 15% (34/241), the values of the other climatic parameters entering into the model being unchanged

Species	Δ climatic parameter	Month	Average change		Mean delay		Mean advance	
			N	days	Nd	days	Na	days
Leaf unfolding								
Oaks	Δ Temp. (+3°C) (a)	January	241	-1.1	38	0.7	203	-1.4
	Δ Temp. (+3°C) (b)	March	241	-3.2	17	1.1	224	-3.5
	Δ Rg. (-5%) (c)	January	241	0.2	144	0.7	97	-0.4
	a + b + c		241	-3.7	34	1.4	207	-4.6
Beech	Δ Temp. (+3°C) (a)	January	169	-2.7	15	0.3	154	-3.1
	Δ Temp. (+3°C) (b)	May	169	-0.4	119	1.3	50	-1.9
	Δ Rg. (-5%) (c)	January	169	0	82	0.5	87	-0.5
	a + b + c		169	-2.5	43	1.4	126	-3.8
Leaf coloring								
Oaks	Δ Temp. (+3°C) (a)	January	241	3.1	193	3.9	48	-0.6
	Δ Temp. (+4°C) (b)	October	241	7.0	236	7.1	5	-1.1
	Δ Rg. (+8%) (c)	October	241	0.3	136	1.3	105	-1.0
	a + b + c		241	9.3	235	9.6	6	-0.9
Beech	Δ Temp. (+3°C) (a)	January	169	2.0	117	3.4	52	-1.3
	Δ Temp. (+4°C) (b)	October	169	4.3	146	5.2	23	-1.3
	Δ Rg. (+8%) (c)	November	169	-0.2	64	1.3	105	-1.2
	a + b + c		169	6.6	134	8.9	35	-2.4

Vosges-Jura Mountains (79)	289	6.0	5.2	7.5	6.8	8.5	7.5	5.3	4.6	9.7	6.6	11.7	8.6	14.9	9.7	7.4	5.5
Alps (200)	285	4.1	3.1	5.9	4.6	7.4	6.1	3.0	2.4	8.3	4.3	10.6	6.4	14.6	8.4	5.5	2.9
Massif Central (347)	288	6.2	5.5	7.8	6.4	10.2	8.6	4.8	3.7	12.2	6.5	15.2	8.5	19.9	11.3	7.2	3.7
Pyrenees (69)	285			4.8	3.9	4.5	3.8			6.5		10.5	5.9	10.3	5.9	3.2	
South-west (371)	301	16.2	14.8	17.8	16.6	19.4	18.7	13.9	9.6	20.9	18.3	21.8	19.9	23.0	21.4	19.4	11.2
Mediterranean area (133)	301	12.0	10.7	12.8	12.3	13.4	12.5	9.7	8.2	14.6	12.2	15.0	13.3	15.5	13.9	12.6	9.2
Corsica (37)	295	13.6	12.2	14.6	13.8	15.3	14.4	11.3	10.0	17.1	12.5	17.5	14.8	18.3	15.6	13.3	9.4
	294	9.1	8.1	10.1	9.1	11.7	10.4	7.7	6.5	14.0	10.4	16.4	11.8	19.4	13.3	9.7	6.9
Length of growing season																	
North-west (282)	199	17.2	14.5	18.9	18.1	18.6	13.5	8.8	8.3	33.7	25.1	35.6	30.5	37.4	25.2	20.6	15.6
Center (399)	199	10.6	8.9	10.1	10.4	11.8	9.3	5.9	6.2	24.7	13.0	27.7	16.3	32.1	14.3	9.0	8.0
North (276)	191	8.5	7.1	6.4	7.8	9.7	7.5	2.9	3.8	11.5	8.4	14.8	9.0	24.4	9.7	4.9	4.0
North-east (267)	189	14.7	13.4	12.0	12.5	13.9	12.9	8.7	8.4	18.9	14.9	18.8	14.4	19.7	13.3	10.2	10.7
Vosges-Jura Mountains (79)	178	16.2	13.3	14.0	13.1	17.3	15.4	9.5	9.0	23.7	17.1	21.5	17.8	24.2	17.9	14.1	10.5
Alps (200)	169	10.3	9.0	13.1	11.7	14.2	11.4	8.1	7.0	17.9	11.5	23.0	15.8	26.9	14.6	12.5	8.2
Massif Central (347)	180	12.6	11.3	13.2	12.1	13.7	11.6	8.4	8.2	20.9	13.6	24.3	17.1	25.0	13.7	11.2	8.8
Pyrenees (69)	169	7.8	6.5	12.6	11.8	8.6	7.7			15.3	9.8	24.6	18.4	18.0	11.7	10.8	7.6
South-west (371)	207	26.2	24.3	29.6	27.8	31.1	27.9	18.4	16.5	34.3	30.4	36.7	33.0	38.1	33.6	29.0	22.2
Mediterranean area (133)	202	25.1	22.4	28.1	27.1	27.8	25.6	20.4	16.9	30.7	27.1	31.6	29.3	32.2	29.9	28.3	20.9
Corsica (37)	191	25.6	23.8	28.7	27.8	27.2	25.7	22.4	19.8	32.6	25.3	35.0	30.5	34.6	28.6	26.9	20.2
	189	15.9	14.0	17.0	16.4	17.6	15.3	11.3	10.4	24.0	17.8	26.7	21.1	28.4	19.3	16.1	12.4

^a The 11 areas correspond to the large-scale French climatic divisions. Numbers in parenthesis correspond to the number of predicted values in each area (grid 15×15 km; 2,460 values for the entire French territory)



◀ **Fig. 4** Predicted variations (in days) at the end of the twenty-first century in spring LU (LU1), autumn LC (LC9) and LGS (LGS19). Each map corresponds to the difference between the average values from the period 1991–2000 and the average predicted values with the climatic scenario A2-HadCM3 for the period 2071–2100. For LU1, negative values correspond to more precocious dates of budburst. For LC9 and LGS19, positive values correspond to a delay in autumn LC and LGS, respectively

beech populations studied. Nevertheless, in the northernmost populations a significant effect on sprouting was attributable also to photoperiodic regime. The interaction chilling \times long day indicates that long days is able to partially substitute winter chilling. Thus, by reducing thermal time requirements, long days may speed up budburst (Sanz-Perez et al. 2009). Other recent studies suggest that photoperiod could also play a crucial role in the regulation of senescence (Estrella and Menzel 2006; Keskitalo et al. 2005; Vitasse et al. 2009b). Our RF models tend to support this hypothesis but the accurate effect of the dual control of autumn temperature and Rg is still poorly understood, and there is no agreement in the literature about the determinants of autumn leaf senescence (Vitasse et al. 2009b).

At the national scale, the most important phenological gradients are observed from southwest (coastal area under oceanic climate) to northeast (lowland and mountain areas with semi-continental climate). They correspond to a delay of foliation, an advance in LC and thus a shortening of the growing season. The growing season lasts between 180 and 190 days in the east and more than 210 days in the west and south-west. This geographical pattern shows a high agreement with the European phenological maps drawn for the period 1961–1998 by Rötzer and Chmielewski (2001). From modeling based on geographical variables only, these authors estimated a difference of the onset of the growing season throughout France of about 15–20 days from the end of March in southwestern coastal areas to the end of April in eastern zones. Similarly to what we observed, these authors also showed relatively less spatial variation of the end of the growing season, most areas having their autumn phase from the end of October to the beginning of November. Finally, the range of the average length of the growing season was quite similar to our values, ranging from less than 180 days to more than 220 days.

Prediction uncertainties on leaf onset obtained by RF modeling (8–9 days) are comparable to estimated values derived from NDVI time-series on the French national scale (Soudani et al. 2008) and with more sophisticated locally fitted models based on daily temperature sums (Chuine 2000; Kramer et al. 2000; Rötzer et al. 2004; Schaber and Badeck 2003; Thompson and Clark 2008). Our values are mostly lower than values obtained from a global prognostic scheme of leaf onset of temperate biomes of about 20 days (Botta et al. 2000). Thus, our large-scale modeling approach

with relatively simple climatic parameters can be used to predict the different phases of leaf development for French forest ecosystems with a satisfying degree of accuracy. For broadleaved trees, the more limited spatial distribution of beech stands in comparison with oak partly explained the lower accuracy of the large-scale models for this species.

Our study period of 10 years is much too short to analyze whether the temperature response of phenological dates varied over the twentieth century. In the near future, the global French phenological database, currently under construction, should make such an analysis possible (<http://www.obs-saisons.fr>). Nevertheless, our results suggest strong differences in the climate responses between both periods and between the hypotheses of warming. A systematic shift in phenological dates towards more precocious foliation and later senescence should be observed only from the second half of the twenty-first century onwards. These shifts should lead to an increase in growing season length of between 20 and more than 40 days in many areas with the more drastic scenario A2-HadCM3, and between 10 and 20 days with the less drastic hypothesis (B2-PCM). Such a difference was expected as GCMs predict greater changes during autumn than during winter or summer. In our study, the simulated rates of budburst hastening for oak and beech were 7.7 days and 6.9 days, respectively, in 100 years (mean for the period 2071–2100) and reach even lower rates if one considers only the next 50 years. Thus, our rates appear lower than the advancing leaf unfolding of between 1.5 and 2.5 days per decade already observed during the last 30–50 years in Europe (Menzel et al. 2006a). The explanation may be linked to the RF modeling, which takes into account the multiple interactions (positive or negative) between the climatic parameters and the nonlinear combinations of the variables. Thus, due to the combined effects of Rg, T and PET in triggering budburst, Rg changes may, for example, reduce the effect that temperature or PET would have on budburst date under a warming scenario (see Table 5). In our study, if we use simple correlations, trends appear steeper. For example, for oak, the simple linear correlation between LU and TMarch is : $LU = -4.7006 \times TMarch + 137.01$ (Lebourgeois et al. 2008). According to this equation, an increase of 3°C leads to an advance of the date of LU of about 14 days. If we consider that this warming will be observed at the end of the century (as predicted by the a2-HadCM3), we can estimate a rate of 1.4 days per decade, which is in agreement with rates already observed.

Even if the long-term consequences remain largely unknown, increased phenological phases should modified annual carbon fluxes by increasing the period during which light can be intercepted for photosynthetic and respiratory activities and thus for growth. A recent study on French deciduous temperate ecosystems by Davi et al. (2006) showed that a 38-day lengthening of the photosynthetically

Table 5 Mean values (for the period 1991–2000) and mean changes (in days) predicted for two periods in phenological dates for oaks and beech. For each future period, the values correspond to the scenario A2-HadCM3. LU1 Leaf unfolding, LC9 leaf coloring, LGS19 length of growing season (in days). All presented changes are significant at the 0.05 level (all pairwise differences, Tukey method, SPLUS 2000)

	Oaks												Beech																							
	LU1						LC9						LGS19						LU1						LC9						LGS19					
	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100	1991–2000	2041–2070	2071–2100									
Mean	96	-3	-8	300	13	20	206	9	17	109	-3	-7	290	5	11	181	2	14																		
North-west (282) ^a	91	-3	-6	299	16	23	209	8	20	109	-4	-11	287	11	21	179	4	29																		
Center (399)	95	-5	-9	298	15	23	205	9	21	107	-2	-2	286	10	15	179	-2	7																		
North (276)	103	-3	-10	298	8	19	195	6	19	109	-4	-5	293	5	9	184	3	3																		
North-east (267)	103	-4	-10	296	9	18	195	9	16	112	-2	-3	290		5	179	-2	-2																		
Vosges-Jura Mountains (79)	106		-6	295	7	12	197	6	7	115	-3	-4	288		2	173																				
Alps (200)	102	-3	-7	297	9	15	202	5	10	117	-5	-8	284	2	8	169	4	13																		
Massif Central (347)	99	-2	-8	298	10	18	205	4	8	111	-3	-5	283	4	11	175	-2	6																		
Pyrenees (69)	103		-5	296	7	12	202		6	116	-5	-10	282		8	170	ns	13																		
South-west (371)	87	-4	-7	306	22	25	217	21	28	106	-2	-14	301	4	12	187	10	39																		
Mediterranean area (133)	84	-2	-4	316	12	14	227	12	17	99	-3	-10	307		4	210	7	20																		
Corsica (37)	91	-6	-8	309	15	18	213	18	22	97	-5	-7	303		6	209	11	16																		

^aThe 11 areas correspond to the large-scale French climatic divisions. Numbers in parenthesis correspond to the number of predicted values in each area (grid 15×15 km; 2,460 values for the entire French territory)

active period should increase NEP by about 150–220 g C m⁻² year⁻¹ from the period 1960–2100 (Davi et al. 2006). As we predict smaller changes, we hypothesize a smaller effect on NEP. However, as proposed by these latter authors, the NEP of oak stands should be more affected globally than beech stands as a result of a greater change in phenological dates for oak. As we observed marked different sub-regional phenological responses, we can also hypothesize significant differences at the national scale; the western stands being globally more affected than the eastern forests (see Fig. 4). During autumn months, recent simulations and observations indicate that northern terrestrial ecosystems may also currently lose carbon dioxide in response to warming, offsetting 90% of the increased carbon dioxide uptake during spring (Piao et al. 2008). In this latter study, the authors suggest that if future autumn warming occurs at a faster rate than in spring, the ability of northern ecosystems to sequester carbon may be diminished earlier than previously suggested. Thus, further investigations using carbon flux models should be undertaken to better highlight these regional effects on forest growth.

A weakness of the global models established here is that they are not physiologically based, and may therefore be too simple. Thus, even if our results forecast significant changes, many studies based on daily modeling with threshold temperature effects suggest that too high temperature during dormancy may modify the expected budburst advancement by modifying the ratio between chilling and forcing temperatures for dormancy release. This effect was illustrated clearly in a recent study on oak and beech (Thompson and Clark 2008). The authors showed that a reduced wintertime chilling duration linked to warming had a greater effect on beech than on oaks. Thus, the flushing date of oak will be advanced by about 37 days for a 4.5°C warming and only by about 16 days for beech. Thus, a logical next step of this work would be to apply this more sophisticated approach, but, unfortunately, the lack of large-scale spatial daily temperature or global solar radiation data makes this modeling impossible at the present time.

In our study, we also hypothesize that climate responses in trees will be stable over time. Although earlier studies have shown a stability of temperature response rates from long-term phenological records (Menzel et al. 2005), it remains possible that climate warming shifts the control of phenology from temperature to soil moisture in most regions where phenology is currently controlled by temperature (Penuelas et al. 2004). Thus, at the end of the century, the length of dry episodes should increase in France by 50%, the number of heat wave days being multiplied by 10 (Déqué 2007). This will lead unavoidably to decreased soil water content and poorer growing conditions for trees. Trees can probably compensate for scattered hot and dry years, but a succession of such climate conditions would noticeably reduce foliar

extension, photosynthetic activity and thus harm forest ecosystems. Other complex interacting effects, also probably species-specific, can greatly complicate the evaluation of the effects of climate change of phenology. Thus, nutrients and CO₂ are known to interact with temperature. For example, on *Picea sitchensis* clones, increasing atmospheric CO₂ delays budburst particularly under low nutrient supply. Increasing temperature counteracts this CO₂ effect, resulting in an advanced budburst, an effect that is nevertheless lower than is the case when only temperature increases (Murray et al. 1994).

We also predict changes in budburst and LC dates in the absence of any response to selection, so any change was due entirely to current phenotypic plasticity. Due to the longevity of trees, the problem is to know if currently growing trees will be adapted to their future environments and if trees have sufficient phenotypic plasticity to accommodate such a change (Kramer 1995; Kramer et al. 2000). Therefore, within-species genetic differences should likely be taken into account whenever possible to make more reliable predictions on the effects of climate change on phenology (Chuine 2000). What can be said is that, as tree species respond differently, the competitive relationships between species, and hence, in the long term, the species composition of forests and possibly the geographical ranges of species will alter. Differences in phenology between species can lead to rather large changes in growth when they grow in mixed forests (Kramer et al. 2000; Rötzer et al. 2004), which might have important implications for the practical management of forests. Typically, the stronger advancement of oak compared to beech predicted in many areas may portend increasing competition pressure for beech trees growing in broadleaved mixed stands.

Finally, although further investigations are required, our study suggests notable modifications of the French forest landscape during the twenty-first century. Climate change will result in a significant change in selection pressure, and phenology is a major aspect of tree functioning that will need to adjust to future climates.

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