

Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break

ISABELLE CHUINE¹, MARC BONHOMME^{2,3}, JEAN-MICHEL LEGAVE⁴, IÑAKI GARCÍA DE CORTÁZAR-ATAURI⁵, GUILLAUME CHARRIER^{2,3}, ANDRÉ LACOINTE^{2,3} and THIERRY AMÉGLIO^{2,3}

¹Centre d'Ecologie Fonctionnelle et Evolutive, UMR CEFE CNRS 5175, 1919 route de Mende, 34293 Montpellier Cedex 05, France, ²INRA, UMR 547 PIAF, F-63100 Clermont-Ferrand, France, ³Clermont Université, Université Blaise Pascal, UMR 547 PIAF, F-63100 Clermont-Ferrand, France, ⁴INRA, UMR 1334 AGAP, F-34398 Montpellier Cedex 5, France, ⁵INRA, US1116-Agroclim, F-84914 Avignon, France

Abstract

The onset of the growing season of trees has been earlier by 2.3 days per decade during the last 40 years in temperate Europe because of global warming. The effect of temperature on plant phenology is, however, not linear because temperature has a dual effect on bud development. On one hand, low temperatures are necessary to break bud endodormancy, and, on the other hand, higher temperatures are necessary to promote bud cell growth afterward. Different process-based models have been developed in the last decades to predict the date of budbreak of woody species. They predict that global warming should delay or compromise endodormancy break at the species equatorward range limits leading to a delay or even impossibility to flower or set new leaves. These models are classically parameterized with flowering or budbreak dates only, with no information on the endodormancy break date because this information is very scarce. Here, we evaluated the efficiency of a set of phenological models to accurately predict the endodormancy break dates of three fruit trees. Our results show that models calibrated solely with budbreak dates usually do not accurately predict the endodormancy break date. Providing endodormancy break date for the model parameterization results in much more accurate prediction of this latter, with, however, a higher error than that on budbreak dates. Most importantly, we show that models not calibrated with endodormancy break dates can generate large discrepancies in forecasted budbreak dates when using climate scenarios as compared to models calibrated with endodormancy break dates. This discrepancy increases with mean annual temperature and is therefore the strongest after 2050 in the southernmost regions. Our results claim for the urgent need of massive measurements of endodormancy break dates in forest and fruit trees to yield more robust projections of phenological changes in a near future.

Keywords: budbreak, climate change impact, endodormancy break, flowering, *Juglans regia*, process-based phenological models, *Prunus armeniaca*, *Prunus persica*

Received 2 February 2016; revised version received 27 April 2016 and accepted 20 May 2016

Introduction

Impacts of current climate change have been observed in a variety of ecosystems and biological processes (Rosenzweig *et al.*, 2008). Because phenological events are strongly responsive to temperature, they have been among the first documented fingerprints of climate change (Menzel & Fabian, 1999), and reported examples are more numerous every year (Menzel *et al.*, 2006). The onset of the growing season of trees has been earlier by 2.3 days per decade during the last 40 years in temperate Europe (Myneni *et al.*, 1997; Parmesan & Yohe, 2003; Root *et al.*, 2003). A recent study has shown that this temporal trend corresponded to a response to

temperature of -3 , 4 days per $^{\circ}\text{C}$ over 1980–2013, which had, however, decreased by 40% the last decade (Fu *et al.*, 2015a). Models project that this trend should continue (Luedeling *et al.*, 2009; Morin *et al.*, 2009; Luedeling & Brown, 2011; Caffarra *et al.*, 2012) according to climate forecasts for the next century (IPCC, 2013); however, some uncertainties remain on its strength, as highlighted by Fu *et al.* (2015a,b).

Increasing phenological changes in temperate woody species will have strong impacts on the distribution of forest trees (Morin *et al.*, 2008; Chuine, 2010; Gritti *et al.*, 2013) and productivity (Loustau *et al.*, 2005; Forrest & Miller-Rushing, 2013), as well as crops cultivation areas (Olesen *et al.*, 2011) and cultivated varieties of fruit trees (Duchêne *et al.*, 2010). Accurate predictions of fruit and forest trees phenology are therefore a

Correspondence: Isabelle Chuine, tel. +33 467 613 279, fax +33 467 613 239, e-mail: isabelle.chuine@cefe.cnrs.fr

prerequisite to understand and foresee the impacts of climate change on forests and agrosystems (Morin *et al.*, 2008; Bennie *et al.*, 2010; Medlyn *et al.*, 2011; Richardson *et al.*, 2013).

The effect of temperature on plants flowering and budbreak in temperate and boreal climates is not linear because temperature has a dual effect on bud development (Arora *et al.*, 2003; Horvath, 2009; Rohde *et al.*, 2011). On one hand, low temperatures are necessary to break bud dormancy, and, on the other hand, higher temperatures are necessary to promote bud growth afterward. Buds go through three main states of development from late summer to spring: paradormancy, endodormancy, ecodormancy (Lang *et al.*, 1987). During paradormancy (midsummer to early autumn), bud cell growth is repressed by active organs (leaves) via inhibitive correlations. During endodormancy (midautumn to midwinter), bud cell growth is inhibited by internal factors which are still not well elucidated but which can be ruled out by low temperatures. The end of this phase classically corresponds to the so-called endodormancy break. During this phase, low temperatures together with decreasing photoperiod also promote cells frost hardening that allows them to withstand further freezing temperatures. Milder winters are therefore also expected to alter trees frost resistance (Charrier & Améglio, 2011; Charrier *et al.*, 2015). During ecodormancy (midwinter to midspring), bud cell growth is inhibited by inadequate external growing conditions (e.g., too low temperatures or too short photoperiod). Different environmental factors thus trigger perennial plants phenology and interact in a complex way all along bud development. Nonlinear response to temperature could also arise due to the effect of other factors such as photoperiod (Körner & Basler, 2010), precipitation and insolation (Fu *et al.*, 2015b), air humidity (Laube *et al.*, 2014a), and nutrient (Jochner *et al.*, 2013).

There have been several models developed in the last decades dedicated to predict the date of budbreak and flowering of several woody species (Erez *et al.*, 1990; Chuine, 2000; Yoon *et al.*, 2003; Luedeling *et al.*, 2009; Pope *et al.*, 2014), but few of them have been used to forecast the evolution of these dates following different climate change scenarios (Morin *et al.*, 2009; Vitasse *et al.*, 2011; Caffarra *et al.*, 2012). These models describe how buds respond to temperature and photoperiod during their development and mainly differ by the development phases they consider (either only ecodormancy, or both endo- and ecodormancy) and the reaction norms of bud development to temperature and photoperiod during each phase (Chuine *et al.*, 2013). Models that consider only the ecodormancy phase make the assumption that endodormancy is always

broken before adequate climatic conditions for cell growth occur (Nendel, 2010). Models which consider both the endodormancy and ecodormancy phases predict the date of endodormancy break, which varies from year to year depending on the climatic conditions during the endodormancy phase. These latter models mostly differ in the way the endodormancy phase and the ecodormancy phase can overlap or not [e.g., growth competence function in Hänninen (1990)]. Experimental studies have shown that the response functions to temperature differed substantially between the endodormancy and the ecodormancy phase, the former ones having their optimum for cooler temperatures (around 5 °C) and the latter ones for warmer temperatures (optimum around 25 °C) with potentially large variations among species (Pouget, 1967; Hauagge & Cummins, 2000). Response functions to temperatures can also vary among populations within the distribution of each species (Vitasse *et al.*, 2013).

So far, one-phase models, describing only the ecodormancy phase, have been able to predict accurately tree budbreak and flowering dates under historical climate (Fu *et al.*, 2012; Basler, 2016). However, because they do not consider what happens prior to ecodormancy, and especially the possible negative effect of winter temperature warming on endodormancy break, it seems unlikely that they can provide accurate predictions in future climate conditions as already pointed out by previous studies (Legave *et al.*, 2008; Garcia De Cortazar-Atauri *et al.*, 2009; Chuine *et al.*, 2010; Vitasse *et al.*, 2011). It has been shown experimentally on fruit trees and on forest trees that a lack of low temperature results either in erratic leaf budbreak pattern, that is only a few buds break mainly at the base of the twigs and at the base of the tree, or in substantially delayed, when not absent, budbreak even in long day length conditions (Erez, 2000; Caffarra *et al.*, 2011b; Laube *et al.*, 2014b). An accurate modeling of the endodormancy break date has thus become a major issue in phenology modeling (Chuine *et al.*, 2010), and no studies so far have addressed it because very few data on endodormancy break are currently available (Jones *et al.*, 2013). Endodormancy break date is indeed very difficult to measure, and available methods (see Material and methods) are destructive, time-consuming, and complicated to implement. Because of the scarcity of endodormancy break observations, previous studies have parameterized phenological models using solely budbreak or flowering dates (Chuine, 2000; Garcia De Cortazar-Atauri *et al.*, 2009; Luedeling *et al.*, 2009; Caffarra *et al.*, 2011a; Legave *et al.*, 2013).

Here, we demonstrate that process-based phenological models may not be parameterized properly without using information on endodormancy break dates, with

a large impact on forecasts of woody species phenology in future climatic conditions. Using series of endodormancy break dates, we evaluated the ability of several process-based phenological models to predict accurately the dates of endodormancy break of three fruit woody species (apricot, peach, and walnut) when parameterized using or not information on endodormancy break dates. We also evaluated the discrepancies in forecasts of budbreak and flowering dates using different climate scenarios when using full vs. defective parameterization of the models.

Materials and methods

Phenological data

Phenological observations realized in the field used in this study are presented in Table 1. Observations were realized at 2-day interval for walnut and peach and twice a week for apricot.

Endodormancy break date characterization

Endodormancy break dates were characterized for the same trees followed in the field for budbreak or flowering.

Peach (*Prunus persica* L.). Endodormancy break dates were obtained using the one-node-cutting test of Rageau (1982), which consists in forcing buds under optimal cellular growth conditions as determined by several previous studies (e.g., Dennis, 2003; Campoy *et al.*, 2011; Vitasse *et al.*, 2014), that is 25 °C and 16-h day length. These temperature and photoperiod conditions are also high enough to be sure that they do not impact endodormancy release. Buds are separated from other parts of the tree to prevent correlative inhibitions (Dennis, 2003). Practically, twigs were sampled from October to March every week on the same trees observed for budbreak date. At each sampling date, twigs were cut in small

fragments of around 7-cm length, leaving only one node at ca. 1 cm below the top end. The top of the cutting was covered by paraffin wax to avoid desiccation and the base of the cutting put into water that was changed once a week (Fig. S1). At each sampling date, around 100 one-node cuttings of axillary buds were made from the central portion of 30 twigs (five twigs per tree) and vegetative buds were followed individually at 3-day interval, recording individual budbreak delay (stage 09 BBCH scale). From individual budbreak delay, a mean time to budbreak is calculated. Note that flowering buds associated with vegetative buds were not removed to avoid damage to the vegetative bud. Previous studies determined that buds of Redhaven peach tree open out after 12 days at 25 °C and 16-h day length when endodormancy is broken (Balandier *et al.*, 1993; Bonhomme *et al.*, 2000). Endodormancy break date was thus obtained by linear interpolation between the two dates giving a postdormancy budbreak delay equal or superior and equal or inferior to 12 days, respectively (Fig. S2).

Walnut (*Juglans regia* L.). Endodormancy break dates were obtained using the same methodology previously described for peach tree. Previous studies determined that buds of Franquette walnut tree open out after 20 days at 25 °C and 16-h day length when endodormancy is broken (Mauget, 1980; Charrier *et al.*, 2011). Endodormancy break date was thus obtained by linear interpolation between the two dates giving a postdormancy budbreak delay immediately equal or inferior to 20 days.

Apricot (*Prunus armeniaca* L.). Endodormancy break dates were estimated using the time-course change of floral primordia fresh weight in orchard conditions. Buds sampling occurred once a week from mid-November of year *n*-1 up to 2–3 weeks after having observed the increase in the buds fresh weight. At each sampling date, 30 short shoots were randomly collected from at least three adult trees. Floral primordia (one per shoot) were extracted under binoculars by removing all bud scales. Mean fresh weights of floral primordia were measured immediately after the sampling. Endodormancy break was estimated using the method of flower primordia fresh

Table 1 Phenological data available for the study. Phenological stage is expressed in the BBCH phenological scale of (Meier, 2001)

Species and variety	Site name	Site coordinates and altitude (m a.s.l)	Period of observation	Number of trees	Number of years	Phenological event	Phenological stage
Apricot – Rouge du Roussillon	Nîmes (INRA)	43°50'N, 4°21'E, 50 m	1997–2010	3	12	Flowering	65
Peach – Redhaven	Clermont-Ferrand (INRA)	45°46'N, 03°08'E, 340 m	1995–2010	5	13	Budbreak	09
Walnut – Franquette	Clermont-Ferrand (INRA)	45°46'N, 03°08'E, 340 m	1976–2009	5	8	Budbreak	09
Walnut – Franquette	Orcival (INRA)	45°40'N, 02°50'E, 1150 m	1978	5	1	Budbreak	09
Walnut – Franquette	Theix (INRA)	45°42'N, 03°1'E, 945 m	1976	5	1	Budbreak	09
Walnut – Franquette	Terrasson (CTIFL)	44°50'N, 00°34'W, 90 m	1976	5	1	Budbreak	09

weight developed by Brown & Kotob (1957) and validated for apricot tree by Legave & Garcia (1982) in the south part of France, where spring is warm enough. Endodormancy break date corresponded to the time when mean fresh weights increase of 15% between two successive sampling dates indicating a transition from low rate of primordia growth, which is characteristic of the endodormancy phase, toward large rate of primordia growth, which is characteristic of the ecodormancy phase.

Temperature data

We used daily temperature data from a meteorological station situated within the orchards for walnut (Meteo France Clermont-Ferrand, 45°78'N, 03°15'E, 331 m a.s.l.; INRA Theix, 45°70'N, 03°02'E, 890 m a.s.l.; INRA Laqueuille, 45°65'N, 02°75'E, 1100 m a.s.l.; INRA Villenave d'Ornon, 44°78'N, -00°58'E, 25 m a.s.l.; SEITA-ITB Bergerac, 44°80'N, 00°51'E, 33 m a.s.l.; CTIFL Bellegarde, 43°75'N, 04°45'E, 52 m a.s.l.), peach (Meteo France Clermont-Ferrand, 45°78'N, 03°15'E, 331 m a.s.l.), and apricot (INRA L'Amarine, 43°50'N, 4°21'E, 52 m a.s.l.).

Process-based phenological models

Endodormancy break dates were modeled using four different one-phase models that differed by the response function of dormancy release to temperature. The one-phase models for endodormancy break were as follows:

$$S_c(t) = \sum_{t_0}^t R_c(t) \quad (1)$$

with S_c , the state of dormancy release at day t , R_c , the rate of dormancy release at day t , which is a function of temperature, t_0 fixed to September 1st.

Endodormancy break occurs when

$$S_c(t_d) = C^* \quad (2)$$

with t_d , the endodormancy break date, and C^* , the chilling requirement for endodormancy break.

The four response functions to temperature ($R_{c,t}$) used were the Chuine function (Chuine, 2000), the smoothed Utah function (Bonhomme *et al.*, 2010), the Erez function (Fishman *et al.*, 1987a,b), and the inverse of the Richardson function (Richardson *et al.*, 1974). These functions are described in the Supporting Information.

The Erez function uses hourly temperatures while the other three functions can either use daily or hourly temperatures. Models using Erez function were thus run with hourly temperatures while models using the smoothed Utah, inverse Richardson, and Chuine function were run both with daily and hourly temperatures. Hourly temperatures were simulated from daily temperatures using the triangular approximation as proposed in Garcia De Cortazar-Atauri *et al.* (2009).

Budbreak and flowering dates were modeled using either a one-phase model or eight different two-phase models (Chuine *et al.*, 2013).

The one-phase model for budbreak and flowering assumes that endodormancy break always occurs before temperature become active on bud growth (Chuine *et al.*, 2013) and predicts that budbreak occurs (t_f) when the state of development (S_f), sum of the daily rates of development (R_f), reaches the critical value F^* :

$$S_f(t) = \sum_{t_d}^t R_f(t) \quad (3)$$

$$S_f(t_f) = F^* \quad (4)$$

with t_d , the starting date of development rate accumulation, which corresponds to the endodormancy break date, and is a parameter of the model. The response function to temperature used was the sigmoid function because it was proven to be the most biologically realistic function (Sarvas, 1974; Hänninen, 1990; Caffarra *et al.*, 2011a).

Two-phase models for budbreak and flowering consider both the endodormancy and the ecodormancy phases. Models used in this study are based either on the sequential model (Hänninen, 1987) or the alternating model (Cannell & Smith, 1983; Chuine, 2000). The sequential model assumes that the phase of bud growth starts only when endodormancy break has occurred, while the alternating model assumes that the ecodormancy phase can start before the end of endodormancy phase, that is before endodormancy break. Sequential models determine the budbreak or flowering date using Eqn (4), with t_d determined by Eqn (2). Alternating models have the same structure except that F^* is no more a parameter but is calculated from the total amount of chilling (S_c) received up to a defined date (t_c), which is a parameter:

$$F^* = we^{-zS_c(t_c)} \quad (5)$$

where w and z are also parameters.

Originally, both types of models have been described with particular response functions for the endodormancy phase and the ecodormancy phase and they have been used with other types of response function since (Chuine, 2000; Chuine *et al.*, 2013). The response functions to temperature used for the endodormancy phase (i.e., $R_{c,t}$) were the Chuine, smoothed Utah, Erez, and inverse Richardson functions. The response function to temperature used for the ecodormancy phase was the sigmoid function. All functions are described in the Supporting Information.

Model parameterization

Models were parameterized using the Phenology Modelling Platform software (<http://www.cefe.cnrs.fr/fr/recherche/ef/forecast/phenology-modelling-platform>) (Chuine *et al.*, 2013). This software proposes fitting different types of phenological models, either selected in a library or defined by the user, using a simulated annealing algorithm following Chuine *et al.* (1998). The optimization algorithm minimizes the mean-squared error, that is the squared difference between the observed dates and the dates predicted by the model (see online PMP documentation, for further details).

Models parameterization proceeded in several steps (Fig. 1). In a first step, the four-one-phase models of endodormancy break dates were fitted to the endodormancy break date series of the three species, using daily temperatures (except model using Erez function) and hourly temperatures. Hourly temperatures were tested to take into account a potential effect of day-time vs. nighttime temperature as Piao *et al.* (2015) recent study suggests. In a second step, the one-phase model of flowering date and budbreak date was parameterized in three different ways: (i) with t_d set to the dates predicted by the best model of endodormancy break date identified in step 2, (ii)

with t_d set to the observed endodormancy break date, and (iii) with t_d fitted as classically done. In a third step, the 82-phase models of flowering or budbreak date were parameterized using solely series of flowering or budbreak dates and associated daily temperatures as classically done.

Model evaluation

Models' performance was characterized by several indices:

the model efficiency (Nash & Sutcliffe, 1970) was defined as follows:

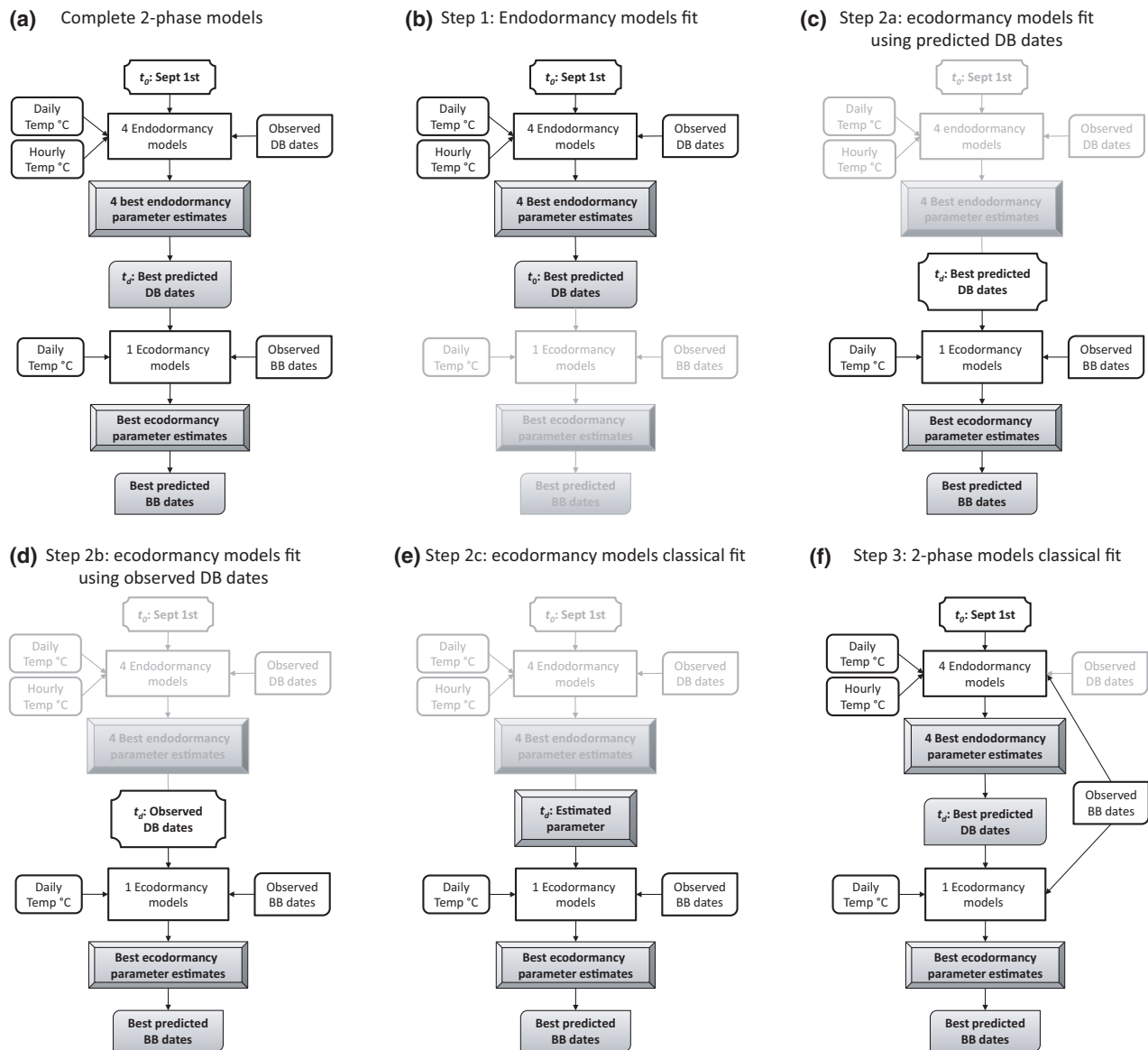


Fig. 1 Graphical representation of the different steps of the models parameterization. (a) Complete 2-phase models; (b) Step 1: Endodormancy models fit; (c) Step 2a: eco-dormancy models fit using predicted dormancy break dates; (d) Step 2b: eco-dormancy models fit using observed dormancy break dates; (e) Step 2c: eco-dormancy models classical fit; (f) Step 3: 2-phase models classical fit. Dashed forms represent outputs of the fitting procedure, either parameter estimates or predicted dates. Open forms represent input variables, models, observed dates. Label like forms represent prescribed dates, plinth like form represent estimated dates, distorted forms represent observed (open) or predicted (dashed) dates. Shaded forms indicate objects unused during the parameterization.

$$EF = 1 - \frac{\sum_{i=1}^n (O_i - P_i)^2}{\sum_{i=1}^n (O_i - \bar{O}_i)^2} \quad (6)$$

the root-mean-squared error (RMSE) was defined as follows:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (O_i - P_i)^2}{n}} \quad (7)$$

the corrected Akaike information criterion (Burham & Anderson, 2002) was defined as follows:

$$AICc = N \times \ln \left(\frac{\sum_{i=1}^n (O_i - P_i)^2}{N} \right) + 2k + \left(\frac{2k(k+1)}{N-K-1} \right) \quad (8)$$

where O_i represents observed dates, P_i represents simulated dates, N is the number of data, and k is the number of parameters.

The EF statistics range between $-\infty$ and +1, yielding +1 for a perfect fit, 0 for a quality of fit equivalent to the null model (overall mean), and a negative value for worse prediction than the null model. The AICc takes into account the number of parameters the model uses. AICc is lowest for the model that explains the highest part of variance in the observed dataset with the fewest parameters.

Due to the limited dataset available, validation was performed using the leave-out-one cross-validation, with

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

as the criterion statistics.

Model projections under climate scenarios

We assessed the divergence among the projections in future climatic conditions of flowering and budbreak dates using (i) the one-phase models with t_d fitted, (ii) the first two best two-phase models fitted with information on the endodormancy break date, and (iii) the first two best two-phase models fitted solely on budbreak and flowering dates. The objective of this comparison is solely to show how much projections can differ when models do not account for the endodormancy phase and when information on the endodormancy break date is taken into account or not in the model parameterization. We insist that the projections must be taken with caution as the data used to parameterize the models for the sake of the models comparison are not sufficient to warrant the robustness of the projections. We used the climatic data generated by the ALADIN-Climat v5 RCM model (CNRM) for the CMIP5 experiment at a 12-km resolution, downscaled at 8-km resolution using quantile–quantile method (<http://www.drias-climat.fr/>). Daily minimum and maximum temperatures of RCP4.5 and RCP8.5 scenarios were extracted on the grid points of three fruit French production areas: Perpignan (42°41'N, 2°53'E, 30 m a.s.l., 15.9°C mean annual temperature MAT), Nîmes (43°50'N, 4°21'E, 118 m a.s.l., 15.2°C MAT), and

Clermont-Ferrand (45°78'N, 03°15'E, 331 m a.s.l., 11.6 °C MAT).

Results

Models performance

First of all, performance of endodormancy models do not show substantial difference when using daily temperature compared to hourly temperature, the latter yielding +0.24 days of RMSE on average over all models (Table 2). Therefore, in the following, we present only the results obtained with daily temperatures.

One-phase models of endodormancy break date show RMSE varying between 2.2 and 3.7, 3.4 and 6.0, and 5.2 and 5.5 for apricot, peach, and walnut, respectively (Table 2). Models yielding the lowest AICc are those using the inverse Richardson function and the Chuine function for the three species. The best fit of the four endodormancy break date models tested were used to fix the parameter values of the endodormancy phase of the two-phase budbreak or flowering date models (sequential and alternating). Among these eight different models, the

Table 2 Performance of the different endodormancy break date models. Chuine, Erez, Richardson and Utah refer to the response function to temperature of the endodormancy phase used in the model. 'Daily' means that the model was run with daily temperatures, and 'Hourly' means that the model was run with hourly temperatures

Species	Model	RMSE	EFF	AICc	N	k
Apricot	Chuine – Daily	2.6	0.854	36.7	12	4
	Chuine – Hourly	2.9	0.825	38.9	12	4
	Erez – Hourly	2.2	0.892	61.4	12	7
	Richardson – Daily	3.1	0.791	36.3	12	3
	Richardson – Hourly	3.1	0.793	36.2	12	3
	Utah – Daily	3.5	0.736	50.1	12	5
Peach	Utah – Hourly	3.7	0.708	51.3	12	5
	Chuine – Daily	3.6	0.902	46.2	13	4
	Chuine – Hourly	4.7	0.829	53.5	13	4
	Erez – Hourly	3.4	0.910	68.5	13	7
	Richardson – Daily	5.7	0.756	53.7	13	3
	Richardson – Hourly	6.0	0.727	55.2	13	3
Walnut	Utah – Daily	5.7	0.755	63.7	13	5
	Utah – Hourly	5.5	0.767	63.1	13	5
	Chuine – Daily	5.4	0.752	51.8	11	4
	Chuine – Hourly	5.5	0.748	52.2	11	4
	Erez – Hourly	5.3	0.762	88.0	11	7
	Richardson – Daily	5.2	0.773	45.7	11	3
	Richardson – Hourly	5.4	0.757	46.5	11	3
	Utah – Daily	5.4	0.755	59.1	11	5
	Utah – Hourly	5.5	0.745	59.5	11	5

RMSE, root-mean-squared error in days; EFF, model efficiency; AICc, corrected Akaike criterion; k , number of fitted parameters; N number of data used to fit the model.

sequential model yields always the lowest AICc, and among the sequential models, that using the inverse Richardson function, the Chuine function or the Utah function yield the lowest and second lowest RMSE (or AICc) (Table 3) and RMSEP in cross-validation (Table S1), with very low differences among models in both cases.

Based on these results, we compared the performance of the best two-phase models and the best one-phase models of budbreak/flowering dates. Two-phase models were sequential models using the inverse Richardson function or the Chuine function for the endodormancy phase and the sigmoid function for the ecodormancy phase. These models were either fitted with no information on endodormancy break date as classically done or fitted using this information, that is parameters of the endodormancy phase were fixed to the parameter estimates obtained for the one-phase (endodormancy) model of endodormancy break date fitted with observed endodormancy break dates. One-phase models use the sigmoid function with t_d either fitted or fixed to the observed endodormancy break date dates. Lowest AICc was obtained for either the one-phase model using observed endodormancy break date (peach) or the one-phase model using endodormancy

break date simulated by the endodormancy models (Table 4). The two-phase models fitted solely on budbreak/flowering dates show the highest AICc due to their higher number of parameters but generate the lowest RMSE (Table 4). However, in cross-validation, they generate the highest RMSEP except that using Chuine function for apricot (Table S1). Finally, two-phase models fitted with information on endodormancy break date provided either slightly higher or slightly lower RMSE (Table 4) and RMSEP (Table S1) than one-phase model using observed t_d , due to error compensation between the endodormancy break date and the budburst/flowering dates.

We compared endodormancy break dates predicted by the two versions of the 2-phase models, that is fitted with and without information on endodormancy break date. Endodormancy break date is best predicted by the two-phase models using information on this variable as we might expect (Fig. 2). RMSEs are two to fourteen times higher with models fitted solely on budbreak/flowering dates, and their error on the mean dormancy date varies from 6 to 78 days (Fig. 2).

Temperature response curves obtained for the ecodormancy phase with the best two-phase models

Table 3 Performance of the two-phase models with parameter values of the first phase (endodormancy) fixed to the parameter estimates of the best one-phase model of endodormancy break date. Chuine, Erez, Richardson and Utah refer to the response function to temperature of the endodormancy phase used in the model. The response function of the second phase is the sigmoid function for all models. Legend as in Table 2

Species	Model		RMSE	EFF	AICc	N	k
Apricot	Sequential	Chuine	2.8	0.887	33.8	12	3
		Erez	3.2	0.854	36.9	12	3
		Richardson	2.5	0.909	31.2	12	3
		Utah	2.7	0.897	32.7	12	3
	Alternating	Chuine	2.8	0.887	44.8	12	5
		Erez	3.6	0.812	50.9	12	5
		Richardson	1.9	0.950	35.1	12	5
		Utah	1.8	0.952	34.6	12	5
Peach	Sequential	Chuine	7.9	0.567	62.4	13	3
		Erez	8.0	0.559	62.7	13	3
		Richardson	8.3	0.519	63.8	13	3
		Utah	7.7	0.585	61.9	13	3
	Alternating	Chuine	7.0	0.661	69.2	13	5
		Erez	7.1	0.646	69.7	13	5
		Richardson	7.1	0.646	69.7	13	5
		Utah	7.0	0.661	69.2	13	5
Walnut	Sequential	Chuine	2.9	0.952	32.9	11	3
		Erez	2.9	0.953	32.9	11	3
		Richardson	3.0	0.950	33.3	11	3
		Utah	3.0	0.947	33.9	11	3
	Alternating	Chuine	9.2	0.525	70.7	11	5
		Erez	5.6	0.822	59.9	11	5
		Richardson	11.7	0.224	76.1	11	5
		Utah	9.7	0.467	72.0	11	5

vary substantially among species (Fig. 3). These response curves show that temperatures below 5 to -5°C no longer sustain growth as it is classically considered (e.g., Bailey and Harrington, 2006; Cannell, 1989; Owens *et al.*, 1977; Rea & Eccel, 2006; Scalabrelli & Couvillon, 1986; Ruml *et al.*, 2011).

Nevertheless, they also show very different midresponse and optimal temperature. Temperature response curves of the endodormancy phase are much more realistic (compatible with the biological knowledge) when fitted with endodormancy break dates (Fig. 3b, d) than not (Fig. 3c, e), that is curve with a narrower optimal temperature range in the case of the Chuine function (Fig. 3d, e), optimal temperature below 10°C for the inverse Richardson function (Fig. 3b, c; Table S3).

Projections of flowering and budbreak across the 21st century

First of all, we compared the endodormancy break and flowering/budbreak dates predicted by the models over the historical period using the simulated climatic data produced by the ALADIN-Climat RCM with the observed endodormancy break and flowering/budbreak dates over the same period (Fig. S3). All models reproduce accurately the mean (0–6 days difference, the precision on the observed dates being 2 days) and the standard deviation (1–6 days difference) of the flowering/budbreak dates. However, only the two-phase models fitted with endodormancy break dates reproduced accurately the mean and, to a lesser extent, the variance of endodormancy break dates. The reason why all models are able to predict correctly budbreak dates over the historical period while diverging in their predictions of the endodormancy break date is because despite global warming, temperature conditions during autumn and winter have remained favorable to endodormancy break so that the endodormancy break date does not affect the budbreak date (there is still a lag between the endodormancy break date and the starting date of cells growth triggered by higher temperatures).

Second, we compared the projections of budbreak or flowering dates over the period 1950–2100 obtained with the two-phase models using the inverse Richardson function and the Chuine function fitted with and without information on the endodormancy break date and obtained with the one-phase model. Projections of endodormancy break and flowering/budbreak dates under RCP4.5 and RCP8.5 climate scenarios differ among species and locations, but most importantly, they differ greatly among models (Figs 4, 5, S4 and S5). Projections differ the most between one-phase model

(green curve) and two-phase models (red and blue curves), although much less in Clermont-Ferrand, the coldest site. This is because temperature conditions are still favorable to endodormancy breakup to the end of the century in this region (see, however, the discrepancy for peach and walnut, the last 30 years especially under RCP8.5) so that endodormancy break does not affect budbreak date almost all along the 21st century, and one-phase models provide similar projections of budbreak or flowering dates as two-phase models. Differences between models increase with MAT and are the strongest at the warmest site (Perpignan) and at the end of the 21st century. Projections of models fitted with endodormancy break dates (red curves) show similar results for the three species: in all locations, they show trends toward later dates of the endodormancy break, which increase with temperature (the trend is weaker in Clermont-Ferrand, the coldest location, than in Perpignan, the warmest location).

They also show similar changes over time of the flowering/budbreak date among the three species: (i) no trend followed by strong trend toward later dates in the warmest region (Perpignan), especially under RCP8.5 (ii) weak trend toward earlier dates followed by strong to weak trend toward later dates in the intermediate region (Nîmes), and (iii) strong trend toward earlier dates (except for peach) followed by no trend in the coldest region (Clermont-Ferrand).

The two-phase model using the Chuine function shows endodormancy break failure due to insufficient chilling accumulation during endodormancy during the 21st century contrary to that using the Richardson inverse function. This is because the active temperature range obtained with the Richardson inverse function is wider than that obtained with the Chuine function. While the two-phase model using the Chuine function shows endodormancy break failure on a vast part of the 21st century in the warmest sites when fitted without information on the endodormancy break date, it shows endodormancy break failure only at the end of the 21st century when fitted with information on the endodormancy break date.

Differences between climate scenarios RCP4.5 (Figs 4 and 5) and RCP8.5 (Figs S4 and S5) lie in the strength of the trends, which are weaker in RCP4.5, and also in the frequency of endodormancy break failure observed when using the Chuine model (Figs 5 and S5).

Discussion

Recently, there has been a growing concern about the effect of declining chilling on temperate woody species due to climate warming and the serious lack of mechanistic understanding of the environmental,

Table 4 Performance of the two-phase models using the Richardson inverse and Chuine functions for the endodormancy phase and of the one-phase models to predict bud-break/flowering dates. Models are all fitted on flowering/budbreak dates. One-phase models use the sigmoid function and differ by the starting date of the ecodormancy phase, that is the endodormancy break date, t_d , which is either the observed date (t_d observed), the date simulated by the endodormancy models using the Richardson inverse or the Chuine function (t_d simulated), or a constant date corresponding to a fitted parameter (t_d fitted). Legend as in Table 2

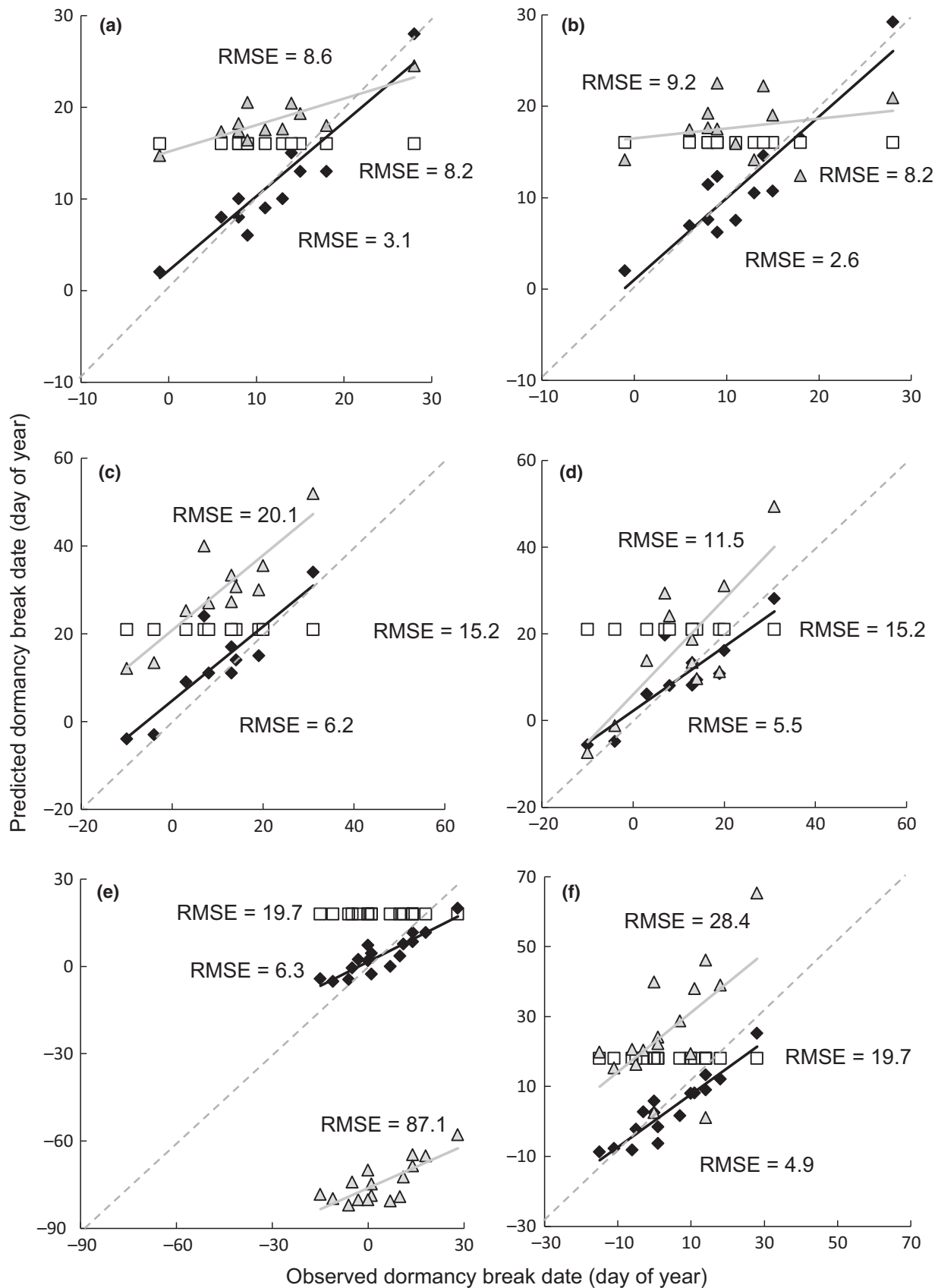
Species	Model	RMSE	EFF	AICc	<i>N</i>	<i>k</i>
Apricot	1-phase t_d observed	2.7	0.896	32.8	12	3
	1-phase t_d simulated with Richardson	2.5	0.909	31.2	12	3
	1-phase t_d simulated with Chuine	2.8	0.887	33.8	12	3
	1-phase t_d fitted	2.7	0.898	37.3	12	4
	2-phase Richardson	1.8	0.956	42.2	12	6
	2-phase Chuine	1.7	0.961	54.1	12	7
	2-phase Chuine fitted	4.3	0.870	74.5	13	7
Peach	1-phase t_d observed	7.7	0.589	61.8	13	3
	1-phase t_d simulated with Richardson	8.3	0.519	63.8	13	3
	1-phase t_d simulated with Chuine	7.9	0.567	62.4	13	3
	1-phase t_d fitted	9.7	0.349	72.1	13	4
	2-phase Richardson	7.2	0.639	77.4	13	6
	2-phase Chuine	4.3	0.870	74.5	13	7
	2-phase Chuine fitted	4.3	0.870	74.5	13	7
Walnut	1-phase t_d observed	3.3	0.937	35.9	11	3
	1-phase t_d simulated with Richardson	3.0	0.950	33.3	11	3
	1-phase t_d simulated with Chuine	2.9	0.952	32.9	11	3
	1-phase t_d fitted	3.1	0.944	39.8	11	4
	2-phase Richardson	2.6	0.962	53.9	11	6
	2-phase Chuine	1.8	0.981	64.5	11	7
	2-phase Chuine fitted	1.8	0.981	64.5	11	7

physiological, molecular, and genetic basis of dormancy (Chuine, 2010; Atkinson *et al.*, 2013; Campoy *et al.*, 2013; Darbyshire *et al.*, 2013; Pope *et al.*, 2013). Recently, Atkinson *et al.* (2013) deplored this situation because we know for long the importance of climate on perennial plants' development and yield. Many studies aimed at estimating chilling requirement for bud endodormancy break using statistical techniques and phenological models (Luedeling *et al.*, 2009; Caffarra *et al.*, 2011a; Chmielewski *et al.*, 2011; Gao *et al.*, 2012;

Jones *et al.*, 2013). However, none of them were able to evaluate the efficiency of the models to predict accurately endodormancy break dates using observed endodormancy break dates so far (Jones *et al.*, 2013).

First of all, it is interesting to note that the best model performance was obtained for apricot which is the species for which endodormancy break dates were obtained by the flower primordial fresh weight and not *a posteriori* determination with forcing of one-node cuttings in growth chambers. This later method can be difficult and less precise (Dennis, 2003). In particular, one needs to know that budbreak delay measured with this method can vary substantially when dormancy is maximal (October and November in temperature climate in the Northern Hemisphere) and that it varies between terminal bud and axillary buds and among axillary buds. This is the reason why several buds per twigs, several twigs per tree, and several trees per species must be sampled to account for this variability. However, this variability is the lowest around the endodormancy break date (<1 day in the species studied here) and does not therefore hamper the estimation the endodormancy break date. Nevertheless, the sudden increment in flower primordial weight corresponds to a water spell in the buds that can occur only if soil and air temperatures are high enough to trigger it. Thus, we would like to highlight that estimation of endodormancy break date (end of endodormancy) with flower primordial weighting right after sampling in orchard (as in this study) will be accurate in climate with mild winters in which temperatures around the end of endodormancy are already sufficient to promote a water spell in the bud and promote cell growth. In such climate, the end of endodormancy corresponds to the start of cell growth and flower primordial weight increment is a good proxy to estimate the end of endodormancy. In colder climates where temperatures around the end of endodormancy are still too low to promote a water spell in the buds, there is a time lag between the end of endodormancy and the time when water spell and cell growth happen. In such climates, flower primordial weight needs to be measured after a short period of forcing in a growth chamber (7 days at 20 °C, 16-h day length). This suggests that new techniques to estimate bud endodormancy break dates should be developed to provide rapidly reliable data for a large

Fig. 2 Comparison of the dates of endodormancy break predicted by the different models vs. observed dates for apricot (a, b), peach (c, d), and walnut (e, f). Predicted dates are obtained using the best two-phase model found for each species fitted either without information on the endodormancy break date (triangles), or with information on the endodormancy break dates (diamonds), and the best one-phase model found for each species (endodormancy break date is fitted and constant every year, squares). Two-phase models use either the inverse Richardson response function (a, c, e) or the Chuine function (b, d, f) for the endodormancy phase. Dashed gray lines represent the 1 : 1 line. Black lines represent the linear regressions on the predictions of the best two-phase model fitted with information on the endodormancy break dates (diamonds).



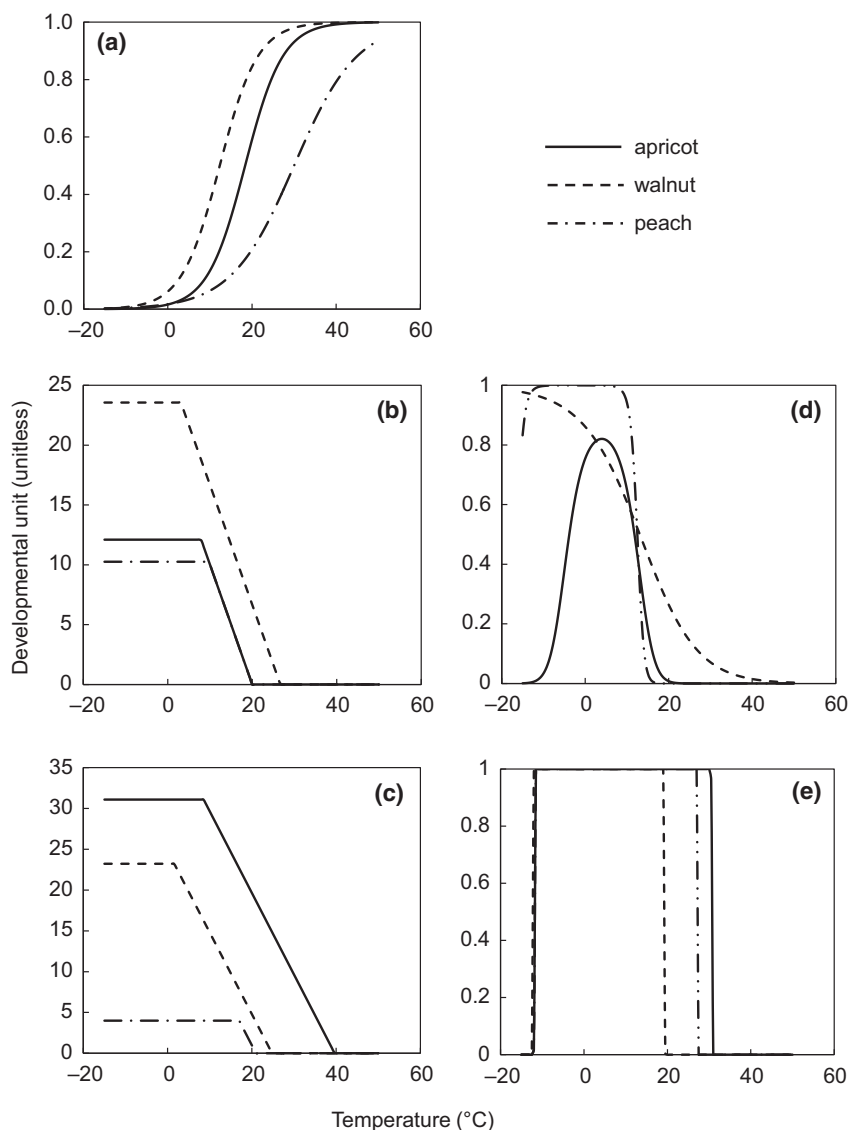


Fig. 3 Best fitted response functions to temperature for the ecodormancy phase (a) and the endodormancy phase (b, c, d, e) using the Richardson inverse function (b, c) and the Chuine function (d, e) when fitted with (b, d) and without (c, e) information on the endodormancy break date. Note the response function for the ecodormancy phase is always the sigmoid function.

number of woody species to parameterize properly phenological models. These techniques would especially be of major importance also for investigating the genetic adaptability of plant species to climate warming using high-throughput plant phenotyping. These techniques, able to estimate the level of dormancy of buds either during dormancy induction or during dormancy release, should ideally be nondestructive, quick, and cheap. This opens an entire field of research and development.

Our results show that two-phase models fitted solely on budbreak or flowering dates, as it is commonly done, are subjected to large errors in the predicted endodormancy break date that can translate into large

errors of budbreak and flowering date predictions in future climate conditions. However, it is interesting to note that in historical conditions and up to 2050 in warmer climate, models fitted without information on endodormancy break date can predict budburst and flowering dates as well as models fitted without this information. Thus, models fitted so far without information on endodormancy break might thus be used confidently to make projections in cold and temperate climates and up to 2050 in warmer climates. However, for long-term projections, our results argue for a better understanding of the endogenous and exogenous determinism of dormancy and endodormancy break and for extensive measurements and also new

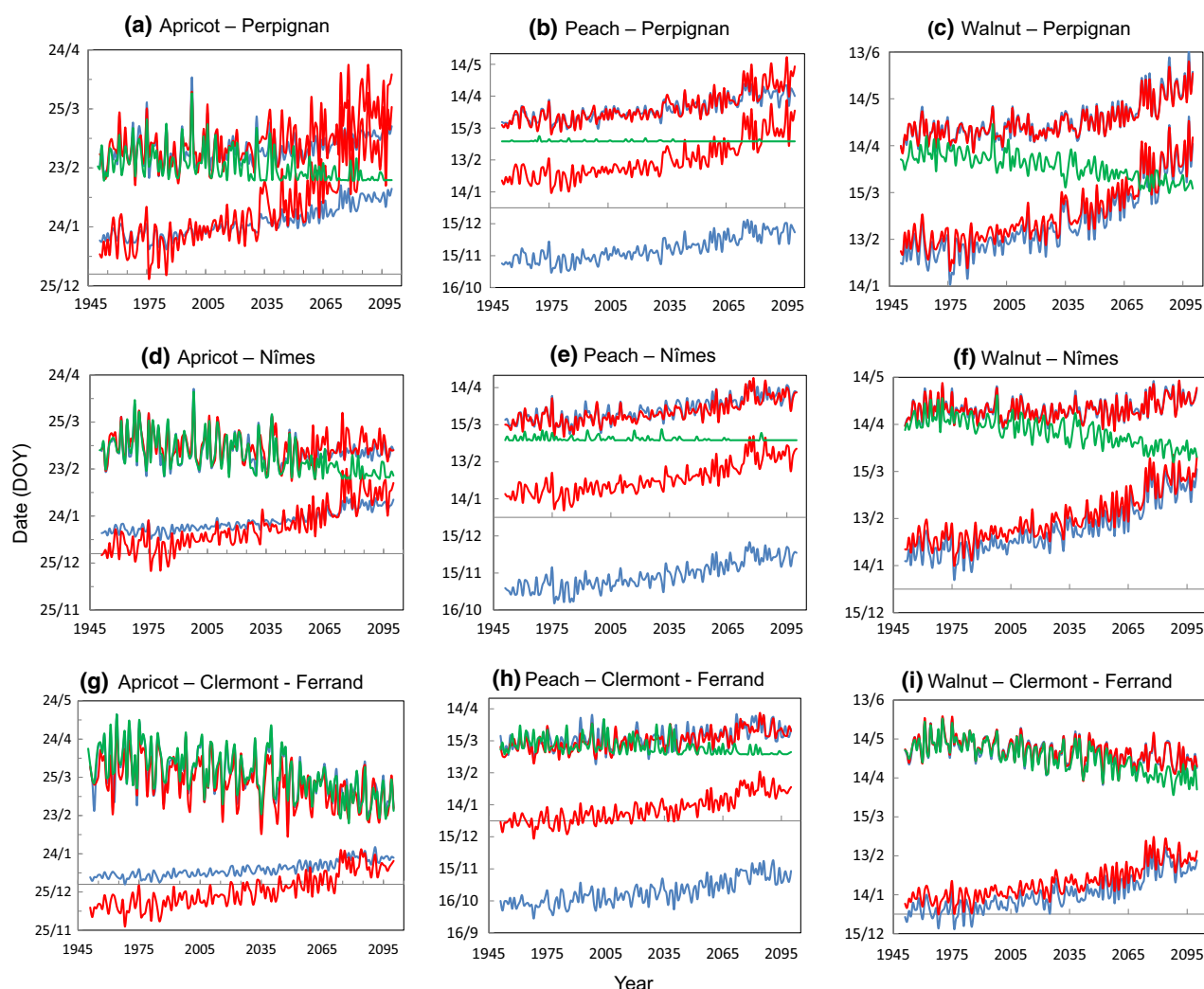


Fig. 4 Projected endodormancy break date (earlier dates) and flowering or budbreak date (later dates) by the best models found under climate scenario RCP8.5 for apricot (a, d, g), peach (b, e, h), walnut (c, f, i) in three locations in France (from South to North): Perpignan ($4^{\circ} 41' \text{ N}$, $2^{\circ} 53' \text{ E}$) (a, b, c); Nîmes ($43^{\circ}50' \text{ N}$, $4^{\circ}21' \text{ E}$) (d, e, f); Clermont-Ferrand ($45^{\circ} 46' \text{ N}$, $03^{\circ} 08' \text{ E}$) (g, h, i). Red curves indicate projections of the two-phase model using the inverse Richardson function for the endodormancy phase fitted with information on the endodormancy break date. Blue curves indicate projections of the same model fitted without information on the endodormancy break date. The green curves indicate flowering or budbreak dates projected by the best one-phase model (where the starting date was also fitted). These last models make the assumption that endodormancy break is always broken before temperature for cell growth become active.

techniques of measurement of endodormancy break. We would like also to point out the necessity to have a critical judgment on the model parameter estimates obtained by statistical inference. Statistical inference can generate several statistically equally similar parameter sets among which only one is actually biologically realistic. Some level of expertise on the species phenology and ecophysiology is therefore usually required to select the most realistic parameter set among the most probable ones, especially when it has to be used to produce projections.

Our results also show dramatic discrepancies between projections of two-phase models and one-phase models as previously shown by Vitasse *et al.* (2011) for forest trees, the latter providing usually the most deviant projections from two-phase models fitted using DB dates. However, it seems that one-phase models can be used to predict accurately budbreak/flowering dates in temperate climate up to 2050. When used with climate warming scenarios, one-phase models thus need to be used with caution if climatic conditions become too warm compared to the training climatic

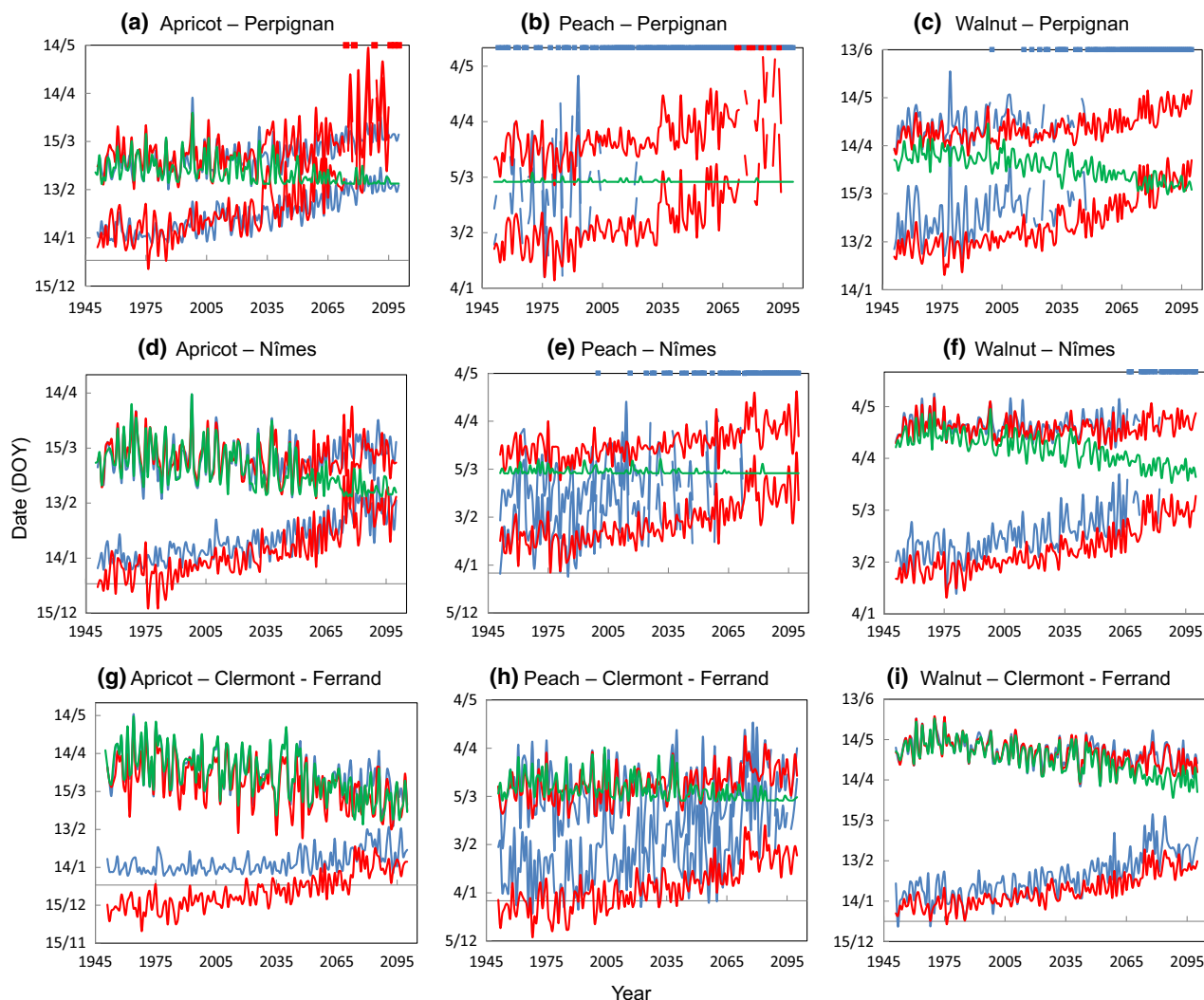


Fig. 5 Projected endodormancy break date (earlier dates) and flowering or budbreak date (later dates) under climate scenario RCP8.5, using the Chuine function for the endodormancy phase in the two-phase sequential model, for apricot (a, d, g), peach (b, e, h), walnut (c, f, i) in three locations in France (from South to North): Perpignan ($4^{\circ} 41' \text{ N}$, $2^{\circ} 53' \text{ E}$) (a, b, c); Nîmes ($43^{\circ} 50' \text{ N}$, $4^{\circ} 21' \text{ E}$) (d, e, f); Clermont-Ferrand ($45^{\circ} 46' \text{ N}$, $03^{\circ} 08' \text{ E}$) (g, h, i). Legend is as in Fig. 4. Blue or red squares indicate years during which temperature conditions do not allow the break of dormancy and thereby flowering and budbreak.

dataset. In such case, it seems preferable to use two-phase models fitted without endodormancy break dates than one-phase models.

Keeping in mind that our projections must be taken with caution as the data used to parameterize the models for the sake of the models comparison are not sufficient to warrant the robustness of the projections, it is nevertheless interesting to compare the tendencies projected by the different models. For the three species, two-phase models fitted using information on the endodormancy break dates show a trend toward earlier flowering and budbreak dates from 1945 to 2000 (warmest sites)/2050 (coldest sites), followed by a trend toward later dates. The strength and the length of these

trends strongly depend on latitude: the first trend toward earlier date is stronger and longer at the coldest location, while the second trend toward later dates is stronger and longer at the warmest locations. Trends toward latter budbreak or flowering dates after 2050 are due to trends toward latter dates of endodormancy break due to insufficient low temperature during autumn and winter. It is particularly noticeable that trends in budbreak and flowering dates predicted by different phenological models can vary substantially between locations distant of a few hundreds of kilometers. These results highlight the importance of the non-linearity of the effect of temperature on bud development and the limits of extrapolating current

linear tendencies in the past (Meier *et al.*, 2007; Maurer *et al.*, 2009) and the future (Chuine *et al.*, 2010) and of comparing tendencies across species and locations (Wolkovich *et al.*, 2012).

Trends in budbreak dates for the 21st century simulated here by the models for fruit trees would probably be similar for forest trees whose phenology does not respond to photoperiod, as they show the same environmental determinism of the occurrence budbreak dates. However, contrary to fruit trees, forest trees are subjected to natural selection, which is expected to be strong on phenological traits especially in the context of climate change. Indeed, heritability of phenological traits is large as well as the genetic variance within the populations, and climate change exerts a strong selective pressure on these traits because they directly affect strongly survival as well as reproductive success (Chuine, 2010). Thus, long-term phenological projections for forest trees should, whenever possible, take into account the genetic evolution of trees phenological response to the environmental cues induced by climate change (Kramer *et al.*, 2008; Oddou-Muratorio & Davi, 2014).

Our results show that models predicting accurately endodormancy break date project endodormancy break failure at the warmest sites after 2050 (Fig. 5). Premises of endodormancy break failure, that is lack of chilling delaying endodormancy break and subsequently budburst date, are actually already visible in long-term phenological series of apple tree in Nîmes (Legave *et al.*, 2015). Endodormancy break failure has been shown to be responsible for local population extinction at species southern range margins in previous modeling studies (Morin *et al.*, 2007). According to observations on temperate fruit trees cultivated in subtropical regions, such as Brazil and Morocco, and experimental results, it is expected that chilling deprivation generate at first a lengthening of the flowering period at the scale of a tree crown, followed by growth disorders, leaves and flowers malformation, and very few budbreak (Erez, 2000; Jackson, 2000; Petri & Leite, 2004; Zguigal *et al.*, 2006; Caffarra *et al.*, 2011b; Laube *et al.*, 2014b). In subtropical/mild regions, dormancy is chemically broken using Dormex®-Hydrogen Cyanamid, which is highly toxic (Sunil *et al.*, 2011). According to climate projections (IPCC, 2013), climatic conditions currently preventing a natural break of bud dormancy in subtropical regions like Morocco are expected to occur in Spain, Italy, Greece, and southern France in a few decades. This is a very short time to adapt the fruit crop sector by selecting for varieties with lower chilling requirement, for example. To meet this challenge, massive data on species and varieties chilling requirement for endodormancy break and efficient phenological models are urgently needed.

Some studies have shown an effect of photoperiod on budbreak timing in tree species such as beech, birch, balsam fir, and Norway spruce (Heide, 1993; Caffarra *et al.*, 2011b; Basler & Koerner, 2012; Laube *et al.*, 2014b). More precisely, some of these studies have shown that long photoperiod during the endodormancy phase could compensate insufficient chilling received during the endodormancy phase. Whether long photoperiod will be able to break dormancy when chilling requirement will not be met anymore at the end of the 21st century remains an open question.

In conclusion, our results demonstrate that two-phase models might not be able to predict accurately endodormancy break date if no information on this variable is used to fit them and thus that they do not necessarily provide accurate projections of budbreak or flowering in future climatic conditions. Yet, they nevertheless provide more accurate projections than 1-phase models can do in regions where autumn and winter temperatures will compromise endodormancy break. We demonstrate it here for fruit trees, but the same conclusions would also apply to other temperate tree species, and in particular forest trees. Considering the major impact of phenology on trees productivity and reproductive success, it seems urgent to collect widely data on the endodormancy break date of major forest and fruit tree species, but also to carry out new experiments and invent new techniques to measure dormancy to better understand its exogenous and endogenous determinism. This is the prerequisite to inventing and testing new phenological models that will be able to provide more robust projections for the future.

Acknowledgements

The authors thank Amelia Caffarra for a thorough reading of a previous version of the manuscript and three anonymous reviewers for their constructive comments which greatly improved the manuscript.

References

- Arora R, Rowland L, Tanino K (2003) Induction and release of bud dormancy in woody perennials: a science comes of age. *Hort Science*, **38**, 911–921.
- Atkinson C, Brennan R, Jones H (2013) Declining chilling and its impact on temperate perennial crops. *Environmental and Experimental Botany*, **91**, 48–62.
- Bailey J, Harrington C (2006) Temperature regulation of bud-burst phenology within and among years in a young Douglas-fir (*Pseudotsuga menziesii*) plantation in western Washington, USA. *Tree Physiology*, **26**, 421–430.
- Balandier P, Bonhomme M, Rageau R, Capitan F, Parisot E (1993) Leaf bud endodormancy release in peach trees: evaluation of temperature models in temperate and tropical climates. *Agricultural and Forest Meteorology*, **67**, 95–113.
- Basler D (2016) Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central Europe. *Agricultural and Forest Meteorology*, **217**, 10–21.
- Basler D, Koerner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, **165**, 73–81.

- Bennie J, Kubin E, Wiltshire A, Huntley B, Baxter R (2010) Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. *Global Change Biology*, **16**, 1503–1514.
- Bonhomme M, Rageau R, Gendraud M (2000) ATP, ADP and NTP contents in vegetative and floral peach buds during winter: are they useful for characterizing the type of dormancy. In: *Dormancy in Plants* (eds Viemont J-D, Crabbé J), pp. 245–257. CAB International, New-York, NY.
- Bonhomme M, Rageau R, Lacombe A (2010) Optimization of endodormancy release models using series of endodormancy release data collected in France. *Acta Horticulturae*, **872**, 51–60.
- Brown D, Kotob F (1957) Growth of flower buds of apricot, peach and pear during the rest period. *Proceedings of the American Society of Horticultural Science*, **69**, 158–164.
- Burham K, Anderson D (2002) Information theory and loglikelihood models: a basis for model selection and inference. In: *Model Selection and Multimodel Inference: A practical Information-Theoretic Approach* (eds Burnham KP, Anderson DR), pp. 32–74. Springer, Berlin.
- Caffarra A, Donnelly A, Chuine I (2011a) Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research*, **46**, 159–170.
- Caffarra A, Donnelly A, Chuine I, Jones M (2011b) Modelling the timing of *Betula pubescens* budburst. I. Temperature and photoperiod: a conceptual model. *Climate Research*, **46**, 147–157.
- Caffarra A, Rinaldi M, Eccel E, Rossi V, Pertot I (2012) Modelling the impact of climate change on the interaction between grapevine and its pests and pathogens: European grapevine moth and powdery mildew. *Agriculture Ecosystems & Environment*, **148**, 89–101.
- Campoy J, Ruiz D, Cook N, Alderman L, Egea J (2011) Clinal variation of dormancy progression in apricot. *South African Journal of Botany*, **77**, 618–630.
- Campoy J, Ruiz D, Nortes M, Egea J (2013) Temperature efficiency for dormancy release in apricot varies when applied at different amounts of chill accumulation. *Plant Biology*, **15**, 28–35.
- Cannell MGR (1989) Chilling, thermal time and the dates of flowering of trees. In: *Manipulation of Fruiting* (ed. Wright CJ), pp. 99–113. Butterworth & Co, London.
- Cannell MGR, Smith R (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of Applied Ecology*, **20**, 951–963.
- Charrier G, Améglio T (2011) The timing of leaf fall affects cold acclimation by interactions with air temperature through water and carbohydrate contents. *Environmental and Experimental Botany*, **72**, 351–357.
- Charrier G, Bonhomme M, Lacombe A, Améglio T (2011) Are budburst dates, dormancy and cold acclimation in walnut trees (L.) under mainly genotypic or environmental control? *International Journal of Biometeorology*, **55**, 763–774.
- Charrier G, Ngao J, Saudreau M, Améglio T (2015) Effects of environmental factors and management practices on microclimate, winter physiology, and frost resistance in trees. *Frontiers in Plant Science*, **6**, 1–18.
- Chmielewski F-M, Bluemel K, Henniges Y, Blanke M, Weber R, Zoth M (2011) Phenological models for the beginning of apple blossom in Germany. *Meteorologische Zeitschrift*, **20**, 487–496.
- Chuine I (2000) A unified model for the budburst of trees. *Journal of Theoretical Biology*, **207**, 337–347.
- Chuine I (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **365**, 3149–3160.
- Chuine I, Cour P, Rousseau D (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant, Cell & Environment*, **21**, 455–466.
- Chuine I, Morin X, Bugmann H (2010) Warming, photoperiods, and tree phenology. *Science*, **329**, 277–278.
- Chuine I, Garcia de Cortazar Atauri I, Kramer K, Hänninen H (2013) Plant development models. In: *Phenology: An Integrative Environmental Science* (ed. Schwarz Md), pp. 275–293. Springer, Dordrecht, The Netherlands.
- Darbyshire R, Webb L, Goodwin I, Barlow E (2013) Impact of future warming on winter chilling in Australia. *International Journal of Biometeorology*, **57**, 355–366.
- Dennis E (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience*, **38**, 347–350.
- Duchêne E, Huard F, Dumas V, Schneider C, Merdinoglu D (2010) The challenge of adapting grapevine varieties to climate change. *Climate Research*, **41**, 193–204.
- Erez A (2000) Bud dormancy: phenomenon, problems and solutions in the tropics and subtropics. In: *Temperate Fruit Crops in Warm Climates* (ed. Erez A), pp. 17–48. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Erez A, Fishman S, Linsley-Noakes G, Allan P (1990) The dynamic model for rest completion in peach buds. *Acta Horticulturae*, **276**, 165–174.
- Fishman S, Erez A, Couvillon G (1987a) The temperature dependence of endodormancy breaking in plants: computer simulation of processes studied under controlled temperatures. *Journal of Theoretical Biology*, **126**, 309–321.
- Fishman S, Erez A, Couvillon G (1987b) The temperature dependence of endodormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. *Journal of Theoretical Biology*, **124**, 473–483.
- Forrest J, Miller-Rushing A (2013) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3101–3112.
- Fu YH, Campioli M, Demaree G, Deckmyn A, Hamdi R, Janssens IA, Deckmyn G (2012) Bayesian calibration of the Unified budburst model in six temperate tree species. *International Journal of Biometeorology*, **56**, 153–164.
- Fu YH, Zhao H, Piao S *et al.* (2015a) Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, **256**, 104–107.
- Fu YH, Piao S, Vitasse Y *et al.* (2015b) Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: effects of chilling, precipitation and insolation. *Global Change Biology*, **21**, 2687–2697.
- Gao Z, Zhuang W, Wang L, Shao J, Luo X, Cai B, Zhang Z (2012) Evaluation of chilling and heat requirements in Japanese apricot with three models. *HortScience*, **47**, 1826–1831.
- Garcia De Cortazar-Atauri I, Brisson N, Gaudillere J (2009) Performance of several models for predicting budburst date of grapevine (*Vitis vinifera* L.). *International Journal of Biometeorology*, **53**, 317–326.
- Gritti E, Gaucherel C, Crespo-Perez M-V, Chuine I (2013) How can model comparison help improving species distribution models? *PLoS ONE* doi:10.1371/journal.pone.0068823.
- Hänninen H (1987) Effects of temperature on dormancy release in woody plants: implications of prevailing models. *Silva Fennica*, **21**, 279–299.
- Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*, **213**, 1–47.
- Hauagge R, Cummins J (2000) Pome fruit genetic pool for production in warm climates. In: *Temperate Fruit Crops in Warm Climates* (ed. Erez A), pp. 267–303. Springer Netherlands, Amsterdam.
- Heide O (1993) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum*, **89**, 187–191.
- Horvath D (2009) Common mechanisms regulate flowering and dormancy. *Plant Science*, **177**, 523–531.
- IPCC (2013) *Working Group I Contribution to the IPCC Fifth Assessment Report. Climate Change 2013: the Physical Science Basis*. Cambridge University Press, Cambridge, UK.
- Jackson JE (2000) Apple production in low latitudes. In: *Temperate Fruit Crops in Warm Climates* (ed. Erez A), pp. 305–342. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Jochner S, Hofer J, Beck I, Gottlein A, Ankerst DP, Traidl-Hoffmann C, Menzel A (2013) Nutrient status: a missing factor in phenological and pollen research? *Journal of Experimental Botany*, **64**, 2081–2092.
- Jones H, Hillis R, Gordon S, Brennan R (2013) An approach to the determination of winter chill requirements for different *Ribes* cultivars. *Plant Biology*, **15**, 18–27.
- Körner C, Basler D (2010) Phenology under global warming. *Science*, **327**, 1461–1462.
- Kramer K, Buiteveld J, Forstreuter M *et al.* (2008) Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. *Ecological Modelling*, **216**, 333–353.
- Lang G, Early J, Martin G, Darnell R (1987) Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. *HortScience*, **22**, 371–377.
- Laube J, Sparks TH, Estrella N, Menzel A (2014a) Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist*, **202**, 350–355.
- Laube J, Sparks T, Estrella N, Höfler J, Ankerst D, Menzel A (2014b) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, **20**, 170–182.
- Legave J, Garcia G (1982) Chilling requirements for blooming in apricot tree determined either by a statistical method or by an experimental method and valued according to an exponential conception of temperature action. *Acta Horticulturae*, **121**, 103–108.
- Legave J, Farrera I, Alméras T, Calleja M (2008) Selecting models of apple flowering time and understanding how global warming has had an impact on this trait. *Journal of Horticultural Science and Biotechnology*, **83**, 76–84.
- Legave J, Blanke M, Christen D, Giovannini D, Mathieu V, Oger R (2013) A comprehensive overview of the spatial and temporal variability of apple bud dormancy

- release and blooming phenology in Western Europe. *International Journal of Biometeorology*, **57**, 317–331.
- Legave J-M, Guédon Y, Malagi G, El Yaacoubi A, Bonhomme M (2015) Differentiated responses of apple tree floral phenology to global warming in contrasting climatic regions. *Frontiers in Plant Science*, **6**, 1054. doi:10.3389/fpls.2015.01054.
- Loustau D, Bosc A, Colin A *et al.* (2005) Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiology*, **25**, 813–823.
- Luedeling E, Brown P (2011) A global analysis of the comparability of winter chill models for fruit and nut trees. *International Journal of Biometeorology*, **55**, 411–421.
- Luedeling E, Zhang M, McGranahan G, Leslie C (2009) Validation of winter chill models using historic records of walnut phenology. *Agricultural and Forest Meteorology*, **149**, 1854–1864.
- Mauget J-C (1980) Dormance et précocité de débourrement des bourgeons chez quelques cultivars de Noyer (*Juglans regia* L.). *Comptes Rendus de l'Académie des Sciences. Série D*, **290**, 135–138.
- Maurer C, Koch E, Hammer C, Hammer T, Pokorny E (2009) BACCHUS temperature reconstruction for the period 16th to 18th centuries from Viennese and Klosterneuburg grape harvest dates. *Geophysical Research*, **114**, D22106. doi:10.1029/2009J D011730.
- Medlyn B, Duursma R, Zeppel M (2011) Forest productivity under climate change: a checklist for evaluating model studies. *Wiley Interdisciplinary Reviews: Climate Change*, **2**, 332–355.
- Meier U (2001) Growth stages of mono- and dicotyledonous plants. In: *Federal Biological Research Centre for Agriculture and Forestry Monograph* (ed. Meier U), pp. 158. Wissenschafts-Verlag, Berlin.
- Meier N, Rutishauser T, Pfister C, Wanner H, Luterbacher J (2007) Grape harvest dates as a proxy for Swiss April to August temperature reconstructions back to AD 1480. *Geophysical Research Letters*, **34**, L20705. doi:10.1029/2007GL031381.
- Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.
- Menzel A, Sparks Th, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.
- Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, **88**, 2280–2291.
- Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, **96**, 784–794.
- Morin X, Lechowicz MJ, Augspurger C, Keef JO, Viner D, Chuine I (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, **15**, 961–975.
- Myneni R, Keeling C, Tucker C, Asrar G, Nemani R (1997) Increasing plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Nash J, Sutcliffe J (1970) River flow forecasting through conceptual models part I – A discussion of principles. *Journal of Hydrology*, **10**, 282–290.
- Nendel C (2010) Grapevine bud break prediction for cool winter climates. *International Journal of Biometeorology*, **54**, 231–241.
- Oddou-Muratorio S, Davi H (2014) Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. *Evolutionary Applications*, **7**, 453–467.
- Olesen J, Trnka M, Kersebaum K *et al.* (2011) Impacts and adaptation of European crop production systems to climate change. *European Journal of Agronomy*, **34**, 96–112.
- Owens J, Molder M, Langer H (1977) Bud development in *Picea glauca*. I Annual growth cycle of vegetative buds and shoot elongation as they relate to date and temperature sums. *Canadian Journal of Botany*, **55**, 2728–2745.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Petri J, Leite G (2004) Consequences of insufficient winter chilling on apple tree bud-break. *Acta Horticulturae*, **662**, 53–60.
- Piao S, Tan J, Chen A *et al.* (2015) Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature Communications*, **6**, 6911.
- Pope K, Dose V, Da Silva D, Brown P, Leslie C, Dejong T (2013) Detecting nonlinear response of spring phenology to climate change by Bayesian analysis. *Global Change Biology*, **19**, 1518–1525.
- Pope K, Da Silva D, Brown P, Dejong T (2014) A biologically based approach to modeling spring phenology in temperate deciduous trees. *Agricultural and Forest Meteorology*, **198–199**, 15–23.
- Pouget R (1967) Méthode d'appréciation de l'évolution physiologique des bourgeons pendant la phase de pré-débourrement. Application à l'étude comparée du débournement de la vigne. *Vitis*, **6**, 294–302.
- Rageau R (1982) Etude expérimentale des lois d'action de la température sur la croissance des bourgeons floraux du pecher (*Prunus persica* L. Batsch) pendant la post-dormance. *Comptes Rendus de l'Académie d'Agriculture de France*, **68**, 709–718.
- Rea R, Eccel E (2006) Phenological models for blooming of apple in a mountainous region. *International Journal of Biometeorology*, **51**, 1–16.
- Richardson E, Seeley S, Walker D (1974) A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience*, **9**, 331–332.
- Richardson A, Keenan T, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, **169**, 156–173.
- Rohde A, Bastien C, Boerjan W (2011) Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiology*, **31**, 472–482.
- Root T, Price J, Hall K, Schneider S, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Rosenzweig C, Karoly D, Vicarelli M *et al.* (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–U320.
- Ruml M, Milatovic D, Vulic T, Vukovic A (2011) Predicting apricot phenology using meteorological data. *International Journal of Biometeorology*, **55**, 723–732.
- Sarvas R (1974) Investigations on the annual cycle of development of forest trees. Autumn dormancy and winter dormancy. *Communications Instituti Forestalis Fenniae*, **84**, 1–101.
- Scalabrelli G, Couvillon G (1986) The effect of temperature and bud type on rest completion and the GDH degree C requirement for budbreak in redhaven peach. *Journal of American Society of Horticultural Science*, **111**, 537–540.
- Sunil H, Uchil S, Shiva K, Punith K (2011) DORMEX®-hydrogen cyanamide poisoning. *Journal of Emergencies, Trauma and Shock*, **4**, 435–437.
- Vitasse Y, Francois C, Delpierre N, Dufrene E, Kremer A, Chuine I, Delzon S (2011) Assessing the effects of climate change on the phenology of European temperate trees. *Agricultural and Forest Meteorology*, **151**, 969–980.
- Vitasse Y, Hoch G, Randin CF, Lenz A, Kollas C, Scheepens JF, Körner C (2013) Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia*, **171**, 663–678.
- Vitasse Y, Basler D, Way D (2014) Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? *Tree Physiology*, **34**, 174–183.
- Wolkovich EM, Cook BI, Allen JM, *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature*, **485**, 494–497.
- Yoon Y, Pope J, Wolfe J (2003) Freezing stresses and hydration of isolated cell walls. *Cryobiology*, **46**, 271–276.
- Zguigal A, Chahbar A, Loudiyi W, Crabbé J (2006) Caractéristiques de la dormance des bourgeons du pommier dans les régions à hivers doux. *Biotechnology Agronomy Society and Environment*, **10**, 131–137.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. A description of the response functions to temperature used in this study.

Figure S1. One-node-cutting test of peach buds.

Figure S2. Typical mean time to budbreak (MTB) curve obtained from one-node-cutting test.

Figure S3. Comparison of the endodormancy break dates predicted by the model using the Richardson inverse function with the observed dates of endodormancy break and flowering/budbreak dates on the historical period of apricot in Nîmes (1988–2010), peach in Clermont-Ferrand (1975–2010) and walnut in Clermont-Ferrand (1976–2009).

Figure S4. Projected endodormancy break date (earlier date) and flowering/budbreak date (later date) by the best models found for each species under climate **scenario RCP4.5** in three locations in France (from North to South): Clermont-Ferrand (45°46'N, 03°08'E), Nîmes (43°50'N, 4°21'E), Perpignan (4°41'N, 2°53'E).

Figure S5. Projected endodormancy break date (earlier date) and flowering/budbreak date (later date) by the best models found for each species under climate **scenario RCP4.5** in three locations in France (from North to South): Clermont-Ferrand (45°46'N, 03°08'E), Nîmes (43°50'N, 4°21'E), Perpignan (4°41'N, 2°53'E).

Table S1. Performance of the two-phase and one-phase models of budbreak/flowering dates in cross-validation.

Table S2. Parameter estimates of the models used to project the budbreak or flowering date of walnut, peach and apricot using A2 and A1B climate scenarios.