

A comprehensive overview of the spatial and temporal variability of apple bud dormancy release and blooming phenology in Western Europe

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Abstract In the current context of global warming, an analysis is required of spatially-extensive and long-term blooming data in fruit trees to make up for insufficient information on regional-scale blooming changes and determinisms that are key to the phenological adaptation of these species. We therefore analysed blooming dates over long periods at climate-contrasted sites in Western Europe, focusing mainly on the Golden Delicious apple that is grown worldwide. On average, blooming advances were more pronounced in northern continental (10 days) than in western oceanic (6–7 days) regions, while the shortest advance

was found on the Mediterranean coastline. Temporal trends toward blooming phase shortenings were also observed in continental regions. These regional differences in temporal variability across Western Europe resulted in a decrease in spatial variability, i.e. shorter time intervals between blooming dates in contrasted regions (8–10-day decrease for full bloom between Mediterranean and continental regions). Fitted sequential models were used to reproduce phenological changes. Marked trends toward shorter simulated durations of forcing period (bud growth from dormancy release to blooming) and high positive correlations between these durations and observed blooming dates support the notion that blooming advances and shortenings are mainly due to faster satisfaction of the heating requirement. However, trends toward later dormancy releases were also noted in oceanic and Mediterranean regions. This could tend toward blooming delays and explain the shorter advances in these regions despite similar or greater warming. The regional differences in simulated chilling and forcing periods were consistent with the regional differences in temperature increases.

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Introduction

Studies undertaken to assess the impact of climate change on plant phenology have reported advances in leafing, flowering and fruiting dates. Higher temperatures are the main factor driving these trends. However, the phenological responses observed in these studies were not the same for different species and sites. In fact, they varied considerably

between species and were found to be more intense in annuals than perennials (Fitter and Fitter 2002). Also, large-scale studies showed that the phenological response of a given species to climate change may vary greatly from one region to another (Menzel and Sparks 2006). This variable phenological response to global warming obviously has worrying ecological and agronomic consequences. More comprehensive studies are therefore required to examine the phenological trends of many species at a given site or those of a single species at different sites (Primack et al. 2009).

Few studies have focused on the flowering responses of temperate fruit trees in the Northern hemisphere. Those that have been undertaken detected a trend toward earlier blooming in both deciduous species (Chmielewski et al. 2004; Miller-Rushing et al. 2007; Guédon and Legave 2008; Nordli et al. 2008; Fujisawa and Kobayashi 2010) and evergreen species (Garcia-Mozo et al. 2009). Similar mean advances in blooming dates have been reported for species of the *Cerasus* genus in Japan (Miller-Rushing et al. 2007) and for pear and apple trees in France and Switzerland (Guédon and Legave 2008). Blooming advances in apple and pear trees have also been reported in the Southern hemisphere, but to a lesser extent (Grab and Craparo 2011). A characteristic feature of blooming advances in Europe is the sudden change that occurred at the end of the 1980s, precisely when temperatures increased (Chmielewski et al. 2004; Guédon and Legave 2008). Changes in the timing of bud and fruit phenology may have consequences on yield regularity and quality (Lopez and Dejong 2007) due to strong links between phenology and fruit production. Particularly, it has been suggested that trends toward earlier bud blooming may increase frost damage in temperate fruit trees (Cannell and Smith 1986). Another future phenological response in perennials might be a divergence in flowering times at any given site between species that currently overlap (Miller-Rushing et al. 2007). Changes in blooming time synchronization in different varieties of a given fruit tree species could arise from interactions between regional changes in temperature and varietal differences in temperature requirements (Spiegel-Roy and Alston 1979). This can affect the cross-pollination phase that determines the annual yield of many fruit tree varieties. Diverging flowering times may also modify insect pollinator resources or impact interspecific gene flow (Menzel et al. 2006; Miller-Rushing et al. 2007). In addition, the planting of fruit tree species is long-term and exacerbates the negative consequences of phenological changes because fruit tree growers cannot rapidly change varieties.

As the few studies previously devoted to fruit tree phenology were restricted to only one or a few sites, and were often based on short-term observations, the objective of our study was to improve the characterization and understanding of blooming changes on a large spatial and temporal scale. Historical analysis is a

necessary first step when considering the impacts of climate change (Darbyshire et al. 2011) and future genetic adaptation (Celton et al. 2011). We considered Western Europe to constitute an ideal starting point for our research due to its great regional diversity of temperature conditions and the marked rise in temperature it has experienced (Chmielewski and Rötzer 2001). We considered the apple tree to be an appropriate species because of its worldwide cultivation. In addition to characterizing the variability observed, we used a modelling approach to reproduce this variability in order to highlight underlying determinisms in terms of temperature requirements for blooming.

Materials and methods

Temperature conditions and blooming data

Study data were drawn from climatic and phenological databases at seven institutes located in contrasting geographic areas (Table 1; Fig. 1). Daily air temperature data were collected from weather stations located no more than a few kilometres from the orchards where blooming dates were recorded. Data were available from autumn 1965 at all sites (except in Trento, no data before 1980) and even earlier in Bonn (1958) and Angers (1962). Monthly temperatures from November to April (i.e. the months mainly involved in blooming) were clearly contrasted between the studied sites, as shown in Fig. 2a. The northern sites of Bonn and Gembloux were characterised by continental climates under an oceanic influence (annual means of 9.7 and 9.5 °C, respectively) and showed relatively low temperatures in March and April. The eastern sites of Conthey and Trento were the highest in altitude and were characterised by continental climates with marked temperature contrasts (annual means of 10.2 °C and 10.9 °C, respectively) and low temperatures in December and January. The western site of Angers was characterised by an oceanic climate (annual mean of 11.9 °C) and showed relatively mild and only slightly contrasting temperatures from November to April. The southeastern site of Forlì showed a Mediterranean climate under a continental influence (annual mean of 14.6 °C) expressed by relatively high temperatures in March and April and contrasting temperatures from November to April. The southern site of Nîmes was characterised by a Mediterranean climate (annual mean of 14.5 °C) and relatively high temperatures from November to April. Mean monthly temperatures from November to April had clearly increased from the late 1980s across all sites as shown by plots over the 1966–2009 period (Fig. 2b). These increases were more marked in January and March than in November and December. They also contrasted greatly at the different sites. In

Table 1 Flowering data collected in climate-contrasting sites for Golden Delicious apple trees

Blooming dates series			Origin of data			
Stage ^a	Observation period	Number of annual data	Site (town)	Latitude/longitude	Altitude (m)	Institute (country)
F1	1958–2011	54	Bonn	50° 37' N / 6° 59' E	179	Bonn University (Germany)
F2	1958–2011	54	Klein-Altendorf ^b			
F1	1984–2011	28	Gembloux	50° 34' N / 4° 41' E	138	CRA-W (Belgium)
F1	1963–2011	49	Angers	47° 28' N / 0° 31' W	38	INRA (France)
E2	1970–2011	42	Conthey	46° 13' N / 7° 22' E	504	Agroscope C-W (Switzerland)
F2	1970–2011	42				
F1	1983–2011	29	Trento	46° 4' N / 11° 7' E	419	CRA-FRF (Italy)
F2	1983–2011	29	Borgo Valsugana ^b			
F1	1970–2011	42	Forlì	44° 13' N / 12° 1' E	34	CRA-FRF (Italy)
F2	1970–2011	42				
F1	1975–2011	37	Nîmes	43° 50' N / 4° 21' E	52	Ctifl (France)
F2	1980–2011	32	Balandran ^b			

^a E2, F1 and F2 stages are respectively stages 59, 61 and 65 in phenological code BBCH (Meier, 1997)

^b Name of the site where records were done; in other cases, they were done near the town cited

particular, great contrasts in monthly increase were noted for the continental climates of Bonn and Gembloux, while the Mediterranean climate of Forlì showed low contrasts.

At all sites experienced observers assessed blooming dates to within 2–3 days on adult trees growing in long-term orchards. The collection of historical data focused on Golden Delicious as this apple cultivar has been ubiquitously grown in Europe for many decades. The data mainly consisted of dates for the F1 stage (early bloom; about 10 % of flowers opened) and F2 stage (full bloom; around 50 % of flowers opened). These correspond to stages 61 and 65 in the international BBCH code. F1 stage dates were

collected at all sites except Conthey, and F2 stage dates at all sites except Gembloux and Angers (Table 1). Dates for the E2 stage (50 % of flowers at balloon stage, stage 59) were also collected in Conthey. In all, 12 chronological series with no missing data were collected for Golden Delicious. The longest was recorded in Bonn (54 years) and the shortest in Gembloux (28 years). Blooming dates available for some other cultivars were also collected in order to compare their variability with that of Golden Delicious. F1 dates were collected in Nîmes for Granny Smith (35 years, 1976–2010) which flowered earlier than Golden Delicious, and F2 dates were collected in Conthey for three cultivars:

Fig. 1 The seven sites where data were collected in Europe



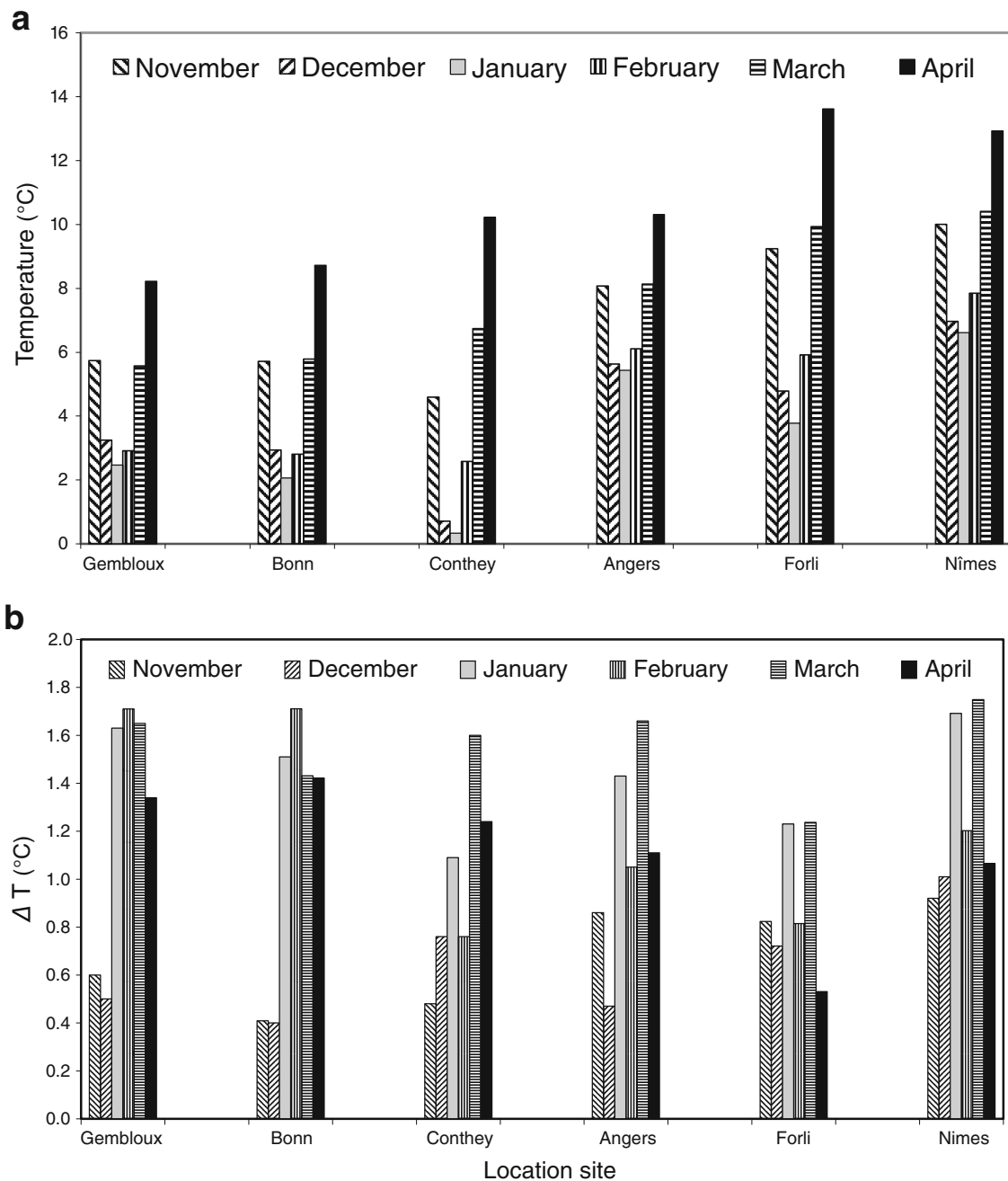


Fig. 2 Characterization of air temperature conditions from November to April at six sites. **a** Monthly mean temperature calculated over 44 years (1966–2009). **b** Mean increase in monthly temperatures in the 1988–2009 period compared to the 1966–1987 period

Idared (41 years, 1970–2010) and Maigold (34 years, 1970–2003) with earlier blooming than Golden Delicious, and Gala (29 years, 1976–2003) that has a similar blooming time. The detection of temporal trends in the chronological series took account of both the different starting years in our data (Table 1) and obviously non-linear changes when curves of annual data were plotted (not shown). The usual analysis of blooming date series by linear regression was therefore discarded because the significance of trends can vary with different starting years in linear regression (Nordli et al. 2008). This statistical method

was also inappropriate when encountering non-linearity (Guédon and Legave 2008). We chose to perform a descriptive analysis of these chronological series using moving averages of observed annual blooming dates, called MAOB, expressed in calendar days. This statistical tool more clearly highlighted spatial and temporal variability than by using current curves of annual observed dates. We tested different time spans when calculating these moving averages and chose five-year averages to highlight main temporal trends and marked short-term changes in these trends.

Blooming date modelling

Our modelling study was based on the usual assumption made for temperate fruit trees that chilling and heating temperatures have successive and independent effects on the endodormancy release and post-dormancy growth that leads to bud break and blooming (Bidabé 1967; Richardson et al. 1974; Fuchigami and Nee 1987; Aono and Moriya 2003; De Melo-Abreu et al. 2004; Rea and Eccel 2006; Farajzadeh et al. 2010). In accordance with this, so-called sequential modelling (Chuine 2000) assumes that a chilling sub-model combined with a heating sub-model can model dormancy release and bud phenology. We tested seven chilling functions and four heating functions covering the entire diversity of the mathematical laws used to model bud phenology. These functions are presented in Table 2 with information on their associated parameters. Differences in the relevance of these functions for modelling are presented in Legave et al. (2008). As heating models used alone have been found to be accurate predictors of bud phenology in some studies (Bidabé 1967; Aono and Moriya 2003), we also studied the simple assumption commonly called thermal time modelling (Chuine 2000). In practice, and using the same data, we compared the thermal time and sequential assumptions by testing each heating sub-model alone then combined with each chilling sub-model. The date of chilling period onset in our chilling sub-models was a time parameter in the year ($n-1$) preceding the blooming year (n), and the sum of daily chilling units (depending on the function) from this date until chilling completion was a quantity parameter corresponding to the chilling requirement. These two parameters were used to generate different simulated annual dates of dormancy release (output data in calendar days) for different annual temperatures during the chilling period. Five-year moving averages for these dates (MADR values) were calculated. No annual date of dormancy release

was simulated in thermal time modelling since the date of forcing period onset was a time parameter (fixed date for each heating model). Similarly, the sum of daily heating units from the simulated date of dormancy release (or fixed date in thermal time) to a given blooming date was another quantity parameter and corresponded to the heating requirement to reach the blooming date. This additional parameter was used to generate different simulated annual dates of blooming stage (output data in calendar days) for different annual temperatures during the chilling and forcing periods. Five-year moving averages for simulated blooming dates (MASB values) were calculated. All parameter values in each tested model were optimized (no prior choice) by maximizing the coefficient of determination (R^2) between observed and simulated dates. The algorithm used for R^2 maximisation was based on the Metropolis algorithm (simulated annealing) described in Chuine et al. (1998). As our study needed to analyse a huge quantity of numerical data, we used ‘Pollenoscope’ modelling software (Legave et al. 2008) including the improvements in the algorithm that shorten calculation times for automatic parameter optimisations. The study focused on modelling Golden Delicious F1 date, as a great deal of contrasting data was available (239 dates; Table 1). Parameter optimization was fitted from a representative sub-group of these data: 96 F1 dates made up of 24 dates recorded in four contrasting climates (Bonn, Angers, Forlì and Nîmes) from 1976 to 1999. This common period was selected because it also included contrasting yearly temperature conditions during the chilling and forcing periods, as previously shown at the French sites (Guédon and Legave 2008). Thus, these 96 F1 dates provided substantial variability in space and time: March 21 (in Nîmes) and May 16 (in Bonn) as the earliest and latest F1 dates, respectively, and April 19 as the mean. Such variability was ideally suited to developing models with broad spatial and temporal adaptation. In practice, Excel files of phenological

Table 2 Mathematical functions and associated parameters tested to model apple F1 date

Sub-model	Temperature (T) function	Function parameter
Chilling sub-model		
Binary chilling	$F_c(T) = 1$ if $T < T_c$, $F_c(T) = 0$ if $T > T_c$	T_c : threshold T^a
Linear chilling	$F_c(T) = T_c - T$ if $T < T_c$, $F_c(T) = 0$ if $T > T_c$	T_c : threshold T^a
Exponential chilling	$F_c(T) = \exp(-T/T_c)$	T_c : specific T^a
Sigmoidal chilling	$F_c(T) = 1 / (1 + \exp[(T - T_c) / S_c])$	T_c : specific T^a ; S_c^b
Triangular chilling	$F_c(T) = 1 - (T - T_c / I_c)$ if $T_c - I_c < T < T_c + I_c$, $F_c(T) = 0$ if not	T_c : optimal T^a ; I_c^c
Parabolic chilling	$F_c(T) = 1 - [(T - T_c) / I_c]^2$ if $T_c - I_c < T < T_c + I_c$, $F_c(T) = 0$ if not	T_c : optimal T^a ; I_c^c
Normal chilling	$F_c(T) = \exp[-(T - T_c)^2 / I_c]$	T_c : optimal T^a ; I_c^c
Heating sub-model		
Binary heating	$F_h(T) = 1$ if $T > T_h$, $F_h(T) = 0$ if $T < T_h$	T_h : threshold T^a
Linear heating	$F_h(T) = T - T_h$ if $T > T_h$, $F_h(T) = 0$ if $T < T_h$	T_h : threshold T^a
Exponential heating	$F_h(T) = \exp(T/T_h)$	T_h : specific T^a
Sigmoidal heating	$F_h(T) = 1 / (1 + \exp[(T_h - T) / S_h])$	T_h : specific T^a ; S_h^b

^a Temperature parameter (°C) depending on the function

^b Slope parameter (number) of the sigmoidal function around T_c or T_h (temperature for which 50 % of maximum daily effect is reached)

^c Temperature interval (°C) defining the range of efficient temperatures around T_c

dates and corresponding temperatures were prepared separately and automatically inputted in the software. The annual temperature files contained daily temperatures from October 1 of year $n-1$ to May 31 of blooming year n . Each temperature file included three sub-files composed of minimum, mean (calculated) and maximum temperatures, each of which was input separately into the software to test which one maximized the R^2 value. Finally, significant models (Fisher's test on the R^2 value at $P < 0.05$) were sought that explained high percentages ($R^2 \geq 0.90$) of the variability selected for model fitting (96 F1 dates) and showed low root mean square errors for simulated dates ($\text{RMSE} \leq 4$ days). An additional criterion for model selection was the consistency of model parameters with knowledge on the biological process of flowering, in particular on chilling period onset (Bidabé 1967) and chilling temperature range (Naor et al. 2003). A final step used to confirm model selection was the validation ($\text{RMSE} \leq 6$ days) of selected models at the four sites used for model fitting (internal validation: only for years not used in model fitting) and at the two sites (Gembloux and Trento) not considered in model fitting (external validation).

Results

Spatial and temporal variability of observed blooming time

MAOB values (Fig. 3) showed latitude to have a great impact on spatial variability since mean blooming dates were clearly earlier at the southern sites of Nîmes and Forlì than at the northern sites of Gembloux and Bonn. For example, the Golden Delicious trees flowered earlier in Nîmes than in Bonn by an average of 22 days over the 1980–2011 period for both

F1 and F2 dates. Intermediate dates were recorded in Angers, Conthey and Trento located at intermediate latitudes. In particular, the Golden Delicious trees flowered only a little earlier in Angers than in Trento (only a 2 day difference in average F1 date over the 1983–2011 period), despite great differences in longitude and altitude between the two sites (Table 1). With regard to the temporal variability, MAOB values showed sudden changes toward earlier dates at the end of the 1980s, and this for all sites and phenological stages (Fig. 3) and for all cultivars (not shown). From this period until 2011, relatively early dates were recorded mainly at continental and oceanic sites, as shown for F1 date of Golden Delicious in Gembloux, Bonn and Angers (Fig. 3a), and for F2 dates in Bonn and Conthey (Fig. 3b). This was also observed in Conthey for E2 dates of Golden Delicious and for F2 dates of other cultivars (Idared, Maygold and Gala) (not shown). This change in the late 1980s was particularly evident for the longest series of F2 dates in Bonn where all five-year average dates were later than May 5 until the 1986–90 period, and all following dates were consistently earlier than May 5 (Fig. 3b). By contrast, MAOB values showed major variations at Mediterranean sites before and after the shift toward earlier dates at the end of the 1980s. In particular, relatively late dates were recorded from the late 1990s for both F1 and F2 dates of Golden Delicious in Forlì and Nîmes, as shown in Fig. 3. A similar trend was observed for the F1 date of Granny Smith in Nîmes (not shown). Thus, no clear trend toward earlier blooming was noted at the Mediterranean sites over the observation periods. A particular trend was observed in Trento where the change period toward earlier dates was longer than at other sites, and was characterized by relatively late dates from 1998 to 2006 (as at the Mediterranean sites). In addition, these regional differences in blooming advance were evaluated by examining differences in mean blooming date between broader successive

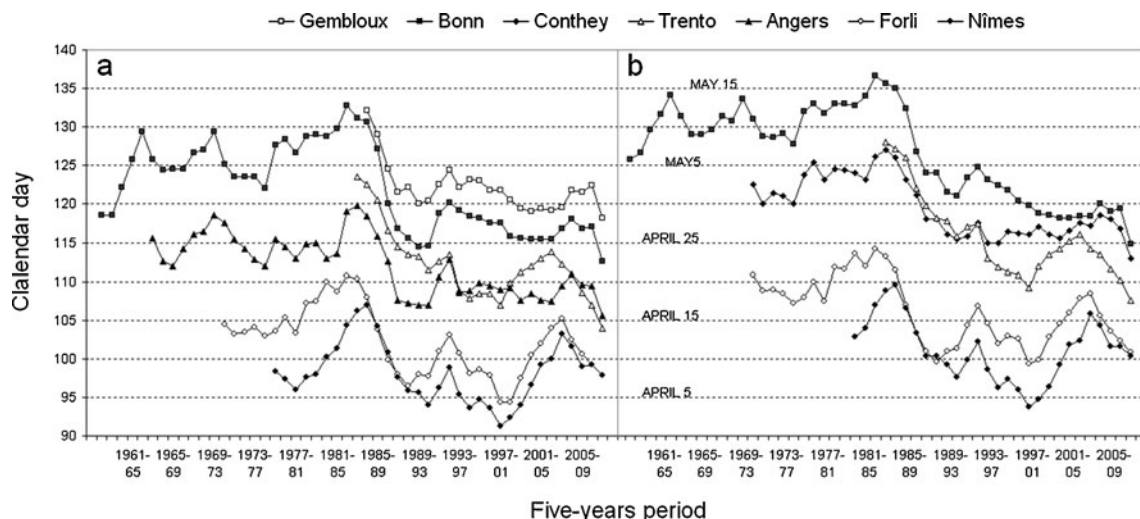


Fig. 3 Time-course changes in moving averages for observed annual dates of two blooming stages (MAOB values) in Golden Delicious, expressed in calendar days from January 1. **a** F1 stage at six sites. **b** F2 stage at five sites

periods. Because 1988 has been identified in Western Europe as a tipping time for both temperature increases and blooming advances in apple (Guédon and Legave 2008), we compared mean dates between more or less long but equal periods ending in 1987 and starting in 1988. This showed that the mean advance in F1 date was 10 days in Bonn compared with 6–7 days in Angers for successive sub-periods 1966–1987 and 1988–2009 (overall period of 44 years). Mean advances were also more pronounced for F1 and F2 dates in Bonn (11–12 days) than in Conthey and Forli (7–8 days) for sub-periods 1970–1987 and 1988–2005 (36 years). Similarly, for sub-periods 1980–1987 and 1988–1995 (16 years), mean advances in F1 and F2 dates reached 11–13 days in Bonn compared to only 5–7 days in Nîmes. Also, and independently of temporal trends, MAOB values showed some marked isolated changes in these trends that expressed the influence of annual variability. In particular, a short-term change toward late F1 and F2 dates was noted for Golden Delicious at all sites over the 1992–1996 period (Fig. 3) despite trends toward earlier dates from the end of the 1980s. This case was mainly due to relatively late dates in 1996 at all sites for Golden Delicious (and for the other cultivars).

Moreover, time-course changes in blooming duration were determined by the number of days between MAOB values (calendar days) for different blooming stages, at sites where chronological series were available for two stages (Fig. 4). In Nîmes, the number of days between five-year average dates for F1 and F2 stages (F1-F2 duration) was

small most of the time (2–3 days), though it reached 4–5 days for a short period at the end of the 1980s. In Bonn, by contrast, F1-F2 duration was relatively long and variable until the early 1990s. In particular, it was also relatively long (7–8 days) at the end of the 1980s. F1-F2 duration thereafter gradually decreased in Bonn, and this surprisingly resulted in similar F1-F2 mean durations in Bonn and in Nîmes from the end of the 1990s. These trends toward shorter F1-F2 durations were also noted in Trento and less clearly in Forli. Finally, short F1-F2 durations (2–3 days) were recorded from the 2003–2007 period onward at all four contrasting study sites. Similarly, the number of days between E2 and F2 mean dates tended to decrease in Conthey, also suggesting that F1-F2 duration was decreasing at this site.

Selection of F1 date models and their validation

As our objective was to undertake a comparative analysis of the effect of temperature on blooming change in a given genetic clone (Golden Delicious grafted trees) at contrasting sites, we needed to use common models (same functions and parameters) at different geographic sites over the same historical periods. Sequential models were considered as appropriate in this task as they are able, unlike thermal time modelling, to simulate and compare series of annual dates for dormancy release. Two sequential models, called F1Gold1 and F1Gold2, were selected since they explained, respectively, 91.7 % and 90.8 % (significant R^2) of the

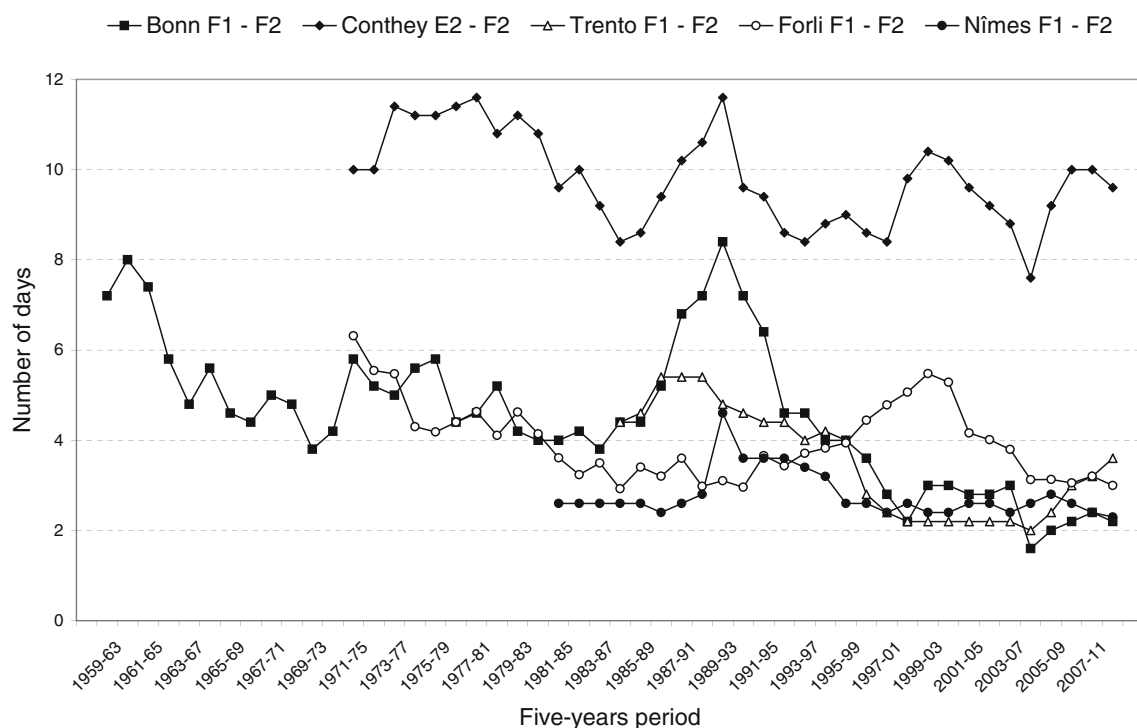


Fig. 4 Time-course changes in moving averages for Golden Delicious blooming durations (days) between the F1 and F2 stages at four sites and between the E2 and F2 stages at one site

Table 3 Characteristics of two best sequential models selected for Golden Delicious apple (model fitting from 96 contrasting F1 dates collected in Europe)

Model	F 1 Gold 1	F 1 Gold 2
Chilling sub-model		
Temperature function	Triangular	Triangular
Daily temperature involved (°C)	Mean	Mean
Function parameters		
Optimal temperature (Tc in °C)	1.1	3.2
Temperature interval (Ic in °C)	20	24
Other parameters		
Chilling period onset (in year $n-1$)	October 30	November 2
Chilling quantity required (C) ^a	56.0	75.0
Heating sub-model		
Temperature function	Exponential	Sigmoidal
Daily temperature involved (°C)	Mean	Mean
Function parameters		
Specific temperature (Th in °C)	9.0	13.9
Slope parameter (Sh, number)	/	6.0
Other parameters		
Heating quantity required (H) ^a	83.58	43.67

^a Sum of daily effects expressed in units depending on the temperature function

variability used to fit them (96 contrasting F1 dates) and showed respective RMSE values of 3.6 days and 3.8 days. Their characteristics are presented in Table 3. The chilling sub-models were similarly based on daily mean temperatures and triangular functions, but were different for the parameter values. Autumnal dates for chilling period onset (October 30 and November 2, respectively) were consistent with literature data for this parameter (Bidabé 1967; Atkinson and Taylor 1994). The two models mainly differed by their heating functions: an exponential function for F1Gold1 and a sigmoidal function for F1Gold2. When compared with F1Gold1 and F1Gold2, optimal thermal time models fitted from the same F1 date variability generally showed lower efficiency. Those based on linear heating functions (temperature sums) gave R^2 values of no more than 88 % and RMSE values of more than 4.3 days; results were poorer for optimal models based on binary functions (R^2 no more than 76.2 % and RMSE more than 6.1 days). Thermal time models based on exponential and sigmoidal functions nevertheless explained 89.2 % to 90.1 % of the variability and gave RMSE values of 3.9 and 4.1 days. This confirmed the advantage of selecting exponential or sigmoidal heating functions when modelling the forcing period, as in the selected F1Gold1 and F1Gold2 models. In order to improve the comparison between best thermal time models based on these functions and our two selected sequential models (F1Gold1 and F1Gold2), R^2 and RMSE values were

calculated by all the models for all the observed dates at each site separately (Bonn, Angers, Forlì and Nîmes). The results confirmed that sequential modelling was the assumption that clearly performed better than the thermal time assumption in the mild climate of Nîmes. As shown in Table 4, F1Gold1 and F1Gold2 explained 81.5 % and 80.3 % of all the variability at the Nîmes site (37 years from 1975 to 2011) and gave RMSE values of around 3 days, compared with only 65.7 % to 64.3 % and 4.1 to 4.2 days for the best thermal time models. In Angers, where 49 years were tested (1963–2011), F1Gold2 also provided a more comprehensive explanation of all the variability than the best thermal time models (around 72 % compared with 65 %). This underlined the advantage of using chilling sub-models in sequential models as they take account of the impact on blooming of possible mild conditions from November to January, particularly at French Mediterranean and oceanic sites characterized by relatively mild conditions (Fig. 2).

To confirm the selection of the F1Gold1 and F1Gold2 models as common models for application at all sites, we validated these models by examining annual deviations between observed and simulated F1 dates (Table 5). In the internal validation (85 annual dates tested), these models explained a relatively large proportion of the variability (71.1 % to 76.9 %) at all the sites except at Angers for F1Gold1 where the proportion explained was lower (56.9 %). RMSE values were in all cases ≤ 5 days. Deviations exceeding 10 days were found only twice with F1Gold1 and three times with F1Gold2 out of 85 tested dates. Similarly, the external validation tested 28 observed dates in Gembloux and 29 dates in Trento. In Gembloux, both models significantly explained a relatively large proportion of the variability (70.7 % and 72.8 %, respectively). RMSE values were ≤ 4 days with no deviation exceeding 10 days. In Trento, both models explained a relatively small

Table 4 Influence of modelling assumption on the efficiency of F1 date simulation in Angers and Nîmes for Golden Delicious (for each modelling, results are shown for two best models fitted)

Modelling assumption	Sequential		Thermal time	
	F1Gold1 ^a	F1Gold2 ^a	Exponential ^b	Sigmoidal ^c
Angers 1963–2011				
RMSE value (days)	4.8	4.2	4.6	4.7
R^2 value	0.637 *	0.722 *	0.657 *	0.653 *
Nîmes 1975–2011				
RMSE value (days)	3.0	3.1	4.1	4.2
R^2 value	0.815 *	0.803 *	0.657 *	0.643 *

^a Sequential models presented in Table 3

^b Exponential model involving mean temperature and the following parameters: Th: 9 °C; H: 69.7 units; Heating onset: February 9

^c Sigmoidal model involving mean temperature and the following parameters: Th: 20 °C; Sh: 8; H: 27.5 units; Heating onset: February 9

* Significant value ($P < 0.05$)

proportion of the variability (51.8 % to 53.3 %) while RMSE values were a little more than 5 days. Poorer validation results in Trento appeared to be due to deviations ≥ 10 days in three years (1989, 1994, 1997) for both models (Table 5). Also, R^2 values were significant for both internal and external validations at all sites except Nîmes where only 13 dates were tested.

Simulation of dormancy release date and forcing period duration by the selected models

Based on the sequential modelling assumption, we defined the duration of the forcing period for a given blooming stage as the number of days between the date of dormancy release and the blooming date corresponding to that stage. The forcing period started when the chilling requirement was satisfied and stopped when the heating requirement was also satisfied. Thus, we used the F1Gold1 and F1Gold2 models to simulate two components of F1 date changes in Golden Delicious at contrasting sites: changes in the date of dormancy release and changes in forcing period duration, and this in relation to various changes in temperature conditions from autumn to early spring. As the two models gave similar results, only the simulations obtained with F1Gold1 are presented (Fig. 5). In the same manner as for the descriptive analysis of observed blooming dates, the simulations were performed on five-year moving averages for both the simulated date of dormancy release (MADR values) and the simulated duration of forcing period, corresponding to the F1 date (MAFP values). In practical terms, MAFP values were obtained by the difference between MADR values and MASB values (simulated dates of blooming stage F1) for the same five-year periods.

Regarding spatial variability, the clear simulated differences noted for MADR values between the sites were consistent with the expected range of earliness of dormancy release. Unlike the spatial variability of observed blooming dates (Fig. 3), this MADR variability did not show any close relationship with site latitude (Fig. 5a and Table 1). As expected, the differences in dormancy release between the sites appeared linked to differences in site temperature from November to January to satisfy the chilling requirement. In particular, the latest dormancy release dates were simulated in Nîmes where temperatures were highest, while the earliest dormancy release dates were simulated in Conthey and Trento where temperatures were coldest (Figs. 2a and 5a). Slightly later dates were simulated in Gembloux and Bonn than in Conthey and Trento (associated with warmer temperatures from November to January in Gembloux and Bonn). Intermediate dates were simulated in Angers and Forlì in accordance with their intermediate temperatures from November to January, and this despite the contrasting latitude and longitude between the two sites (Fig. 5a and Table 1). Regarding duration of forcing period (MAFP values), greater differences were noted between the sites than for dormancy release (Fig. 5a and b). Although this spatial variability

in forcing period appeared to be more related to latitude than for dormancy release (Fig. 5b and Table 1), the forcing period simulations suggested that it was mainly differences in site temperature from January to April (particularly February and March) that had an impact. As expected (Figs. 2a and 5b), the shortest forcing period durations were simulated in Nîmes where temperatures were highest over this period, while the longest were simulated in Gembloux, Bonn, Conthey and Trento where temperatures were coldest. Intermediate durations were simulated in Angers and Forlì (shorter in Forlì than in Angers), consistent with their intermediate temperatures from January to April (warmer in Forlì).

Regarding temporal variability, noticeable trends toward later dormancy release dates were highlighted by MADR values in Nîmes, Angers and Forlì. This effect was less pronounced or unclear at the other sites (Fig. 5a). Our simulations suggested that dormancy release has been occurring since the end of the 1980s in Nîmes. This delay appeared to have occurred more gradually in Angers and later in Forlì (from the early 1990s). By contrast, simulations of forcing period durations (MAFP values) clearly showed that forcing periods have been shorter at all sites since the end of the 1980s (though more gradually at Forlì; Fig. 5b). This shortening of forcing period appeared to be less marked in Nîmes and Angers from the end of the 1990s.

Determinisms of F1 date advance and regional patterns

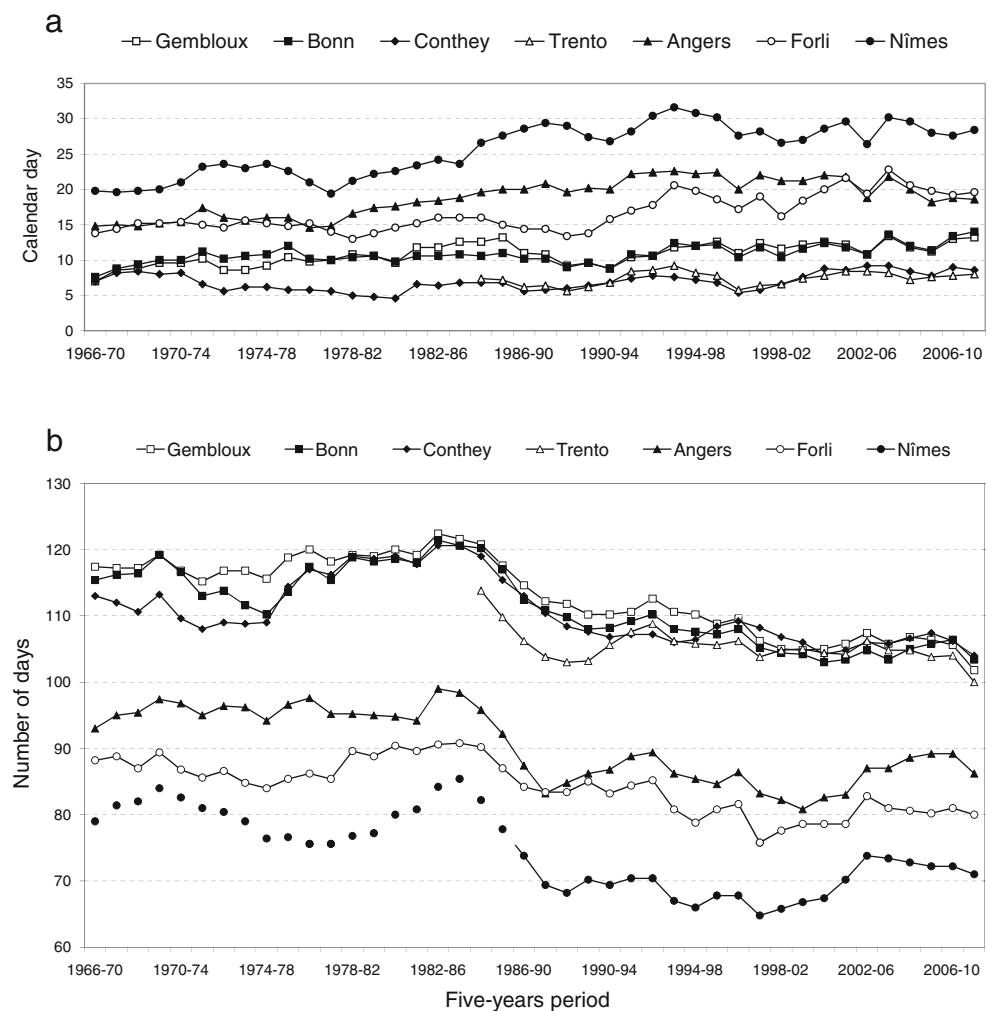
Finally, marked similarities were shown between temporal trends in observed dates (MAOB values; Fig. 3) and simulated forcing period durations (MAFP values; Fig. 5b). We therefore calculated the correlations between the annual values for observed F1 date and annual values for estimated forcing duration period obtained from the F1Gold1 and F1Gold2 models. This resulted in high, positive and significant Pearson's coefficients (r) at all sites for both models and for all periods tested. The coefficient varied from 0.84 to 0.89 in Bonn and from 0.70 to 0.78 in Angers depending on the model tested and the observation period. Similarly, high values were obtained for the shortest series in Gembloux (0.83–0.86), Trento (0.70–0.81), Forlì (0.76–0.85) and Nîmes (0.69–0.78). The results obtained with F1Gold2 used to simulate forcing period duration from 1984 to 2011 (common observation period) are presented in Fig. 6 (similar results were obtained with F1Gold1). Despite some regional differences, a very large proportion of the annual variability in observed F1 dates was explained at all sites by the annual variability in forcing period duration. It may therefore be concluded that faster satisfaction of the heating requirement since the end of the 1980s (Fig. 5b) was the main determinism of F1 date advances. By contrast, Pearson's coefficients calculated between the observed annual F1 date and the simulated annual date of dormancy release were very low at all sites for both models and all periods tested (−0.17 to +0.22). The

Table 5 Deviation (in days) between observed and simulated dates of Golden Delicious F1 stage according to selected models F1Gold1 and F1Gold2

Blooming year		Gembloux		Trento		Blooming year		Bonn		Angers		Forlì		Nîmes	
		F1Gold1	F1Gold2	F1Gold1	F1Gold2			F1Gold1	F1Gold2	F1Gold1	F1Gold2	F1Gold1	F1Gold2	F1Gold1	F1Gold2
1983	/	/	-6	-8	-6	1959	+6	+8	/	/	/	/	/	/	/
1984	-1	0	-3	-3	-3	1960	+4	+6	/	/	/	/	/	/	/
1985	+1	+2	-1	0	-1	1961	+11	+8	/	/	/	/	/	/	/
1986	0	+3	-3	-3	-3	1962	-9	-3	/	/	/	/	/	/	/
1987	+8	+5	0	0	0	1963	+8	+5	-6	-6	-9	/	/	/	/
1988	-2	0	-1	-1	-1	1964	+1	+2	-2	-2	-2	/	/	/	/
1989	+2	+1	-14	-14	-14	1965	-4	-3	-4	-4	-2	/	/	/	/
1990	-3	-2	-3	-3	-4	1966	0	-1	-7	-3	-3	/	/	/	/
1991	+2	+5	-3	-3	-3	1967	0	0	-4	-1	-1	/	/	/	/
1992	-5	-4	-3	-3	-4	1968	-5	-1	-1	-1	0	/	/	/	/
1993	+3	+6	+4	+4	+4	1969	-2	+2	-8	-8	+6	/	/	/	/
1994	-4	-2	+10	+10	+10	1970	-1	+1	-12	-7	-7	-2	-2	/	/
1995	-4	-3	+9	+9	+7	1971	0	+2	-5	-2	-2	-1	-1	/	/
1996	+4	+9	+2	0	+2	1972	+2	+2	-5	-5	-5	+4	+4	/	/
1997	+2	+2	+10	+10	+10	1973	0	0	0	0	+1	-7	-8	/	/
1998	-3	-5	+2	+2	+1	1974	+6	+13	-5	-5	-2	-3	-3	/	/
1999	-7	-4	+4	+4	+4	1975	-5	-5	0	0	+1	-4	-3	+8	+8
2000	-2	-3	+2	+2	+3	2000	-2	-4	-6	-6	-9	-2	-3	-2	-2
2001	-6	-7	-4	-2	-4	2001	-3	-3	-8	-8	-10	-2	-2	0	+1
2002	-2	+2	+2	+2	0	2002	+2	+7	-6	-6	+3	-2	-1	-2	+3
2003	+5	+5	0	0	0	2003	+5	+6	+1	+1	0	+1	-1	+2	-1
2004	-2	-2	-1	-1	-1	2004	-2	-2	0	0	0	-5	-7	-1	-2
2005	-2	-1	-1	-1	-2	2005	-3	0	-1	-1	0	-2	-3	+4	+1
2006	-4	-3	+4	+4	+4	2006	-1	0	-2	-2	-2	-3	-3	-2	-3
2007	+1	0	+2	+2	+2	2007	+2	+2	-1	-1	-2	0	-3	-1	-3
2008	-9	-5	+1	+1	+1	2008	-1	+4	-8	-8	-3	+2	+2	+4	+2
2009	-6	-5	+8	+8	+8	2009	+5	+5	+1	+1	+3	-1	-1	+1	0
2010	-2	-2	+9	+9	+9	2010	+9	+7	+3	+3	+1	+6	+3	+1	0
2011	-1	+1	0	0	+2	2011	+9	+10	+1	+1	+3	+2	+2	+3	+1
RMSE value (days)	4.0	3.9	5.3	5.3	5.2		4.8	5.0	5.0	5.0	4.1	3.3	3.4	3.1	2.9
R2 value	0.707*	0.728*	0.518*	0.518*	0.533*		0.749*	0.730*	0.569*	0.711*	0.765*	0.730	0.745*	0.730	0.769

RMSE root mean square error; +, - represent the simulated date respectively later or earlier than observed; value 0 refers to the same date; / means the observed date is not available; * Significant R2 value at $P < 0.05$

Fig. 5 Simulated time-course changes in Golden Delicious bud phenology by the F1Gold1 model at seven sites. **a** Moving averages for the simulated annual date of dormancy release in calendar days from January 1 (MADR values). **b** Moving averages for the simulated annual duration (days) of the forcing period up to the F1 stage (MAFP values)

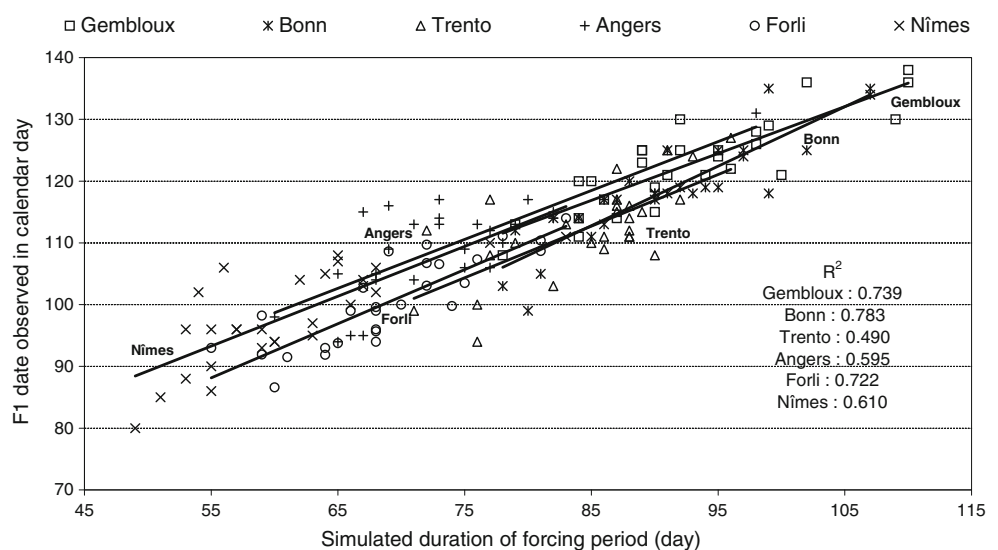


highest values were obtained under the mild conditions prevalent in Nîmes, and this for both models (round +0.20). Thus, the annual variability in observed F1 date appeared to be poorly (mild conditions) or not at all determined by annual variability

dormancy release. However, when average values were calculated for simulated chilling period over 44 years (1966–2009), the chilling requirement was seen to have been satisfied later since the end of the 1980s, in particular in Nîmes and Angers

i n

Fig. 6 Linear relationships between the annual forcing period duration simulated by the F1Gold2 model and the annual observed F1 date at six sites over the same 1984–2011 period (R^2 values provided for each site were all significant at $P < 0.01$)



(in accordance with the trends previously shown in Fig. 5a). Finally, the mean advance in F1 date in the recent past was seen to have been due to different regional patterns in the satisfaction of chilling and heating requirements, as illustrated graphically in Fig. 7 for four contrasting sites and using F1Gold1 model simulations over the 1966–2009 period. In Bonn, the mean advance resulted in a 10-day decrease in forcing period (heating satisfaction), balanced by a short delay in chilling satisfaction (1–2 days). In Angers, a 10 day decrease in forcing period (as in Bonn) was balanced by a longer delay in chilling satisfaction (4–5 days) than in Bonn. This may explain the greater mean advance observed in Bonn than in Angers, previously cited in the results. Similar mean advances simulated in Angers and Forli resulted in different changes, i.e. a smaller decrease in forcing period (7–8 days) and a shorter delay in chilling satisfaction (3–4 days) in Forli. Similar mean advances simulated in Forli and in Nîmes resulted in more marked changes in Nîmes, i.e. a more pronounced shortening of the forcing period (11–12 days) and a longer delay in chilling satisfaction (7–8 days). This delay in Nîmes compared to the short delay simulated in Bonn (1–2 days) may explain the shorter mean advance observed in Nîmes than in Bonn, as previously cited in the results.

Despite regional differences, the simulations showed that mean forcing period was shortened more than the mean delay in chilling satisfaction at all sites (Fig. 5 and 7), and this appeared to be consistent with the greater temperature increases from January to April (forcing period) than from November to January (chilling period) recorded at all sites (Fig. 2b). Likewise, the different regional patterns for F1 date advance, suggested by the modelling, appeared to be consistent with the

regional differences in temperature increase. In particular, the short delay in chilling satisfaction simulated in Bonn was consistent with small temperature increases in November and December, while the longest delay simulated in Nîmes was consistent with the marked temperature increases over the same period (Fig. 2b and 7). Both the greater delay in chilling satisfaction and the greater decrease in forcing period in Nîmes than in Forli (Fig. 5 and 7) were consistent with the more marked temperature increases in Nîmes than in Forli from November to April (Fig. 2b).

Discussion

Blooming variability

Most of the studies conducted to assess the impact of warming on bud phenology have focused on responses within species (Menzel et al. 2006; Miller-Rushing et al. 2007; Primack et al. 2009). Very few studies have been conducted on responses within growing regions even though this is critical when determining phenology adaptation strategies in the fruit tree industry (Eccel et al. 2009). Our study was therefore designed to assess blooming variability in apple trees across Western Europe and thereby provided information on regional differences. In particular, trends toward shorter blooming advances in oceanic and Mediterranean regions than in continental regions and shorter blooming phase durations in continental regions (that are usually characterised by extended blooming) might be insights into future phenological changes in temperate fruit

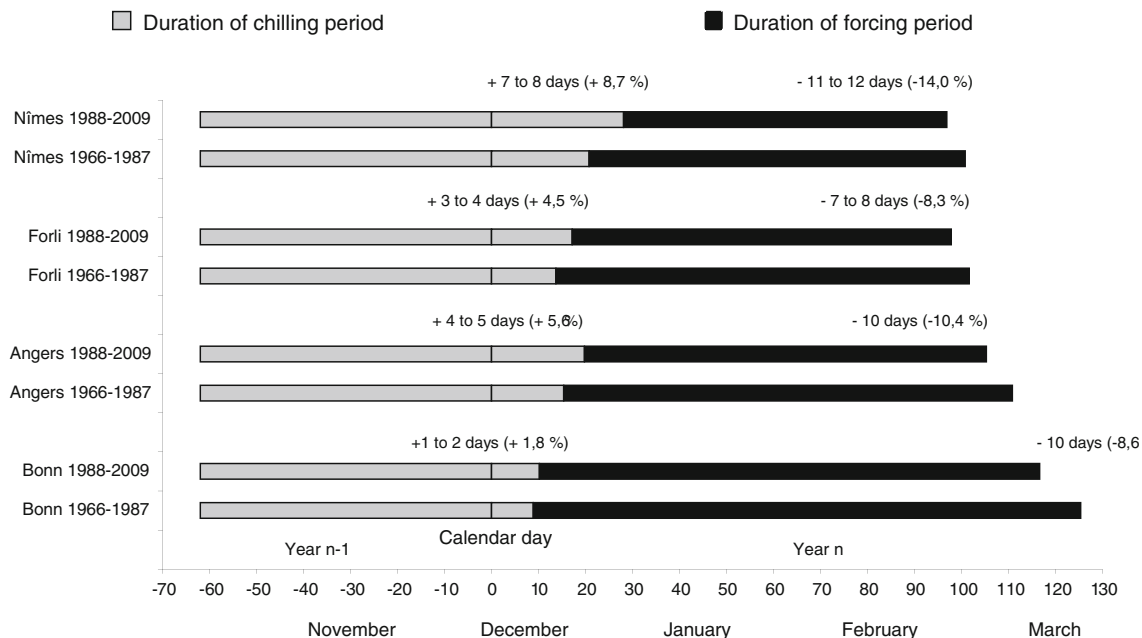


Fig. 7 Differences in mean chilling and forcing period durations between the 1966–1987 period and the warmer 1988–2009 period (see Fig. 2b) for Golden Delicious buds at four contrasting sites, as simulated by the F1Gold1 model

trees in the Northern hemisphere. Information recently provided by Fujisawa and Kobayashi (2010) in northern Japan suggested that the trend toward blooming advance was little different between growing regions for the Fuji apple tree. These authors also noted that trends in the recent past were linear, whereas blooming changes in apple and pear trees in Western Europe were characterized by marked advancement in the late 1980s, as shown in our study and in preliminary work (Guédon and Legave 2008). In Norway, Nordli et al. (2008), studying forest species, noted that advances in the oceanic region were more pronounced than in colder central regions, i.e. quite the opposite to our results. Such apparently opposing observations probably underline a broad range of regional phenological responses to global warming in the Northern hemisphere. As suggested by Primack et al. (2009), and as supported by our results, these responses would appear to result from various interactions between contrasting regional climates and regional differences in temperature increase, depending on the geographical characteristics of the area considered (longitude, latitude, altitude). For example, both late blooming and marked trends toward earlier and shorter blooming in the continental region of Bonn resulted from a relatively cold climate that was subject to pronounced warming mainly during the forcing period. By contrast, early and short blooming with an unclear trend toward earlier blooming in the Mediterranean region of Nîmes resulted from a mild climate being subjected to pronounced warming during both the chilling and forcing periods. Other interactions led to similar blooming times and temporal trends despite clearly contrasting climates, as shown for Angers (western flat region) and Trento (eastern mountainous region). Finally, the result of regional differences in blooming advance was the decrease in the spatial variability of Golden Delicious blooming dates in the explored area. In particular, the time interval between F2 dates in Bonn (late blooming) and in Nîmes (early blooming) decreased by an average of 8–10 days between the 1980s and the 2000s. Strong parallelism in blooming advance within apple cultivars (as observed in our study) or within pear cultivars (Guédon and Legave 2008) may suggest that the spatial variability of blooming time is decreasing in Western Europe for these species. By contrast, Menzel et al. (2006) noted that spatial variability in spring phenophases increased in Germany in response to temperature changes, and this for a range of perennial species. Such observations that are apparently contradictory to our own in apple indicate that further investigations are necessary on bud phenology changes in European perennial plants.

Modelling and determinisms of blooming changes

Sequential modelling has been found to provide more accurate simulations of blooming time than thermal time modelling for apple tree in Western Europe, as shown in France (Legave et

al. 2008). Sequential modelling predictions for certain forest species in the 21st century have highlighted that chilling effects can be insufficient at low altitude in southwestern France (Vitasse et al. 2011). It is therefore crucial to consider dormancy release in the future phenology modelling of temperate trees in Western Europe. Sequential modelling can easily simulate annual dates of chilling satisfaction, whereas the current forcing tests used to estimate these dates are too time consuming and are generally unavailable (Hauagge and Cummins 1991). The triangular function and optimal temperatures used in our selected chilling sub-models were consistent with the biological knowledge of the chilling process in fruit trees (Fuchigami and Nee 1987; De Melo-Abreu et al. 2004) and with results obtained for Golden Delicious (Naor et al. 2003). In addition, these selected chilling functions were similar to that used in the 'Utah model' (Richardson et al. 1974) employed worldwide. A modified version of this model was the approach that performed best for Golden Delicious in the Trento region (Rea and Eccel 2006). The exponential heating function, as used in our F1Gold1 model, is accurately predicting blooming time in apple (Bidabé 1967). A sigmoidal heating function (used in the F1Gold2 model) appeared to be biologically meaningful by estimating the limited effects of high temperatures. Substantial validation of our selected models lent a great deal of weight to the simulations obtained and they may therefore be used in Western Europe to predict future blooming changes in apple tree. Similarly, in olive tree, Garcia-Mozo et al. (2009) concluded that it should be possible to fit models for all of Mediterranean Europe.

Although based on contrasting heating functions, the two selected models showed that advances in F1 date were mainly determined by faster satisfaction of the heating requirement since the end of the 1980s. Advances in F2 date might be similarly explained. The trend toward shorter F1-F2 phase, highlighted in continental regions (Bonn particularly), would appear to be due to high rates of heating satisfaction during this phase. This was supported by very marked temperature increases in April (full blooming phase) in continental regions (Bonn particularly). Apple blooming advances in Japan were also found to be closely correlated with temperature increases in April (Fujisawa and Kobayashi 2010). But the satisfaction of chilling requirements must be also considered in order to have a full understanding of the regional differences in blooming advance. For instance, our modelling results suggested that chilling completion dates were particularly delayed in Nîmes. This would tend to delay blooming time in an inverse relationship with the more rapid satisfaction of the heating requirement. Similarly, trends toward a declining satisfaction of chilling requirement were found in the United Kingdom and Australia (Sunley et al. 2006; Darbyshire et al. 2011). Our modelling results also pointed to a gradual and limited reduction in chilling accumulation (also shown by Sunley et al.

2006) contrary to the sudden change toward faster satisfactions of the heating requirement. This is consistent with more pronounced temperature increases in winter and early spring (forcing period) than in autumn (chilling period) across all of Western Europe (Chmielewski et al. 2004). Finally, two opposing and unequal impacts of temperature increases determined the extent of blooming advances in Western Europe (Fig. 7). This resulted in shorter mean advances at sites where warming was relatively marked (Nîmes particularly), and highlighted the non-linearity between blooming advance and warming intensity.

Implications of blooming changes

Earlier blooming dates might increase the risk of spring frost damage, as suggested by Cannel and Smith (1986) in Britain. More recently, spring frosts in southern regions of the United Kingdom have been seen to be decreasing both in frequency and severity (Sunley et al. 2006). Likewise, investigations into the frost risk for apple in northern Italy (Eccel et al. 2009) concluded that the risk is lower now than in the past, and suggested that it will remain stable or decrease slightly in the future. The frost risk during fruit tree blooming in Europe will be probably more open to debate in the future context of climate change because of regional differences both in the magnitude of blooming advances and the frequency of negative temperatures. In particular, our results suggest that the French Mediterranean coastline (Nîmes) may at present be little subject to frost risk because blooming advances are only slight. By contrast, this risk might be a true worry for growers in continental regions because of more pronounced blooming advances, as in Germany (Bonn). In addition, shorter blooming phase durations in these regions could heighten the risks of both frost damage and insufficient pollinations due to enhanced tree vulnerability (more opened flowers in few days when frost or poor pollination can occur). By contrast, oceanic and Mediterranean regions may be gradually affected in the future by excessive delays in chilling satisfaction, particularly in southern France where such delays already occurred, as shown by our modelling results in recent past. On the orchard scale, this could cause future phenological disorders (Fuchigami and Nee 1987) such as poor blooming synchronization between cultivars that require cross-pollination, and excessively long blooming durations that may excessively increase fruit maturity time. Moreover, decreases in the spatial variability of blooming time on the European scale, as also shown in our study, could affect the regional ranges of maturity time that are such an essential commercial feature.

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