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This study aimed to improve the modelling of flowering time in fruit trees and to understand to what extent global warming has affected this trait since the end of the 1980s. The onset of flowering time (F1 stage) in apple trees has advanced by 7 – 8 d in France since the late 1980s. In this context, a sequential model composed of a chilling sub-model and a heat sub-model was considered. The input data consisted of F1 dates for 'Golden Delicious' apple in three French cropping areas from the North-West to South-East over the period 1976 – 2002 (81 F1 dates). A user-oriented software package, called 'Pollenoscope', automatically optimised combinations between seven chilling and three heat temperature functions. This was achieved by maximizing the R^2 values between the observed and simulated flowering dates. The study provided comparative information for assessing the respective effects of temperature functions commonly used for modelling flowering time in temperate trees. Three selected models explained 82 – 86% of the observed variability in flowering. Their fitness for an accurate prediction of the F1 date was validated using independent flowering datasets. All three models simulated similar time-course changes in the duration of the chilling effect at all three locations [i.e., a mean increase in the duration of this effect (by 3 – 5 d) since the end of the 1980s]. Consequently, it suggested that the duration of the heat effect had decreased (10 – 13 d) to explain the advance in flowering time. Hence, our results support the idea that global warming has, simultaneously, exerted two opposing effects in France between 1976 – 2002: (i) a slower mean rate of completion for the chilling requirement, and (ii) a higher mean rate of completion for the heat requirement. A more marked effect on completion of the heat requirement may have resulted from more pronounced warming from January to April, corresponding to the active growth phase of floral primordia, than from October to January, corresponding to the dormancy-breaking phase.

A relatively marked increase in mean air temperature has been observed in many parts of the World since the end of the 1980s (Houghton *et al*., 2001). As plant phenology is mainly influenced by temperature, global warming has stimulated renewed interest in phenological methods and observations to address important questions related to the modelling of global changes (Schwartz, 1999). Long-term phenological series at specific sites provide useful measures of species-level biological responses to climate change. Clear responses in plant phenology have been observed in European countries, where an earlier onset of the growing period was associated with global warming (Chmielewski and Rötzer, 2001). Most reports focus on changes in natural vegetation and annual crops (Chuine, 2000), while few studies deal with phenological trends in perennial horticultural crops (Schultz, 2000). Nevertheless, over the last 40 years, similar trends towards an advancement in flowering times have been described in several fruit species in distant countries in the northern hemisphere and related to global warming (Omoto and Aono, 1990; Kai *et al*., 1993; Chmielewski *et al*., 2004; Legave and Clauzel, 2006).

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In fruit tree orchards, changes in the timing of flowering phenology could have important impacts on fruit production, because of the indirect influences of phenology on Spring frost damage, pollination, and fruit-set efficiency (Cannell and Smith, 1986; Atkinson and Taylor, 1990; Atkins and Morgan, 1990; Zavalloni *et al*., 2006).

In temperate climates, the buds of deciduous fruit trees are dormant during the Autumn and Winter. It is commonly assumed that this rest period is composed of an endodormancy phase, followed by an ecodormancy phase (Lang *et al*., 1987). Endodormancy involves growth-controlling perception events that are entirely within the floral primordia. Chilling temperatures, during Autumn and Winter, are perceived by the flower primordia and cumulative chilling effects (chilling requirement) are generally considered to be the main factor in the endodormancy-breaking process. Long-term floral databases do not, in general, contain estimated dates for the onset and end of endodormancy-breaking because reliable and easy-to-use biological markers are lacking (Tromp, 2005). Following release from endodormancy, the ecodormancy phase is associated with unsuitable environmental conditions for active growth of the floral primordia, due to low

temperatures, nutrient deficiency, or water stress. In standard orchard practice, the cumulative effects of moderate and high temperatures during Winter and Spring (heat requirement) are generally considered to be the main factor that determines the active growth phase, resulting in flower bud opening.

With regard to the modelling of flowering time in temperate trees, many papers have described different types of mathematical functions to simulate chilling and heat responses, although they have rarely been compared with each other (Chuine, 2000). The chilling function was chosen rather arbitrarily in fruit trees, according to Sunley et al. (2006). Modelling studies in fruit trees are commonly based on only one or two temperature response functions (Bidabé, 1967; Richardson et al., 1974; Erez et al., 1990; Rojas-Martinez et al., 1999; Honjo et al., 2006). Moreover, different temperature response functions are frequently compared on the basis of reduced climatic variability, or heterogeneous data (Virtudes Andres and Duran, 2000). It is therefore difficult to assess the fitness of the phenological models thus developed.

This work aimed to improve the modelling of flowering time in fruit tree species by comparing various temperature functions on the basis of phenological data recorded under contrasting climatic conditions. As a result, we also sought to improve our understanding of the impact of global warming on flowering time. With these goals in mind, the possibilities recently offered by 'Pollenoscope' modelling software (Alméras et al., 2003) were explored using long-term data for apple phenology recorded in different growing areas in France.

MATERIALS AND METHODS
Plant material and environmental conditions

Flowering data concerning 'Golden Delicious' apple were analysed, as this cultivar has been cropped ubiquitously in France for many years. As this study aimed to analyse time-course changes in flowering phenology, only one flowering stage was considered per year. Of the common phenological data used, the F1 flowering stage (approx. 10% of flowers opened) was chosen as it is easily detected in orchards, and consequently is a reliable marker of flowering time. Accurate F1 dates, recorded in adult orchards managed by commercial practices and contained in a database called PhenoClim® (Domergue et al., 2004), were selected at three locations representative of the main cropping areas of France. The first location was the INRA Research Station near Angers (47° 28 N; 0° 33 W) in the Pays de Loire region. An intermediate location was a farm at Domaine de Castang near Bergerac (44° 51 N; 0° 29 E) in the Aquitaine region, and the third location was the Ctifl professional Station near Nîmes (43° 50 N; 4° 21 E) in the Languedoc region. The longest chronological series of data was collected at Angers (1963 – 2006). The other two series were shorter and covered different periods: 1967 – 1972 and 1976 – 2002 at Bergerac, and 1974 – 2006 at Nîmes. Additional data were composed of F1 dates collected in 1984 – 2006 at the Walloon Research Centre (50° 34 N; 4° 41 E) near Gembloux in Belgium.

Regional differences in temperature in France were assessed using temperature records from the INRA climate database located in Avignon (Agroclim Unit). We used 27 successive years (1976 – 2002) for which F1 dates were recorded at all three locations. A gradual range in annual mean temperature was recorded according to latitude. Angers, located further to the North and characterised by an oceanic climate, had the coldest mean temperature (11.9°C), and Nîmes characterised by a Mediterranean climate had the warmest mean temperature (14.5°C). Bergerac, located to the South-East of Angers, showed an intermediate mean temperature (12.9°C). Monthly mean temperatures showed a similar pattern, with the lowest being recorded at Angers and the highest at Nîmes (data not shown). We considered two sub-periods (1976 – 1988, 1989 – 2002) to highlight temperature increases since the end of the 1980s. The sub-period 1989-2002 clearly showed increases in monthly mean temperatures at all three locations in comparison with the sub-period 1976 – 1988, except for September (Table I). Annual mean temperatures had increased by 1°C at all three locations. This included noticeable monthly differences for the months involved in the annual flowering process: warming was relatively limited in October, November and December (+ 0.4°C to + 0.9°C), whereas it was more pronounced in January, February and March (+ 1.1°C to + 2.0°C). In comparison with the three French locations, Gembloux clearly showed the coldest climate, with the lowest annual mean temperature (9.7°C).

Temperature functions and modelling parameters

The flowering model was based on the usual hypothesis that chilling temperatures and heat temperatures had successive and independent effects on fruit trees (sequential modelling; Richardson et al., 1974; Atkins and Morgan, 1990). Thus, the model included, firstly, a chilling sub-model and, secondly, a heat sub-model. In the chilling sub-model, seven temperature functions, representative of a large diversity of mathematical laws, were chosen to compare their respective fitness. These functions and their associated parameters are presented in Table II. Four were based on increasing chilling effects as temperatures fell (binary, linear, exponential and sigmoidal chilling). The binary, linear and exponential chilling functions offered the advantage of involving only one parameter. The relevance of using the exponential chilling function to predict flowering time has been highlighted in apple

TABLE I
Mean variations in monthly and yearly mean temperatures (°C) at three locations in France in 1989 – 2002 compared with 1976 – 1988

Month	Angers	Bergerac	Nîmes
January	+ 1.7	+ 1.3	+ 1.4
February	+ 1.6	+ 1.1	+ 1.2
March	+ 1.8	+ 1.8	+ 2.0
April	+ 0.7	+ 0.7	+ 0.8
May	+ 2.1	+ 2.4	+ 1.7
June	+ 0.6	+ 0.8	+ 0.9
July	+ 0.8	+ 0.6	+ 1.0
August	+ 2.0	+ 2.0	+ 1.9
September	+ 0.1	– 0.1	– 0.2
October	+ 0.4	+ 0.5	+ 0.6
November	+ 0.8	+ 0.9	+ 0.7
December	+ 0.4	+ 0.8	+ 0.8
Year	+ 1.0	+ 1.0	+ 1.1

+, – ; increase or decrease, respectively.

TABLE II
Temperature functions and associated parameters available in 'Pollenoscope' software, involved in the chilling and heat sub-models

Sub-model	Temperature function	Temperature parameter (°C)
Chilling sub-model		
Binary chilling (BC)	Fc (T) = 1 if T<Tc, Fc (T) = 0 if T>Tc	Tc: threshold T°
Linear chilling (LC)	Fc (T) = T–Tc if T<Tc , Fc (T) = 0 if T>Tc	Tc: threshold T°
Exponential chilling (EC)	Fc (T) = exp – (T/Tc)	Tc: specific T°
Sigmoidal chilling (SC)	Fc (T) = 1 / 1 + exp (T–Tc / Ic)	Tc: specific T°
		Ic: specific interval[1]
Triangular chilling (TC)	Fc (T) = 1– T–Tc / Ic if Tc– Ic <T< Tc+ Ic	Tc: optimal T°
	Fc (T) = 0 if not	Ic: specific interval[2]
Parabolic chilling (PC)	Fc (T) = 1– [(T-Tc) / Ic]² if Tc– Ic <T< Tc+ Ic	Tc: optimal T°
	Fc (T) = 0 if not	Ic: specific interval[2]
Normal chilling (NC)	Fc (T) = exp [(T–Tc)2/ Ic]	Tc: optimal T°
		Ic: specific interval[2]
Heat sub-model		
Linear heat (LH)	Fh (T) = 0 if T<Th , Fh (T) = T-Th if T>Th	Th: threshold T°
Exponential heat (EH)	Fh (T) = exp (T/Th)	Th: specific T°
Sigmoidal heat (SH)	Fh (T) = 1 / 1 + exp (Th – T / Ih)	Th: specific T°
		Ih: specific interval[1]

[1]Parameter linked to the slope of the sigmoidal function around Tc or Th depending on the sub-model.
[2]Parameter defining the range of efficient temperatures around Tc.

trees in comparison with the simplest binary function (Bidabé, 1967). The sigmoidal chilling function involved two parameters, but offered the advantage of attaching limited importance to negative temperatures in comparison with linear and exponential functions. The three other chilling functions (triangular, parabolic and normal) similarly delineated an optimal chilling effect associated with an optimal temperature, and decreasing effects around this optimum according to a range of temperatures efficient in breaking dormancy. Although such chilling functions involved two parameters, they were more in agreement with the physiological characteristics of the chilling effect (Fuchigami and Nee, 1987). For a given temperature function, the date of onset of the chilling effect (called the Oc stage) and the sum of daily effects until chilling completion (C) were considered as two parameters (Table III).

With regard to the heat effect, it has been shown that flowering models that consider only daily heat effects cumulated from a fixed date to a given sum (Chuine, 2000) can provide accurate flowering time predictions (Bidabé, 1967; Honjo *et al.*, 2006). Thus, in the heat sub-model, we considered only three temperature functions (linear, exponential and sigmoidal) that are broadly involved in the chemical or enzyme-catalysed reactions of growth events. These functions and their respective parameters are presented in Table II. The sigmoidal heat function differed from the two others in estimating limited effects for high temperatures. For all three functions, the sum of daily heat effects (H) from the date of completion of sum C, to the F1 date constituted another sum parameter. Also, the lack of a chilling sub-model (Thermal Time modelling) was tested to evaluate the part of F1 date-variability that is explained only by

TABLE III
Parameters involved and number of elementary tests performed for each of the combinations tested between the different chilling and heat temperature functions available in the 'Pollenoscope' software

Function combination[2]	Temperature parameter[2]	Time parameter[3]	Sum parameter[4]	Number of parameters	Number of tests[5]
LH[1]	Th	Oh	H	3	3
BC × LH	Tc, Th	Oc	C, H	5	9
LC × LH	Tc, Th	Oc	C, H	5	9
EC × LH	Tc, Th	Oc	C, H	5	9
SC × LH	Tc, Ic, Th	Oc	C, H	6	9
TC × LH	Tc, Ic, Th	Oc	C, H	6	9
PC × LH	Tc, Ic, Th	Oc	C, H	6	9
NC × LH	Tc, Ic, Th	Oc	C, H	6	9
EH[1]	Th	Oh	H	3	3
BC × EH	Tc, Th	Oc	C, H	5	9
LC × EH	Tc, Th	Oc	C, H	5	9
EC × EH	Tc, Th	Oc	C, H	5	9
SC × EH	Tc, Ic, Th	Oc	C, H	6	9
TC × EH	Tc, Ic, Th	Oc	C, H	6	9
PC × EH	Tc, Ic, Th	Oc	C, H	6	9
NC × EH	Tc, Ic, Th	Oc	C, H	6	9
SH[1]	Th, Ih	Oh	H	4	3
BC × SH	Tc, Th, Ih	Oc	C, H	6	9
LC × SH	Tc, Th, Ih	Oc	C, H	6	9
EC × SH	Tc, Th, Ih	Oc	C, H	6	9
SC × SH	Tc, Ic, Th, Ih	Oc	C, H	7	9
TC × SH	Tc, Ic, Th, Ih	Oc	C, H	7	9
PC × SH	Tc, Ic, Th, Ih	Oc	C, H	7	9
NC × SH	Tc, Ic, Th, Ih	Oc	C, H	7	9

[1]No chilling involvement.
[2]Defined in Table II.
[3]Expressed in calendar date.
[4]Expressed in different units depending on the temperature function.
[5]Corresponding to all possibilities for separately testing the three daily temperatures (min, mean, max).

heat effects cumulated from a given date (Oh), which constituted the time parameter in this case (Table III).

Parameter values and simulated dates

'Pollenoscope' software, previously developed to predict pollen emissions (Alméras *et al.*, 2003), was used to test all possible combinations between the seven chilling functions and the three heat functions selected, including no chilling involvement (Table III). The observed F1 dates constituted the phenological input data. We considered twelve data files, defined by four location groups (Angers, Bergerac, Nîmes, and the cumulative dates from all three locations) and three data recording periods (sub-periods 1976 – 1988 and 1989 – 2002; and the global period 1976 – 2002). The corresponding temperature files (climate input data), obtained from the INRA database, were composed of temperatures from 15 August of year $n-1$ (preceding flowering year n) to 31 May of year n. Each file included three sub-files composed of minimum (min), mean and maximum (max) daily temperatures, each of which was used separately. The total number of parameters involved (output data) varied according to the combination tested (three-to-seven; Table III). The number of temperature parameters varied from one-to-four, depending on the combination and the temperature function. Only a single time parameter was involved in each combination (Oc or Oh). The sum of heat effects (H) was a common parameter for the different combinations, while the sum of chilling effects (C) was an additional parameter when chilling and heat functions were combined.

For each combination and data file, the software automatically searched for the optimal values of the parameters involved which maximised the coefficient of determination (R^2) between the observed F1 dates (input data) and the simulated F1 dates (output data). The algorithm of R^2 maximisation was based on the Metropolis algorithm (simulated annealing) described in Chuine *et al.* (1998). Some improvements to this algorithm were added to the 'Pollenoscope' software to shorten calculation times when numerical data were analysed in thousands, as in our study (Alméras *et al.*, 2003). In practical terms, the automatic search for optimal parameter values was conducted through a user-oriented
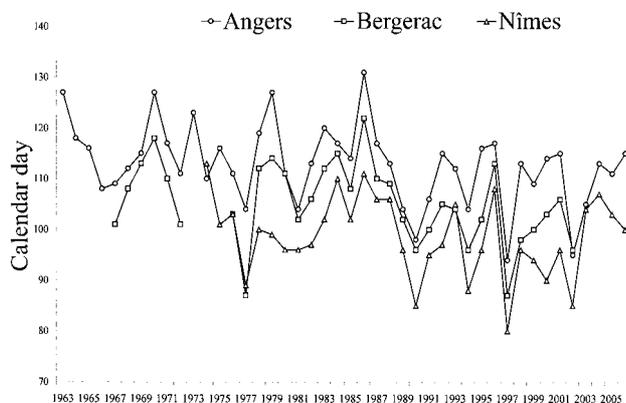
Excel interface (visual basic). It allowed easy switching between the different input files and the different combinations of chilling and heat functions. Thus, for each F1 date file, a total of 198 tests were performed: nine tests without chilling (3 heat functions × 3 daily temperatures tested for each) added to 189 tests corresponding to 21 function combinations, each involving nine tests because of all the possible combinations between three daily temperatures (Table III).

Also, for each combination tested from a given data file, the simulated dates of the F1 stage, and the completion of sum C, were obtained automatically by considering the optimal values found for the different parameters as fixed values, and using the simulation module provided by the software.

Parameter validation

As usual (Chuine *et al.*, 1999), the fitness of certain selected combinations was validated by examining the deviation (in days) between the observed and simulated F1 dates for flowering and the temperature data (location × year situations) which were not used previously for parameter determination. Thus, data collected at Angers, Bergerac and Nîmes before 1976 and after 2002, and at Gembloux, were used (including 29 and 23 F1 dates, respectively). The simulated F1 dates were obtained by using the simulation module on the basis of parameter values corresponding to the selected combinations and the temperature data files of the situations considered.

Statistical tools

'Pollenoscope' software automatically calculated both the R^2 significance of each maximised value, by Student's test, and the corresponding standard deviation (SD) for the simulated F1 date ($P = 0.05$). Statistica® software (Version 7.1) was used for additional tests. The non-parametric Kruskal-Wallis test was chosen for multiple comparisons of mean R^2 values that were not normally distributed. An analysis of variance (ANOVA) and mean comparisons by the Newman-Keuls test were used for normally distributed variables.

RESULTS

Variability within the observed dates for the F1 stage

In France, time-course changes in observed F1 dates showed that flowering times were different according to location and recording period, despite the usual yearly fluctuations (Figure 1). Firstly, clear differences in flowering time were recorded between the three regional series for the period 1976 – 2002. The F1 date was consistently earlier at Nîmes than at Angers, while, most of the time, an intermediate date was observed at Bergerac. The mean F1 dates over this period were 22 April at Angers, 14 April at Bergerac and 7 April at Nîmes. The same range of variability in mean dates was observed between the three locations when means were considered separately over the 1976 – 1988 sub-period (25 April, 19 April, and 11 April, respectively) and the 1989 – 2002 sub-period (18 April, 11 April, and 4 April, respectively). These data also underline the constant advance in flowering time in France from North-West to South-East as flowering was 6 – 8 d earlier at Bergerac

Fig. 1
Time-course changes in the observed date of the F1 stage in 'Golden Delicious' apple trees recorded at three representative locations in the French cropping area. Each date is expressed in calendar days from 1 January of the flowering year (n).

Chilling function involved	R^2 value[†]
No chilling	0.72 a[‡]
Linear (LC)	0.78 ab
Binary (BC)	0.85 ab
Exponential (EC)	0.85 b
Parabolic (PC)	0.88 b
Normal (NC)	0.88 b
Triangular (TC)	0.88 b
Sigmoïdal (SC)	0.89 b

[†]Mean of 18 values derived from independent tests, using independent data files (Angers 1976 – 1988, Angers 1989 – 2002, Bergerac 1976 – 1988, Bergerac 1989 – 2002, Nîmes 1976 – 1988, Nîmes 1989 – 2002).

[‡]Means followed by different lower-case letters are significantly different by the Kruskal-Wallis test ($P = 0.05$).

than at Angers, and 7 – 8 d earlier at Nîmes than at Bergerac. The F1 date was also consistently earlier over the period 1984 – 2006 at Angers than at Gembloux in Belgium, where the mean F1 date was the latest (data not shown).

On the other hand, time-course changes in observed F1 dates highlighted a trend toward more frequent early dates at all three locations in France. This trend was particularly clear for the longest series (Angers, 1963 – 2006; Figure 1). At all three locations, the mean F1 date over the 1989 – 2002 sub-period was 7 – 8 d earlier than over the previous 1976 – 1988 sub-period. This means that, since the end of the 1980s, flowering at Angers occurred at the same mean time (18 April) as over the previous period (1976 – 1988) further south at Bergerac (19 April). The same change was observed at Bergerac, since the end of the 1980s, where flowering occurred at the same mean time (11 April) as it previously did further south at Nîmes (11 April).

Maximising the R² value

The R^2 values corresponding to 2,376 tests were compared (12 input data files × 198 tests per file). All the tests using minimum temperature in the heat sub-model showed low or relatively low R^2 values. Thus, the comparison focussed on R^2 values given by tests involving minimum, mean, and maximum temperatures in the chilling sub-model, and only mean and maximum temperatures in the heat sub-model. This reduced the comparison to 1,584 tests (12 files × 132 tests per file).

Firstly, we explored the possible effect of the data file on the R^2 value, regardless of temperature functions involved in the chilling and heat sub-models (data not shown). The mean R^2 value was high (close to 0.80 or higher) for all data files. Data location had no effect. In particular, mean R^2 values were similar (0.81 – 0.85) for the three files corresponding to data from Angers, Bergerac and Nîmes covering the global period (1976 – 2002). The data recording period had no effect, as shown by similar mean R^2 values (0.79 – 0.83) for the three files including cumulative data of three locations over 1976 – 2002, 1976 – 1988, and 1989 – 2002. Thus, given that the data file had no effect, the analysis focussed on the effects of chilling and heat functions.

To do this, we compared the results provided by six independent data files: Angers 1976 – 1988, Angers 1989 – 2002, Bergerac 1976 – 1988, Bergerac 1989 – 2002, Nîmes 1976 – 1988, and Nîmes 1989 – 2002. The effect of the heat function appeared to be insignificant, although

higher mean R^2 values were obtained for the sigmoidal function than the linear function. Intermediate values were generally obtained for the exponential function (results not shown). Nevertheless, without any chilling involvement, the mean R^2 value reached relatively high levels for all three heat functions (0.69 – 0.75). When a chilling function was involved, this increased the mean R^2 values for the seven chilling functions regardless of the heat functions (Table IV). A significant increase in the mean R^2 value was obtained by using five chilling functions (exponential, parabolic, normal, triangular and sigmoidal). The significant increase reached 0.13 – 0.17, according to these chilling functions, in comparison with the mean R^2 value reached without chilling.

Model selection

Three criteria were considered; the goal being to select only a few reliable models. In line with Chuine *et al.* (1999), the first criterion was the percentage of variance (R^2) explained by the combination of sub-models constituting the model. Following our initial results which provided numerous combinations with relatively high R^2 values, we selected a pool of combinations which reached R^2 values of 0.85 or higher. These were selected from the combinations fitted with the F1 dates at all three locations covering the global period 1976 – 2002, in order to fit the parameter values of selected models on the basis of the largest date file (81 F1 dates). In this way, combinations were pre-selected, all involving chilling and heat functions (Table V). They also showed high R^2 values when tested separately with the data from Angers, Bergerac and Nîmes covering the global period 1976 – 2002 (results not shown).

Since the temperature functions were different (non-linear, non-nested, different number of parameters), it was inappropriate to compare combinations of chilling and heat functions by statistical tools. Thus, the second criterion was to consider the consistency of functions involved and parameters fitted on the basis of the biological knowledge of the flowering process (Fuchigami and Nee, 1987). Two elements were used: the chilling function involved, and the date of onset of the chilling effect (Oc parameter). Models involving chilling functions based on weighted efficiency of temperature (triangular, parabolic and normal functions) appeared more adequate, according to Richardson *et al.* (1974). Also, we preferentially selected models characterised by onsets of the chilling effect before the end of October, according to Bidabé (1967). Thus, the choice of models was limited to a few combinations. Unfortunately, all contained a relatively large number of parameters (six-to-seven).

The third criterion for model selection was the number of parameters, with the goal of selecting relatively simple models involving the lowest possible number. Finally, parameter consistency and number were considered together to select three models covering the diversity of best combinations (Table V).

Thus, we selected a model, called "Model 1", involving only five parameters (fitted from 81 F1 dates; $R^2 = 0.82$), despite the lower consistency of the chilling function (exponential) and Oc parameter (26 November). Two other models fitted from 81 F1 dates ($R^2 = 0.86$), called "Model 2" and "Model 3", were selected for the

Table V
Pre-selected combinations and associated parameters fitted with F1 dates at all three locations covering the global period 1976 – 2002

Function combination	Daily temperature involved[1]	R^2 value	Number of parameters	Onset of chilling	Chilling parameter Temperature[2]	Sum	Heat parameter Temperature[3]	Sum
EC × EH*	max., max.	0.82	5	26 Nov.	15	80	12	97
BC × SH	min., mean	0.85	6	1 Dec.	10	65	11 ; 5	55
SC × LH	min., mean	0.85	6	11 Nov.	4 ; 16	90	1	107
SC × LH	mean, mean	0.85	6	22 Oct.	2 ; 14	85	2	96
TC × LH	mean, mean	0.85	6	11 Nov.	2 ; 30	75	2	89
PC × LH	mean, mean	0.85	6	21 Nov.	1 ; 18	65	1	109
SC × EH	min., mean	0.85	6	17 Oct.	4 ; 10	100	9	81
SC × EH	mean, mean	0.85	6	21 Nov.	11 ; 2	95	9	86
SC × EH	max., max.	0.85	6	6 Nov.	15 ; 8	95	13	88
PC × EH	mean, mean	0.85	6	16 Nov.	2 ; 14	55	9	84
NC × EH	mean, mean	0.85	6	21 Nov.	1 ; 32	45	9	85
TC × EH	mean, mean	0.86	6	17 Oct.	1 ; 24	75	7	104
TC × EH**	max., max.	0.86	6	22 Oct.	6 , 20	60	12	98
PC × EH	max., max.	0.86	6	6 Nov.	4 , 20	65	13	87
NC × EH	max., max.	0.86	6	27 Oct.	7 , 28	60	12	101
SC × SH	mean, mean	0.85	7	17 Oct.	4 ; 12	90	12 ; 4	48
SC × SH	max., max.	0.85	7	12 Oct.	2 ; 16	75	16 ; 6	61
TC × SH	min., mean	0.85	7	27 Oct.	1 ; 30	90	11 ; 5	53
TC × SH	max., max.	0.85	7	22 Oct.	5 ; 24	65	16 ; 6	64
PC × SH	mean, mean	0.85	7	11 Nov.	1 ; 20	75	11 ; 4	54
PC × SH	max., max.	0.85	7	22 Oct.	1 ; 26	75	16 ; 5	30
PC × SH	min., mean	0.85	7	27 Oct.	1 ; 18	95	12 ; 5	48
NC × SH	min., mean	0.85	7	16 Nov.	1 ; 32	70	9 ; 4	67
NC × SH	mean, mean	0.85	7	16 Nov.	2 ; 28	50	14 ; 6	49
SC × SH	min., mean	0.86	7	17 Oct.	1 ; 14	95	12 ; 5	52
TC × SH***	mean, mean	0.86	7	17 Oct.	1 ; 24	75	16 ; 5	30

*, **, ***, Model 1, Model 2, and Model 3, respectively.
[1]Daily temperature used in chilling and heat functions, respectively.
[2]Temperature(s) used in chilling function (Tc or Tc ; Ic depending on function, see Table III).
[3]Temperature(s) used in heat function (Th or Th ; Ih depending on function, see Table III).

consistency of the chilling function (triangular) and Oc parameter (22 October and 17 October, respectively) despite the larger number of parameters (six and seven respectively). These three selected Models showed significant R^2 values and simulated F1 dates within ± 4.2 d (SD) for "Model 1", and ± 3.7 d for "Model 2" and "Model 3" ($P = 0.05$).

Validation of the selected models

The three selected Models predicted F1 dates with small deviations for most of the 23 years considered at Gembloux in Belgium (Table VI). Deviations of ≤ 3 d were recorded 17 times for "Model 1" and "Model 2", and 13 times for "Model 3". The greatest deviation was limited to 8 d for "Model 1" and 9 d for "Model 2", while it was 15 d for "Model 3". Deviations exceeding 10 d were recorded only three times for 'Model 3". In some cases, relatively poor validations were recorded for all three Models (1984; 1987). Similar promising results were obtained for validation tests done with the 29 location × year situations retained for this purpose within the data collected in France (results not shown). However, in this case, "Model 1" gave the lowest predictions compared to the other two Models. Thus, "Model 2" showed the best predictions of F1 date when the total number of validation tests was considered (52 location × year situations).

Chilling effect completion and duration

Time-course changes in the date of completion of the chilling effect (date of sum C completion) were simulated for the global period (1976 – 2002) using the mean date of estimated dates given by the three selected chilling sub-models for each year. A consistently later date was obtained at Nîmes than at Angers (Figure 2). Most of the time, an intermediate date was obtained at

Bergerac. The same results were obtained when the selected sub-models were used separately (data not shown). As the onset of the chilling effect (parameter Oc) was the same at all three locations, for each of the three Models, these simulations showed a gradient in the duration of the chilling effect in reverse regional order compared to the gradient of flowering times. Whatever sub-model was used, the mean duration of the chilling effect increased significantly ($P = 0.01$) from Angers to Nîmes, and to the same degree during the sub-periods 1976 – 88 and 1989 – 2002 (2 – 8 d between two adjacent locations; Table VII).

On the other hand, time-course changes in the completion of the chilling effect highlighted a trend toward more frequent late dates, as shown for Angers and Nîmes (Figure 2). The same trends were noticeable when the selected sub-models were used separately. Whatever sub-model was used, the mean duration of the
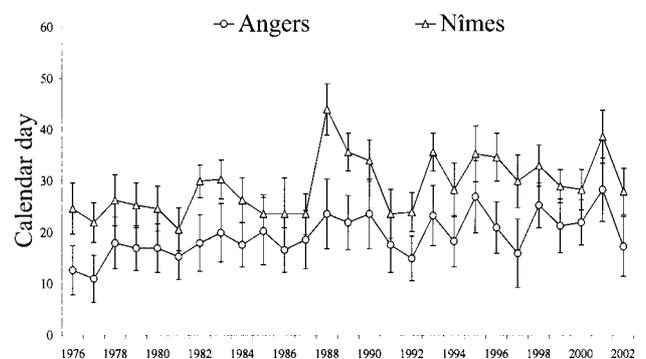
Fig. 2
Simulated dates for completion of the chilling effect (sum C) expressed in calendar days from 1 January of the flowering year (n) at two locations in France. Each simulated date is the mean of three estimated dates provided by the three selected chilling sub-models. Bars represent ± standard error of the mean.

TABLE VI
Deviation (in d) between the observed and simulated dates of F1 stage given by the three selected Models for flowering data collected at Gembloux in Belgium

Year	Model 1	Model 2	Model 3
1984	− 8	− 9	+ 7
1985	0	1	+ 3
1986	− 1	0	+ 4
1987	5	5	+ 11
1988	− 3	− 3	+ 3
1989	+ 3	− 2	+ 6
1990	− 3	− 1	+ 2
1991	0	− 1	+ 11
1992	− 2	− 4	+ 2
1993	+ 1	+ 1	+ 5
1994	−2	− 4	+ 1
1995	− 4	− 2	0
1996	− 4	+ 2	+ 15
1997	+ 1	+ 5	+ 5
1998	+ 5	− 3	− 1
1999	− 4	− 4	− 4
2000	+ 2	+ 1	+ 1
2001	− 1	− 1	− 2
2002	+ 1	+ 3	+ 1
2003	+ 1	+ 2	+ 6
2004	− 2	− 2	− 1
2005	− 1	− 1	0
2006	− 3	− 1	− 1

+, − ; earlier or later simulated date than observed date, respectively.

chilling effect presented higher values (by 3 – 5 d) for the sub-period 1989 – 2002 compared to simulated values for the sub-period 1976 – 1988, at all three locations. This increase was significant in most cases (*P* = 0.05; Table VII).

DISCUSSION
Improvement in the modelling of flowering time

A large number and a great diversity of combinations between chilling and heat functions appeared to explain a major part of the variance in flowering time (80% or more), estimated by the R^2 value. Different methodological aspects might explain such results, and contribute to improving the modelling of flowering time. First, the user-oriented 'Pollenoscope' software provides the advantage of an automatic search for optimal values for all parameters in each model tested; its power being based on a high-performance algorithm. We exploited this advantage by using a large and balanced variability of flowering data with regard both to geographical origin (large latitude gradient) and to observation period before and after the warming at the end of 1980s. Modelling improvements are commonly achieved without such an exhaustive parameter optimisation (Erez *et al.*, 1990). Another aspect might be the importance attached to the choice of heat functions. Preliminary tests led us to discard certain heat functions (binary, triangular, normal) due to results not being efficient at explaining the variance in flowering time

(data not shown). Conversely, the three heat functions selected (linear, exponential and sigmoidal) were probably an appropriate choice, as suggested by the relatively high values (69 – 75%) of variance explained when these functions were tested without chilling involvement. Numerous growing-degree models have demonstrated the advantages of a linear heat function, even if the limitations of its use were emphasised (Richardson *et al.*, 1974; Bonhomme, 2000; Zavalloni *et al.*, 2006; Normand and Léchaudel, 2006).

In apple and pear trees, the relevance of an exponential heat function has been demonstrated in various climatic conditions (Bidabé, 1967; Honjo *et al.*, 2006). A sigmoidal function was frequent in plant enzyme reactions and has been used in forest tree modelling (Chuine *et al.*, 1999). Our study also focussed on the effect of different chilling functions to improve prediction of the F1 date. Surprisingly, similar increases in the variance explained were reached using mathematical functions of varying degrees of complexity to simulate the chilling effect. Only the linear chilling function was of little interest. The increase in explained variance reached 13% for binary and exponential functions, and 17% for the sigmoidal function, although these functions were relatively inconsistent with physiological knowledge of the chilling effect. Conversely, the increases in explained variance by using parabolic, normal and triangular functions appeared to be quite similar (16%), although such functions consider the existence of optimal and efficient temperatures that are the main physiological characteristics of the chilling effect (Fuchigami and Nee, 1987).

In the past, the modelling of flowering time in fruit tree species has been improved through a more accurate account of chilling mechanisms (Richardson *et al.*, 1974). In particular, possible chilling enhancement and negation by high temperatures, during dormancy breaking, have been demonstrated in peach trees (Erez *et al.*, 1979a) and apple trees (Young, 1992). Following these findings, a relatively complex model was proposed for peach trees (Erez *et al.*, 1990). Nevertheless, our results emphasise that the most physiologically correct models are not necessarily the most accurate (Schwartz, 1999). To develop an operational tool to forecast the flowering time, we selected only three models which took account of the explained variance, the consistency, and the number of fitted parameters. The accuracy of predictions of F1 dates by these models, for such diverse conditions as the climates in the South and West of France and a relatively cold climate in Belgium, appear promising, but this must be confirmed by tests under broader environmental conditions (Bidabé, 1967; Erez *et al.*, 1990). The models selected could be improved by

TABLE VII
Mean number of days from onset of the chilling effect (date Oc) to the date of completion of the chilling effect (sum C) estimated by the three selected chilling sub-Models at three locations in France for the sub-periods 1976 – 1988 and 1989 – 2002

Location	Model 1			Model 2			Model 3		
	1976 – 88	1989 – 2002	Period effect	1976 – 88	1989 – 2002	Period effect	1976 – 88	1989 – 2002	Period effect
Angers	50 a[†]	54 a	*	82 a	85 ab	*	103 a	108 ab	*
Bergerac	55 ab	59 b	*	89 bc	93 cd	*	106 ab	110 b	ns
Nîmes	59 b	64 c	*	93 cd	97 d	ns	111 b	116 c	*
Location effect	**	**		**	**		**	**	

*, **; significant effect at *P* = 0.05 and *P* = 0.01 respectively (ANOVA). ns; not significant.
[†]Means followed by different lower-case letters are significantly different by the Newman-Keuls test (*P* = 0.05).

adapting the panel of parameters to regional gradients (time parameters) and genetic differences in tree phenology (temperature and sum parameters).

Impact of recent warming on dormancy breaking and flowering time

The trend toward an advance in flowering time, as exhibited by 'Golden Delicious' apple trees in France, is consistent with phenological observations recorded in natural vegetation as well as in fruit trees in other countries in the northern hemisphere (Chmielewski *et al.*, 2004; Honjo *et al.*, 2006). This advance was clearly highlighted when mean values for F1 dates were compared between the sub-periods 1976 – 1988 and 1989 – 2002. Such agreement with the temperature increase at the end of the 1980s allows us to consider this advance in flowering to be a perceptible impact of climate warming on apple phenology. The mean range in flowering advance was equal to the mean range of flowering time differences between adjacent cropping areas. Thus, as a result of the warmer period (1989 – 2002) in France, 'Golden Delicious' is now flowering at the northern location of Angers within the same time range it was previously flowering further south, at Bergerac. The same relative change was observed between Bergerac and Nîmes. At present, such a regional impact does not matter (except for cross-pollination), although the mechanism by which climate warming exerts its influence must be investigated (Atkinson and Taylor, 1990).

Interestingly, the three models selected simulated converging results regarding time-course changes in the duration of the chilling effect. Longer durations of chilling were simulated in the warmer climate of Nîmes, in contrast to shorter durations in the colder climate of Angers, while intermediate durations were simulated at Bergerac. These consistent results would tend to indicate that the three models are reliable for exploring the possible impact of climate warming on the duration of chilling, which is rarely considered in the literature. The three models simulated longer mean durations of chilling for the warmer period (1989 – 2002) compared with simulations for the colder period (1976 – 1988) at all locations. This suggests a general increase in the duration of dormancy-breaking affected by global warming.
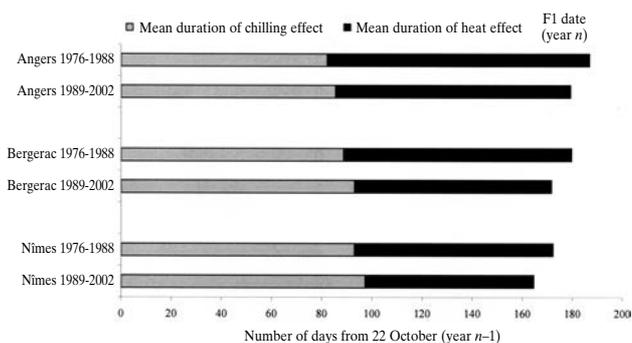
FIG. 3
Sequential time representation of the chilling and heat effects from the onset date of chilling (date Oc) to the observed F1 date in 'Golden Delicious' apple trees, according to location and sub-period. The mean duration of the chilling and heat effects were estimated by using the parameters fitted in chilling sub-Model 2. In accordance with this simulation, chilling effects were cumulated from 22 October (date Oc) in the year ($n – 1$) before the flowering year (n).

Similarly, lower amounts of chilling since the end of 1970s were recorded in the United Kingdom (Sunley *et al.*, 2006).

Finally, our study suggests that global warming exerted two simultaneous and opposing effects in France between 1976 – 2002: a longer mean duration (by 3 – 5 d) to satisfy the chilling requirement and a shorter mean duration (by 10 – 13 d) to satisfy the heat requirement, explaining the observed mean advance in flowering time (7 – 8 d), regardless of regional differences (Figure 3). A more pronounced impact of climate warming on heat completion than on chilling completion would be in agreement with the greater increase in warming from January to April (the active growth phase) than from October to January (the dormancy-breaking phase), as observed in other countries (Chmielewski and Rötzer, 2001).

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