



A Unified Model for Budburst of Trees

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Accurate plant phenology (seasonal plant activity driven by environmental factors) models are vital tools for ecosystem simulation models and for predicting the response of ecosystems to climate change. Since the early 1970s, efforts have concentrated on predicting phenology of the temperate and boreal forests because they represent one-third of the carbon captured in plant ecosystems and they are the principal ecosystems with seasonal patterns of growth on Earth (one-fifth of the plant ecosystems area). Numerous phenological models have been developed to predict the growth timing of temperate or boreal trees. They are in general empirical, nonlinear and non-nested. For these reasons they are particularly difficult to fit, to test and to compare with each other. The methodological difficulties as well as the diversity of models used have greatly slowed down their improvement. The aim of this study was to show that the most widely used models simulating vegetative or reproductive phenology of trees are particular cases of a more general model. This unified model has three main advantages. First, it allows for a direct estimation of (i) the response of bud growth to either chilling or forcing temperatures and (ii) the periods when these temperatures affect the bud growth. Second, it can be simplified according to standard statistical tests for any particular species. Third, it provides a standardized framework for phenological models, which is essential for comparative studies as well as for robust model identification.

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Introduction

Vegetation phenology, the study of recurring vegetation cycles and their connection to climate, plays a prominent role in regional or global ecosystems simulation models (Running & Hunt, 1993) as well as coupled biosphere/atmosphere general circulation models (GCMs) (Sellers, 1996). Different phenological models have been developed to predict animal phenology (Podolsky, 1984) and plant phenology (Landsberg, 1974; Sarvas, 1974; Cannell & Smith, 1983; Kobayashi & Fuchigami, 1983a, b; Murray *et al.*, 1989; Hänninen, 1990; Moorman *et al.*, 1990;

Hunter & Lechowicz, 1992; Kramer, 1994b; Chuine *et al.*, 1999). Plant phenological models are used to simulate the length and the timing of the growing season which controls the dynamics of carbon and water cycles (White *et al.*, 1997). They are also used to predict the response of tree performance of climate changes which may alter competitiveness, geographic range and density of populations (Kramer *et al.*, 1996; Kramer & Mohren, 1996). However, available phenological models are found not to be very effective for these tasks (Kramer *et al.*, 1996) and consequences of a global climate change on phenology remain controversial (Hänninen, 1991, 1995, 1996; Hänninen *et al.*, 1993; Kramer, 1994a).

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Phenological models, used to simulate leaf unfolding, i.e. the start of the growing season, are based on the response of bud growth to forcing temperatures (temperatures that force growth during spring when dormancy has been released) and/or to chilling temperatures (temperatures that break dormancy). This response has been described with different types of mathematical functions, derived from experimental results on particular species (Sarvas, 1974; Cannell & Smith, 1983). Such functions have been used in different models predicting either reproductive (dates of flowering) or vegetative (leaf unfolding) phenology for several temperate tree species (deciduous or evergreen) (Robertson, 1968; Landsberg, 1974; Sarvas, 1974; Cannell & Smith, 1983; Kobayashi & Fuchigami, 1983a, b; Murray *et al.*, 1989; Hänninen, 1990; Moorman *et al.*, 1990; Hunter & Lechowicz, 1992; Kramer, 1994b; Chuine *et al.*, 1999). These models are nonlinear and non-nested within each other (Chuine *et al.*, 1998) so that classical comparative tests are impossible (likelihood ratios or *F* tests). As a result, phenological models have been rarely compared with each other (but see Hunter & Lechowicz, 1992; Kramer, 1994a, b; Chuine *et al.*, 1999). The lack of standardization in phenology modelling and the difficulty in comparing and testing model predictions, have greatly slowed down the improvement of phenological models despite the wide literature on this subject.

In the present study, I show that former existing models are particular cases of a more general model (unified model). This unified model allows for a direct estimation of (i) the type of response of bud growth to chilling and forcing temperatures, (ii) the period when these temperatures affect bud growth, (iii) the relationship between the amount of forcing units required for budburst and the achieved amount of chilling units experienced, and (iv) the species specific parameters. Finally, the unified model provides a statistical framework for standard model identification, comparison and simplification.

Generalization of the Phenological Models

RESPONSES OF BUD GROWTH TO TEMPERATURE

Phenological models assume that leaf unfolding is regulated by temperature and is induced by

a period with chilling temperatures followed by a period with forcing temperatures (Nienstaedt, 1974; Richardson *et al.*, 1974). The simplest models consider that only forcing temperatures cumulated from a fixed date to a given sum explain the dates of budburst [Thermal Time model (Cannell & Smith, 1983) also named Spring Warming model (Hunter & Lechowicz, 1992), ForcSar and ForcTT models (Chuine *et al.*, 1999)]. More sophisticated models also consider the effect of chilling temperatures, which are involved in the break of buds dormancy during the autumn/winter. This latter family of models includes mainly the *Parallel* model (Landsberg, 1974; Hänninen, 1990; Kramer, 1994b), the *Sequential* model (Hänninen, 1990; Kramer, 1994b), the *Alternating* model (Murray *et al.*, 1989), the *Deepening Rest* model (Kobayashi *et al.*, 1982), the *Four-Phase* model (Vegis, 1964), the *SeqSar* model and the *ParSar* model (Chuine *et al.*, 1999). In addition to breaking dormancy, chilling temperatures have also been shown to accelerate bud growth from the state of quiescence (i.e. when dormancy is broken) to the state of burst (Nelson & Lavender, 1979; Cannell & Smith, 1983; Murray *et al.*, 1989; Hänninen *et al.*, 1993), i.e. the more chilling temperatures are received, the less forcing temperatures are subsequently needed to reach budburst. This negative relationship between the state of forcing and the state of chilling has been taken into account in different models (Cannell & Smith, 1983; Murray *et al.*, 1989; Kramer, 1994b; Chuine *et al.*, 1999).

The state of forcing (S_f) is described as a daily sum of rates of forcing

$$S_f = \sum_{t_1}^{t_b} R_f(x_t) \quad (1)$$

(with t_1 the starting date of cumulating, t_b the date of budburst and x_t the mean temperature of the Julian day t). Rates of forcing are either growing degree-days (Murray *et al.*, 1989) [Fig. 1(a)],

$$R_f = GDD(x_t) = \begin{cases} 0 & \text{if } x_t < Tb_1 \\ x_t - Tb_1 & \text{if } x_t \geq Tb_1 \end{cases}, \quad (2)$$

(with Tb_1 the degree-day base temperature) or a sigmoid function of the temperature (Kramer,

1994b; Hänninen, 1990) [Fig. 1(a)],

$$R_f = SF(x_t) = \begin{cases} 0 & \text{if } x_t < 0, \\ \frac{28.4}{1 + e^{-0.185(x_t - 18.4)}} & \text{if } x_t \geq 0. \end{cases} \quad (3)$$

Numerical values of eqn (3) were fitted by Hänninen (1990) using Sarvas (1974) experimental results on the Finnish birch seedlings, but are probably species-specific and, thus, might not be fixed *a priori*.

The state of chilling (S_c) is described as a daily sum of rates of chilling,

$$S_c = \sum_{t_0}^{t_1} R_c(x_t) \quad (4)$$

(with t_0 the starting date of dormancy, t_1 the date of quiescence and x_t defined as above). Rates of chilling are either chilling days (Murray *et al.*,

1989) [Fig. 1(b)],

$$R_c(x_t) = CD(x_t) = \begin{cases} 1 & \text{if } x_t < Tb_2, \\ 0 & \text{if } x_t \geq Tb_2 \end{cases} \quad (5)$$

(with Tb_2 the chilling day base temperature) or a triangular function of the temperature (Kramer, 1994b; Hänninen, 1990) [Fig. 1(b)],

$$R_c(x_t) = TC(x_t)$$

$$= \begin{cases} 0 & x_t \leq -3.4 \text{ or } x_t \geq 10.4, \\ \frac{x_t + 3.4}{T_0 + 3.4} & -3.4 < x_t \leq T_0, \\ \frac{x_t - 10.4}{T_0 - 10.4} & T_0 < x_t < 10.4 \end{cases} \quad (6)$$

with T_0 the optimal chilling temperature. As for eqn (3), numerical values in eqn (6) were fitted by Hänninen (1990) using Sarvas (1974) experimental results on the Finnish birch seedlings.

Although very similar, the different functions describing the response of bud growth to temperature have always been used per pair: CD with GDD (*Alternating model*) and TC with SF (*Deepening Rest, Four Phase, Sequential or Parallel model*). GDD is very similar to SF , especially when the base temperature (Tb_1) is close to 5°C [Fig. 1(a)]. SF is a sigmoid function of the type

$$\frac{1}{1 + e^{b(x-c)}} \quad (7)$$

(with $b < 0$ and $c > 0$). Coefficient 28.4 of the numerator in eqn (3) is of little use since forcing units are arbitrary. If parameter b is positive and high, then the sigmoid function is equivalent to CD , and parameter c is equivalent to the base temperature (Tb_2). In conclusion, the functions SF , GDD and CD are particular cases of eqn (7). The function TC cannot be a particular case of eqn (7), but can be a particular case of the function type,

$$\frac{1}{1 + e^{a(x-c)^2 + b(x-c)}} \quad (8)$$

Depending on the values of the parameter set (a, b, c), eqn (8) describes a sigmoid curve and is equivalent to the function TC for a particular parameter set. Therefore, CD , TC , SF and GDD are particular cases of eqn (8), called in the

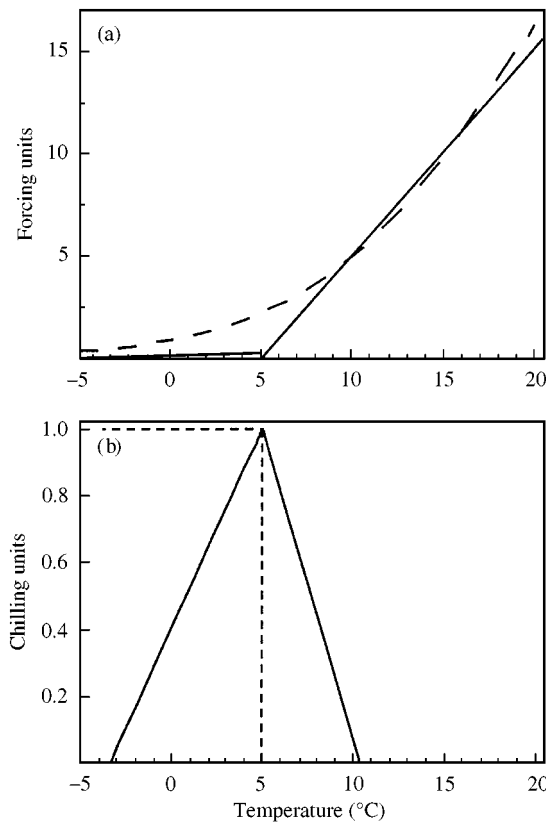


FIG. 1. Responses of the bud growth to forcing and chilling temperatures. Four types of response are presented: (a) (---) SF ; (—) GDD . (b) (—) TC ; (---) CD .

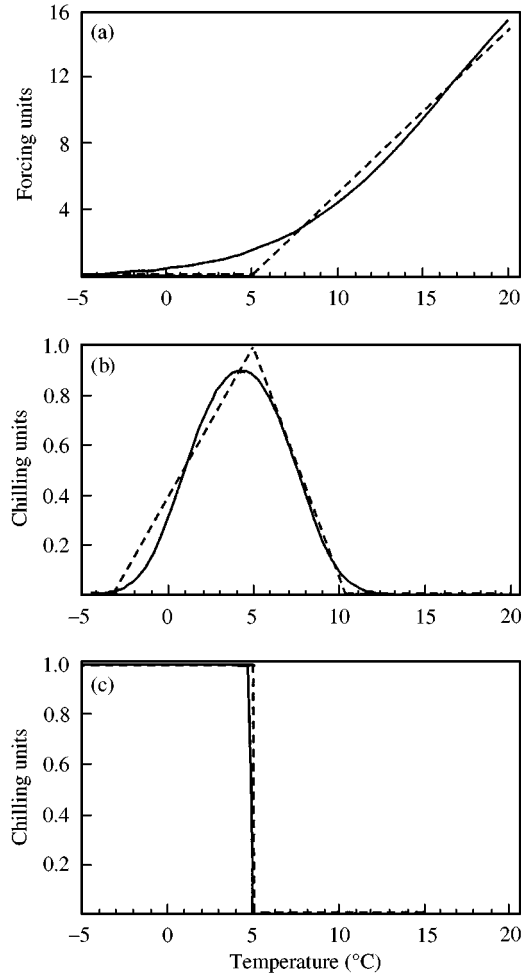


FIG. 2. CF functions fitted to the four types of response to temperature presented in Fig. 1. (a) GDD and CF with fitted parameter values $a = 0.002975$, $b = 0.15587$, $c = -19.56$: (—) CF ; (---) GDD . (b) TC and CF with fitted parameter values $a = 0.07613$, $b = 0.0000086$, $c = -4.2$: (—) CF ; (---) TC . (c) CD and CF with fitted parameter values $a = 0.5$, $b = 50$, $c = -5$: (—) CF ; (---) CD .

following text CF (C for chilling and F for forcing). The particular parameter set (a, b, c) for which CF is equivalent to CD , SF , TC and GDD are shown in Fig. 2.

A UNIFIED PHENOLOGICAL MODEL

Phenological models are defined by three main assumptions: the type of response of bud growth to temperature, the dependency of chilling and forcing temperatures effect, and the time windows when buds are assumed to be receptive to chilling and forcing temperatures. In the unified

model, the CF function was chosen to describe the response of bud growth to temperature. I call $CF_f(0, b_f, c_f, x_t)$ the response to forcing temperatures and $CF_c(a_c, b_c, c_c, x_t)$ the response to chilling temperatures. Since a negative relationship between the state of forcing and the state of chilling has been shown experimentally (Cannell & Smith, 1983; Murray *et al.*, 1989; Heide, 1993; Myking & Heide, 1995), the critical state of forcing needed for leaf out (F^*) was described as a function of the total state of chilling achieved (C_{tot}) as follows:

$$F^* = w e^{k C_{tot}} \quad (9)$$

with $w > 0$ and $k < 0$.

Three different periods during which forcing and chilling temperatures can affect bud growth can be distinguished (Fig. 3): (i) chilling temperatures (ct) active from the onset of dormancy (t_0) to the onset of quiescence (t_1), and forcing temperatures (ft) active from t_1 to budburst (t_2); (ii) ct active from t_0 to $t > t_1$ and ft active from t_1 to t_2 ; (iii) ct active from t_0 to $t > t_1$ and ft active as soon as chilling units have been accumulated (t'_0) to t_2 . t_0 can be fixed to 1st September because chilling temperatures do not occur before this time in the temperate zone and buds are already dormant at the end of summer. Let t_1 be the day when S_c (state of chilling) becomes higher than C^* (critical state of chilling) and t'_0 the day when S_c becomes strictly positive. The three different cases can thus be described with two parameters: C^* and t_c ,

$$t_1 \text{ such as } \sum_{t_0}^{t_1} R_c(x_t) = C^*, \quad (10)$$

$$t_c \text{ such as } \sum_{t_0}^{t_c} R_c(x_t) = C_{tot}, \quad (11)$$

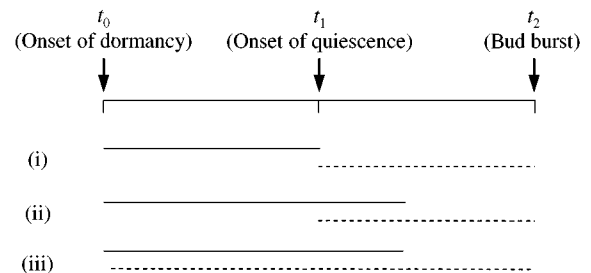


FIG. 3. The four different assumptions concerning the period when bud growth is affected by forcing and chilling temperatures: (—) chilling period; (---) forcing period.

The three different cases can be formalized as follows:

- (i) $t_c = t_1$ and $C^* > 0$,
- (ii) $t_c > t_1$ and $C^* > 0$,
- (iii) $t_c > t'_0$ and $C^* \approx 0$.

From the above considerations, a unified model with nine parameters ($a_c, b_c, c_c, b_f, c_f, w, k, C^*$ and t_c) can be defined as follows. The response to chilling temperature is defined by $CF_c(a_c, b_c, c_c, x_t)$ and the response to forcing temperature by $CF_f(0, b_f, c_f, x_t)$. Forcing units are accumulated as soon as a critical state of chilling (C^*) is reached, and the critical state of forcing needed to burst (F^*) is a function of the total state of chilling reached at t_c ($F^* = we^{kC_{tot}}$).

Application of the Unified Model

METHOD

The unified model was fitted using reproductive phenological data (dates of flowering) from Montpellier, France, described in Chuine *et al.* (1998, 1999), for two main reasons. First, phenological models can be used to predict reproductive phenology (Boyer, 1973; Chuine *et al.*, 1998, 1999) as well as vegetative phenology (Cannell & Smith, 1983; Kramer, 1994b; Hänninen, 1990; Chuine & Cour, 1999). Second, this data set has already been used to fit and test phenological models, so that the fitted unified model could be compared to the best model found previously for each species. The unified model was fitted using the flowering dates of *Aesculus hippocastanum* L., *Buxus sempervirens* L., *Olea europaea* L., *Platanus acerifolia* Willd., *Taxus baccata* L. and *Ulmus minor* Mill. in Montpellier from 1974 to 1992.

Adjustments were realized by minimizing the least-squares function in the parameters space using a simulated annealing method (Chuine *et al.*, 1998). The optimization procedure used was the Metropolis algorithm. The name “simulated annealing” derives from a thermodynamic principle on the manner in which metals cool and anneal or liquids freeze and crystallize. This principle is described by the Boltzmann probability distribution, $\text{Prob}(E) \approx \exp(-E/kT)$:

a system in thermal equilibrium at temperature T has its energy probabilistically distributed among energy states (E). Metropolis *et al.* (1953) first used this principle for numerical calculations and optimization algorithms. Considering that a set of parameter values is analogous to a thermodynamic state (S) of a system, and the sum of square is analogous to the energy (E) of that system, the range of possible states (S) is explored by randomly changing from S_1 and S_2 according to the following rule. The probability of transition from S_1 to S_2 is 1 if $S_2 < S_1$, and equals $\exp(-(S_2 - S_1)/rT)$ if $S_2 > S_1$, with r and T parameters of the procedure decreasing with the number of steps. An infinite decrease of T leads to the convergence of the system towards its state of minimum energy (Press *et al.*, 1989). The first set of parameters is arbitrary, and then all the parameters are changed by a random amount. The Marsaglia procedure (Marsaglia *et al.*, 1990) was used as the generator of random changes. This generates a random walk, which tends to avoid local minima and converge toward the global minimum. Since the number of local minima of the least-squares function of phenological models is very high, global searches were performed several thousand times with few iterations and beginning each time with random parameter values in the parameter ranges, so that the initial conditions did not influence the search of the global minimum. Then, a classical global search was performed starting at the best point found so far with more iterations than previously.

Percentages of variance explained by the model was computed and compared with that of the best models found for each species in Chuine *et al.* (1999) adjusted with the same data set.

ANALYSIS OF THE MODEL ESTIMATES

Percentages of variance explained by the model varied between 53 and 92% depending on the species (Table 1). However, the fitted unified model did not explain significantly more variance than the null model (model with the mean of the observations as single parameter) for two species (*Aesculus hippocastanum* and *Taxus baccata*). This is due to the high number of parameters fitted compared with the number of data used to fit them. Three main conclusions arise from the

TABLE 1
Estimates of the unified model for each species and percentages of variance explained

	a_c	b_c	c_c	b_f	c_f	w	k	C^*	t_c	t_1		R^2
										Mean	S.E.	
<i>Aesculus hippocastanum</i>	0.191	1.18	-13.36	-4.09	-9.59	87.6	-5.0E-8	10.6	93	67.2	9.9	0.68ns
<i>Buxus sempervirens</i>	3.045	-9.21	-5.39	-1.49	-10.90	15.6	-9.0E-8	26.9	195	155.6	16.2	0.78*
<i>Olea europaea</i>	1.268	-12.45	-3.07	-0.29	-14.61	48.7	-1.0E-8	65.7	244	135.5	11.6	0.90†
<i>Platanus acerifolia</i>	0.670	-24.00	11.81	-0.62	-8.33	31.9	-2.1E-5	170.0	176	172.0	1.3	0.75*
<i>Taxus baccata</i>	0.100	-24.51	9.14	-1.02	-4.76	33.3	-3.0E-5	143.0	210	143.0	0.0	0.53ns
<i>Ulmus minor</i>	0.624	18.39	-10.60	-0.66	-7.28	21.0	-9.0E-8	54.1	195	136.8	6.7	0.80*

Note: t_1 = date when C^* is reached (vary from year to year). S.E. = standard error. ns = non-significant. t_c as Julian date from 1st September.

* $p < 0.05$.

† $p < 0.001$.

analysis of the unified model estimates. First, forcing temperatures were never accumulated before a minimum state of chilling was reached (Table 1). Second, the slope of the negative exponential curve was zero (k always inferior to $-10E-4$ and usually inferior to $-10E-7$, see Table 1), so that F^* is constant and equal to w whatever be the variations of C_{tot} . Therefore, the negative relationship does not improve the model predictions for the six species studied, and the parameter set (w, k) can be replaced by ($F^*, 0$) (fixed amount of forcing units required for bud-burst every year). Third, chilling temperatures do not explain the inter-annual variability in the dates of flowering of *Platanus acerifolia* and *Taxus baccata*. This is shown by the means and standard errors of t_1 , the date when C^* is reached. Each year, t_1 equals C^* , or almost, because CF_c always equals 1 over the temperature range of these species. It also means that each year the response of bud growth to forcing temperature starts at almost the same time.

MODEL SIMPLIFICATION

The Unified model can be simplified into two different models, *UniChill* requiring seven parameters ($a_c, b_c, c_c, b_f, c_f, C^*, F^*$) and *UniForc* requiring four parameters (b_f, c_f, F^*, t_1). Both models predict that flowering occurs at the state of forcing, S_f , reaches a particular value F^* . In *UniChill*, S_f is a sum of forcing units cumulated from the fixed date when C^* is reached. In *UniForc*, S_f is a sum of forcing units cumulated from the date t_1 . According to the previous analysis of the unified model estimates, *UniChill* should be effective for predicting the phenology of *Aesculus*, *Buxus*, *Olea* and *Ulmus* and *UniForc* should be effective to predict the phenology of *Platanus* and *Taxus*.

The *UniChill* model led to identical percentages of variance explained to the unified model that were all significant except for *Taxus* (Table 2). Since this model explains as much variance as the unified model using less degrees of freedom, it is a better model than this latter whatever the species. The *UniForc* model led to high and significant percentages of variance explained except for *Aesculus* (Table 3). According to F tests, the *UniChill* model was significantly

TABLE 2
Estimates of the UniChill model for each species and percentages of variance explained

	a_c	b_c	c_c	b_f	c_f	C^*	F^*	R^2
<i>Aesculus hippocastanum</i>	0.191	1.18	− 13.36	− 4.09	− 9.59	10.6	87.6	0.68*
<i>Buxus sempervirens</i>	3.045	− 9.21	− 5.39	− 1.49	− 10.90	26.9	15.6	0.78†
<i>Olea europaea</i>	1.268	− 12.45	− 3.07	− 0.29	− 14.61	65.7	48.7	0.90‡
<i>Platanus acerifolia</i>	0.670	− 24.00	11.81	− 0.60	− 8.24	170.0	31.9	0.75†
<i>Taxus baccata</i>	0.100	− 24.51	9.14	− 1.04	− 4.72	142.9	33.3	0.53ns
<i>Ulmus minor</i>	0.418	18.38	− 10.60	− 0.66	− 7.28	54.1	21.0	0.80†

Note: ns = non-significant.

* $p < 0.05$.

† $p < 0.01$.

‡ $p < 0.001$.

TABLE 3
Estimates of the UniForc model for each species and percentages of variance explained

	F^*	b_f	c_f	t_1	R^2
<i>Aesculus hippocastanum</i>	149.8	− 15.00	− 4.60	76	0.29ns
<i>Buxus sempervirens</i>	16.5	− 4.53	− 10.40	167	0.67†
<i>Olea europaea</i>	85.7	− 0.25	− 9.97	126	0.84‡
<i>Platanus acerifolia</i>	32.0	− 0.60	− 8.39	170	0.72‡
<i>Taxus baccata</i>	34.0	− 0.83	− 4.80	141	0.50†
<i>Ulmus minor</i>	18.8	− 0.61	− 7.59	140	0.68‡

Note: ns = non-significant.

* $p < 0.05$.

† $p < 0.01$.

‡ $p < 0.001$.

better than the UniForc model only for *Aesculus*, but in every other cases the UniForc model was better than the UniChill and the unified model.

RESPONSE OF BUD GROWTH TO TEMPERATURE

The estimates of the response to chilling and forcing temperatures in the UniChill model and the unified model are identical (Tables 1 and 2). The optimal forcing temperature (for which $SF = 1$) varies a lot among species, from 10°C for *Aesculus* [model UniChill, Fig. 4(a)] to 25°C for *Olea* (model UniForc, Fig. 5), but is, on an average, between 10 and 15°C. The slope of the response to forcing temperature varies also a lot among species: it is very smooth for *Olea*, which seems able to respond to temperature from 0 to 20°C (Fig. 5) and very steep for *Aesculus* and *Buxus* which both seem to respond as soon

as temperature reaches 10°C [Fig. 4(a)]. The response to chilling temperature takes place between 0 and 15°C except for *Taxus* and *Platanus* for which chilling temperatures do not explain variance. The temperature range varies a lot among species. It can be very narrow (*Aesculus*, *Buxus*), as in the *Parallel* model or the *Sequential* model, broad (*Olea*), or very broad, as in the *Alternating* model, with a threshold temperature below which temperature has no effect (*Ulmus*) [Fig. 4(a)].

Discussion and Conclusion

COMPARISON WITH OTHER PHENOLOGICAL MODELS

The analysis of the unified model estimates is consistent with the former studies on phenological models comparison. First, estimates show

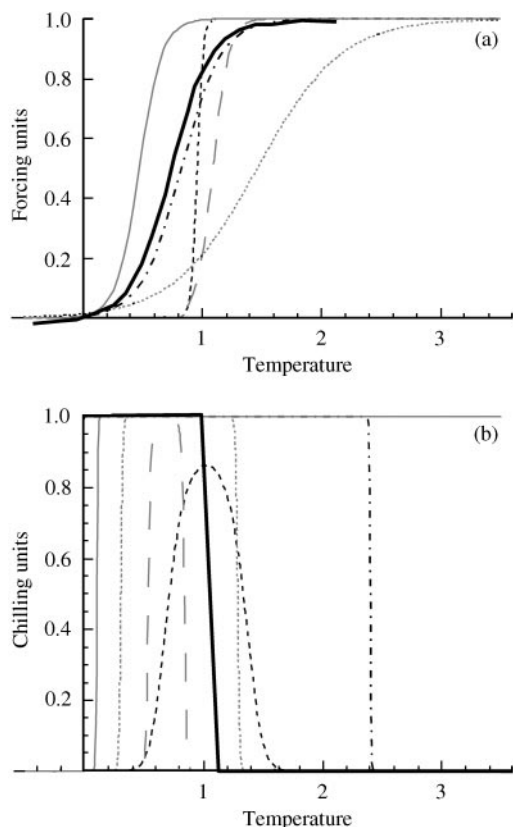


FIG. 4. Fitted responses to temperature of *Aesculus*, *Buxus*, *Olea*, *Platanus*, *Taxus* and *Ulmus*: (a) responses to the forcing temperature of the *UniChill* model and the unified model (same responses), (b) responses to the chilling temperature of the *UniChill* model: (---) *Aesculus*; (—) *Buxus*; (.....) *Olea*; (-.-.-) *Platanus*; (—) *Taxus*; (—) *Ulmus*.

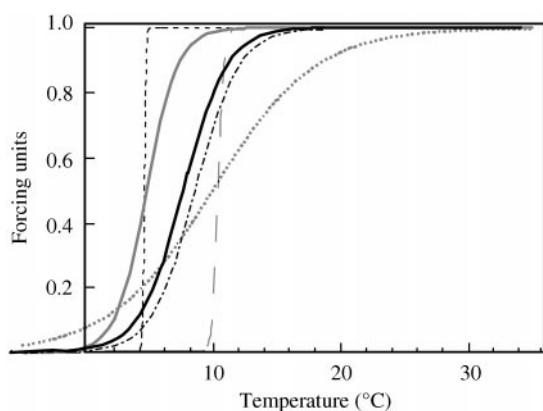


FIG. 5. Fitted responses of bud growth to forcing temperature of the *UniForc* model: (---) *Aesculus*; (—) *Buxus*; (.....) *Olea*; (-.-.-) *Platanus*; (—) *Taxus*; (—) *Ulmus*.

that forcing temperatures play a prominent role compared to chilling temperatures in phenology modelling. Previous studies on phenology

modelling have shown that the *Spring Warming* (or *Thermal Time*), *ForcSar* or *ForcTT* models, which involve only forcing temperatures, give generally the highest percentages of variance explained regarding their number of parameters (Hunter & Lechowicz, 1992; Chuine *et al.*, 1998, 1999). Such models give, however, better predictions for late flowering species or populations living in southern Europe than for early flowering species or populations living in northern Europe because the latter species experience longer chilling conditions and shorter forcing conditions. Second, estimates show that bud growth does not respond to forcing temperatures before a minimum amount of chilling units is reached. However, the unified model fitted to the data set of Montpellier does not show that the negative exponential relationship between F^* and C_{tot} improves the models fit as it has been shown in a previous study (Chuine *et al.*, 1999). This result is discussed in the next paragraph.

Percentages of variance explained by the *UniChill* and *UniForc* models are usually higher than those found for other phenological models fitted to the same data set (Chuine *et al.*, 1998, 1999). However, their accuracy of prediction should be tested with external data and for different places before using them for phenology predictions.

RELATIONSHIP BETWEEN STATE OF CHILLING AND STATE OF FORCING

The relationship $F^* = we^{k C_{tot}}$ has been shown experimentally (Cannell & Smith, 1983; Murray *et al.*, 1989; Heide, 1993; Myking & Heide, 1995; Chuine & Cour, 1999) and used in the *Alternating* model (Cannell & Smith, 1983; Kramer, 1994a; Murray *et al.*, 1989), *SeqSar* model and *ParSar* model (Chuine *et al.*, 1999). The use of this relationship in phenological models has been shown to improve the model effectiveness (Chuine *et al.*, 1999), but is found useless in our analysis using the unified model. Two hypotheses can be put forward to explain this result.

First, as pointed out by Chuine and Cour (1999), this relationship may be an artefact due to a wrong estimation of the response to temperature. The specific responses to chilling and forcing temperatures and the period when they take place are unknown, mainly because we are

unable to record development stages prior to leaf unfolding. These responses and the period when they take place have been tracked indirectly assuming particular types of response and particular parameter values. At the end of the bud development, a decreasing amount of forcing temperatures was usually observed following an increasing amount of chilling temperatures. However, part of the “assumed” chilling temperatures may have been inactive and part of the “actual” forcing temperatures may not have been taken into account, so that the relationship observed may be artefactual. The unified model does not assume a particular type of response nor particular parameter values, so that we expect an unbiased estimation of the responses to temperature contrary to the previous models. If this expectation is verified, it is likely that the relationship was previously an artefact due to wrong estimation of these responses.

Second, as pointed out by Chuine *et al.* (1999), F^* does not vary a lot from one year to another in a single place especially in a warm climate like in Montpellier. Information is thus lacking for a correct fit of the relationship $F^* = we^{kC_{tot}}$. There should be scope for an estimation of this relationship if population from different origins were used since the range of C^* and F^* would be expanded. However, such method requires to check for no genetic differentiation of phenology among the populations used to fit the model.

RESPONSE OF BUD GROWTH TO TEMPERATURE

The fitted responses to chilling temperature of the *UniChill* model are consistent with the experimental background, i.e. either an optimal chilling temperature (Sarvas, 1974) or a threshold temperature (Cannell & Smith, 1983; Kramer, 1994a; Murray *et al.*, 1989) does exist. However, optimum and threshold values vary with species and are not fixed as usually assumed [Fig. 4(b)]. The fitted responses of bud growth to forcing temperatures, generally vary greatly from one species to another (slope or inflexion) [Figs 4(a) and 5].

The unified model shows that the timing of flowering of *P. acerifolia* does not require chilling temperatures to be explained. This result is supported by different studies. First, the *Spring*

Warming model, which involves only forcing temperatures, has been shown to be particularly effective to predict the dates of flowering of this Mediterranean species (Hunter & Lechowicz, 1992; Chuine *et al.*, 1998, 1999). Second, some experiments have shown that the phenology of *P. acerifolia* (vegetative or reproductive since both take place at the same time) was not significantly influenced by the chilling temperatures in contrast to most temperate-zone tree species (Chuine & Cour, 1999). This type of response to temperature may be the result of an adaptation to the climate of the provenance of this species, the Middle East (Davis, 1982). This result is particularly important for species originated from the Middle East and the Tropics. Such responses have also been shown for populations of *Acer rubrum* from Florida (Perry & Wang, 1960), which flower earlier when not exposed to chilling temperature than when exposed to an increasing chilling period, contrary to northern populations. A lack of true chilling requirements has also been reported also for other species or races of species (Perry, 1971).

The optimal chilling temperature and the range of chilling temperature are different from those measured by Sarvas on Finnish birch seedlings and are different for each species considered. In particular, the response function can be always optimal below a certain threshold temperature or can be optimal for a wider range of temperature than assumed in the Parallel model or Sequential model (Hänninen, 1990; Kramer, 1994b).

THE USEFULNESS OF A UNIFIED MODEL

A unified model helps in finding the best model for each species and allows for a logical search of the best model by considering in turn the different assumptions underlying the phenological models. Until now, every model proposed in the literature had to be fitted to data to find the best one. The *CF* function allows a direct estimation of the type of response of bud growth to temperature which may be one of the previously used (*GDD*, *SF*, *CD*, *TC*) or a different one. The multiple formalization of this response was one of the reasons for multiple models. Assumptions concerning the response of bud growth to temperature and the period of its occurrence are likely

to influence the results of phenological models. This has been illustrated by Myking (1997), who showed that contrary to the previous experimental results, variable chilling temperatures were not less efficient than constant temperatures in regulating the break of dormancy. Myking showed that previous results were incorrectly analysed due to misleading assumptions concerning the periods of temperature (chilling and forcing) effects on bud growth.

Many unknown factors remain in our understanding of tree phenology. For instance, chilling and forcing temperature ranges overlap and we still do not know to what point bud growth remains affected by chilling temperatures or begins to be affected by forcing temperatures. Models can improve our understanding of biological processes if their assumptions are not *a priori* too much constrained. The use of the unified model should help in this task.

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