

Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling

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ABSTRACT

Classical budburst models (Spring Warming, Sequential, Parallel and Alternating) are unable to fully predict external data, partly because of the methods of optimization used to adjust them. The purpose of this study was to examine different assumptions of budburst models and select those which are best supported by the data, defining new models able to predict external data. Eight models, each differing in one assumption, were fitted and tested using external data. The dataset used to test the models was deduced from aeropalynological data at two stations in France. The results show that some of the models proposed are able to accurately predict external dates of flowering of most of the studied species. The assumptions of those models have been individually tested and shown to improve the models accuracy. Robust estimates of the best predictor models of 12 tree species are presented. The analysis of hypothetical provenance transfer of two species, *Buxus sempervirens* and *Platanus acerifolia*, between the two study sites, shows that *P. acerifolia* estimates are similar in both environments whereas *B. sempervirens* estimates are variable. This result, which agrees with the genetic characteristics of both species, shows that local adaptation of phenology can also be studied through modelling approaches.

Key-words: budburst models; dates of flowering; external validity; local adaptation of phenology to climate.

INTRODUCTION

Since the early 1970s, phenology has been recognized to play a prominent role in the modelling of ecosystem productivity (Lieth 1971). Models predicting the timing of budburst of trees are now widely used to predict the consequences of a global warming on tree phenology (Hänninen 1991; Hänninen *et al.* 1993; Kramer 1994a; Hänninen 1995; Kramer 1995; Hänninen *et al.* 1996; Hänninen 1996)

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but also on terrestrial carbon productivity (Lieth 1971; Kramer, Friend & Leinonen 1996; Kramer & Mohren 1996). Phenology modelling requires four essential steps (i) a model definition (ii) a data collection (iii) adjustments of the model to the data, and (iv) tests of the model hypotheses.

Different models predicting the dates of budburst or flowering have been described in the literature. Temperature is recognized as being the main variable which regulates the timing of budburst. Some models consider only the action of forcing temperatures (Thermal Time model (Cannell & Smith 1983) also named Spring Warming model (Hunter & Lechowicz 1992)), while others consider also the action of chilling temperatures (Parallel model (Landsberg 1974; Hänninen 1990; Kramer 1994b); Sequential model (Sarvas 1974; Hänninen 1990; Kramer 1994b); Alternating model (Murray, Cannell & Smith 1989)).

Four types of phenological data can be distinguished: (i) observations of trees in natural or planted populations (Cannell & Smith 1983; Nizinski & Saugier 1988; Hunter & Lechowicz 1992; Kramer 1994a,b; Hänninen, Linkosalo & Hari 1995) (ii) observations of clones in different environments (phenological gardens) (Schnelle & Volkert 1974; Kramer 1995) (iii) greenhouse experiments (Perry & Wang 1960; Nelson & Lavender 1979; Mauget 1983; Murray *et al.* 1989; Hänninen *et al.* 1993; Heide 1993; Cecich, Kang & Chalupka 1994; Hänninen 1995; Myking & Heide 1995), and (iv) measurements of pollen emissions in the atmosphere indicating the timing of flowering of populations (Boyer 1973; Richard 1985; Andersen 1991; Frenguelli *et al.* 1992; Chuine, Cour & Rousseau 1998).

The adjustment of models to these data first requires an adapted optimization algorithm that ensures correct convergence. Classical optimization algorithms are in general unable to converge (Kramer 1994b), leading to unreliable estimates. This nonconvergence is primarily due to the fact that the likelihood functions of budburst models have many local maxima in the parameter space considered. Unreliable estimates have been shown to be partly responsible for the lack of external validity of budburst models, i.e. they do not accurately predict external data. Even if the appropriate optimization algorithm is used, classical models (Thermal Time, Sequential, Parallel, Alternating)

are still unable to predict external data with accuracy (Chuine *et al.* 1998). Testing of external validity is particularly important for budburst models which are used to make predictions in climatic conditions that differ from those used to fit them (e.g. in a globally warmed climate).

Long time series of phenological data of the same location are very rare and we are often compelled to use different data sampled in different locations to adjust and test phenological models. However, this method can lead to wrong model estimates and wrong tests if the phenology of the species studied is locally adapted to climate. A trait is locally adapted if it is significantly different from one population to another (differentiated populations) and if this difference is adaptive. Both conditions have been proven for the phenology of some herbaceous species (Reinartz 1984; Fox 1989; Dominguez & Dirzo 1995). Transfer experiments on tree seedlings (Perry & Wang 1960; Kuser & Ching 1980; Billington & Pelham 1991; Ducouso, Guyon & Krémer 1996; Li *et al.* 1997a,b) have demonstrated that populations of some tree species were differentiated for their phenology. Such transfer experiments do not lead however, to a clear statement of a local adaptation of phenology to climate. Some transplants show earlier flushing of southern-origin seedlings (Ducouso *et al.* 1996), others show a earlier flushing of northern-origin seedlings (Mergen 1963; Beuker 1994; Falusi & Calamassi 1996), or show no difference between origins for the same species studied (Lieth 1974). Differentiation of tree phenology remains a part of phenology modelling that has not been extensively studied. Beyond its interest for evolutionary biology, its study for phenology modelling is necessary to assess the conditions of application of the models for natural populations.

The aims of this paper are (1) to propose models capable of predicting the timing of flowering of trees using external data, i.e. data not used to adjust the model; (2) to test the different hypotheses involved in budburst models; and (3) to compare models estimates of a species in two different environments in order to estimate the differentiation between both populations. The only variable used in the models is temperature. Models involving the action of photoperiod have not been considered for two main reasons. First, photoperiod is unlikely to influence inter-annual variation of any variable in a single place since it does not vary from one year to another. Second, experiments in controlled environmental conditions show that contrary to many annual plant species, flowering does not appear to be under photoperiodic control in most woody perennials (Sedgley & Griffin 1989).

Classical models, although different, share some hypotheses which have never been tested against each other. The eight models proposed in this study are a combination of three different types of hypotheses: (1) hypotheses about the coupling of forcing and chilling temperatures; (2) hypotheses about the period during which forcing and chilling temperatures influence bud growth; and (3) hypotheses about the functions of response to temperature. The models have been constructed in order

to test each hypothesis independently. The eight models are compared to one another and to the classical models (Thermal Time, Sequential, Parallel and Alternating models) on the basis of their external validity. Adjustments of the models and tests are performed using the dates of flowering of tree populations in two locations in France. The conditions needed to obtain reliable models and estimates are discussed. Hypothetical transfers of the species shared by both locations are analysed to estimate their differentiation for the timing of flowering.

MATERIALS AND METHODS

Data

Pollen data

The dates of flowering were extracted from aeropalynological data. These data consist of pollen concentrations in the atmosphere as weekly averages from two localities in France, one near Montpellier (43.3°N, 3.6°E) and another near Lyon (45.6°N, 5.2°E), over 19 (1974–92) and 16 (1982–97) years, respectively. Pollen was trapped on filters fixed vertically on a wind-cock which continuously orientated the filters to the wind. The filters were exposed throughout the year and were changed every week. The density of pollen deposited on the filters was estimated for each identified taxon according to Cour (1974). Using data of the amount of wind that passed through the filters and was measured by an anemometer, the concentration of pollen per cubic metre air for each taxon was calculated. This method allowed the determination of the temporal variation in pollen concentrations of each taxon present in the atmosphere.

Pollen identification was made to the genus level since the pollen morphology of the different possible species of a plurispecific genus is too similar to be discriminated. In the present study, only the monospecific genera were considered. The identification of the species concerned was made using regional flora and vegetation maps (1/200000). The species chosen for the study were: *Aesculus hippocastanum* L., *Alnus glutinosa* Gaert., *Betula verrucosa* Ehrh., *Buxus sempervirens* L., *Carpinus betulus* L., *Castanea sativa* Mill., *Corylus avellana* L., *Olea europaea* L., *Platanus acerifolia* Willd., *Taxus baccata* L., *Ulmus minor* Mill. and *Ulmus montana* L. Two species were common to Lyon and Montpellier: *B. sempervirens* and *P. acerifolia*.

Dates of flowering

From the annual pollen spectrum of each species the week of maximum concentration was determined. The middle-day of this week was assumed to be the mean date of anthesis of the population of each species around the pollen sampling station (approximately 50 km around for the principal pollen taxa, Cour & Villemur 1985). The models tested here were used to predict the dates of anthesis which corresponded either to the date of flowering of the male flowers (*A. glutinosa*, *B. verrucosa*, *C. betulus*, *C. sativa*, *C. avellana*, *P. acerifolia*, *T. baccata*), or to

the date of the male maturation stage of the bisexual species (*A. hippocastanum*, *B. sempervirens*, *O. europaea*, *U. minor*, *U. montana*).

Meteorological data

At both sampling stations pollen traps were placed in the meteorological station near the airport (Frejorgues, 6 km south of Montpellier and Bron, 2 km east of Lyon). Daily minimum and maximum temperatures, wind speed, and weekly precipitation were recorded. The average temperature of each day was estimated to be the mean of the daily minimum and maximum temperatures. The speed of the wind was used to calculate the weekly pollen concentration in the atmosphere. The weekly precipitation were used to control whether the pollination was disturbed by unfavourable meteorological conditions which would bias the dates of flowering. In favourable meteorological conditions, pollen peak occurs over 1 week. If during the week of pollination, it rained more than 20% of the time, the atmosphere was cleaned from pollen (Richard 1985) so that the pollen peak was bimodal and did not correspond exactly with the week of theoretical maximal pollination. When rain was the cause of a bimodal peak, the week between the two peaks was taken as the week of maximum pollen abundance as it would have been if it had not rained. Data were not recorded if the cause of a bimodal peak was not obvious.

Models

Eight different models were proposed. Each model is empirical; that is, it simulates a physiological process, and is a combination of three types of hypotheses. The models

proposed are used to predict the dates of flowering but they could be also used for the prediction of vegetative budburst. In the following text they will be referred to as budburst models.

Four hypotheses can be tested independently in comparing two models differing only by one hypothesis. The hypotheses tested are:

- (i) Does the use of chilling temperatures improve the accuracy of budburst models?
- (ii) Has the negative relationship assumed between state of forcing and state of chilling to be taken into account in the models?
- (iii) Do the forcing and chilling rate functions as defined in Hänninen 1990, i.e. a sigmoidal function and triangular function of the temperature, better account for the action of temperature than degree-days and chilling days?
- (iv) How do the period of forcing and the period of chilling overlap?

Two models (ForcSar and ForcTT, Forc for forcing, Sar for Sarvas and TT for Thermal Time) consider only the action of the forcing temperatures. Both assume that budburst occurs when a critical state of forcing (F^*) is reached, the state of forcing being a sum of daily rate of forcing (R_f), which is a function of temperature only. Model ForcSar, the simplest, has one parameter: F^* , and R_f is a sigmoid curve (Sarvas 1974 in Hänninen 1990) (see Table 1). Model ForcTT has one additional parameter: T_b , the base temperature and considers R_f as degree-days ($x_t - T_b$, x_t being the daily temperature). ForcTT model is equivalent to the Thermal time model (Cannell & Smith 1983) without the t_0 parameter (starting date of the sum of temperatures).

Table 1. Forc models assumptions

y	date of flowering
x_t	daily mean temperature (°C)
$R_f(x_t)$	forcing rate function
F^*	critical value of state of forcing for the transition from quiescence to flowering
t_0	1 January
T_b	base temperature
Model ForcSar	

y such as $f_c(y) = F^*$

$$f_c(t) = \sum_{t_0}^t R_f(x_t)$$

$$R_f(x_t) = \frac{28.4}{1 + e^{-0.185(x_t - 18.4)}} \quad x_t > 0^\circ\text{C} \text{ (from Sarvas 1974 in Hänninen 1990)}$$

Model ForcTT

y such as $f_c(y) = F^*$

$$f_c(t) = \sum_{t_0}^t R_f(x_t)$$

$$R_f(x_t) = \begin{cases} 0 & \text{if } x_t < T_b \\ x_t - T_b & \text{if } x_t \geq T_b \end{cases}$$

Degree-days are accumulated when the temperature exceeds T_b as soon as photoperiod increases (1 January).

Models SeqTT, SeqSar, Par1TT, Par1Sar, Par2TT and Par2Sar (Par for Parallel and Seq for Sequential) also consider the action of chilling temperatures involved in the break of bud dormancy during the autumn/winter. Chilling temperatures are also considered here to be involved in the speeding up of the bud growing during the forcing in the spring as in the Alternating model (Cannell & Smith 1983; Murray *et al.* 1989; Kramer 1994b): the more chilling temperatures, the less forcing temperatures are needed. Thus, budburst occurs when the critical state of forcing dependent of the state of chilling is reached. Rates of chilling and forcing can be considered as chilling days and degree-days or as specific functions of the temperature. Each model is a combination of two types of hypotheses (see Table 2). First, a hypothesis defining the period of action of chilling and forcing. Three cases are distinguished (A1, A2 or A3, Table 2): chilling temperatures active from the onset of dormancy to the onset of quiescence (A1) or to the flowering (A2 and A3) and forcing temperatures active from the onset of quiescence (A1 and A2) or the onset of dormancy (A3) to budburst. Second, a hypothesis defining the modelling of the forcing and chilling rates. Two cases are distinguished: degree-days and chilling days (B1) or forcing and chilling units which are a function of the temperature (B2).

Parameter estimation

Models were fitted using the least square method (for details see Chuine *et al.* 1998). The function $f(x) = \sum [r_i(x)]^2$ is minimized in the parameter space \tilde{x} , where $r_i(x)$ is the residual ($r_i(x) = d_i(x) - d_{i\text{obs}}$), $d_i(x)$ is the predicted date

and $d_{i\text{obs}}$ the observed date of the year i . Parameter estimations were performed using the Metropolis algorithm (1953), a simulated annealing method. The accuracy of the estimates found by this algorithm was checked by replication. The quality of the convergence was measured by the standard error on each parameter for 10 repetitions.

Tests

Internal and external validity

Parameters were fitted using 9 years of the Montpellier dataset (odd years from 1975 to 1991). The internal validity of each model was measured by the percentage of variance explained by the model computed with the data used to fit it (R^2), and tested for each species separately using F -tests. The external validity (Lebreton *et al.* 1992) was measured by the percentage variance explained by the model computed with data not used to fit it (10 even years from 1974 to 1992). External validity was tested as follows: the percentage variance explained was considered as a coefficient of determination and its associated correlation coefficient was compared to critical values for correlation coefficients (Rohlf & Sokal 1969).

Since the models are nonlinear and non-nested (i.e. each model is not a submodel of the other), they were compared using their external validity. The external validity of pairs of models that differed for one hypothesis were compared for each species to choose the most accurate hypotheses. The Thermal Time, Sequential, Parallel and Alternating models have also been used for these comparisons since they have already been fitted with the same dataset in Chuine *et al.* (1998). Since no test exists to combine the comparisons made for different species and for different

Table 2. Seq and Par models assumptions

y	date of flowering
x_t	daily mean temperature ($^{\circ}\text{C}$)
$R_f(x_t)$	forcing rate function
$R_c(x_t)$	chilling rate function
S_f	state of forcing
S_c	state of chilling
C^*	critical value of state of chilling for the transition from rest to quiescence
F^*	critical value of state of forcing for the transition from quiescence to flowering
t_0	date of onset of rest
t_1	date of onset of quiescence
T_b	base temperature
T_o	optimal temperature of the rate of chilling
a, b	constants ($a > 0, b < 0$)

Models	Hypotheses	d.f.	Parameters
SeqTT =	A1 + B1	4	T_{b1}, T_{b2}, a, b
SeqSar =	A1 + B2	4	T_o, a, b, t_1
Par1TT =	A2 + B1	5	$T_{b1}, T_{b2}, a, b, t_1$
Par1Sar =	A2 + B2	4	T_o, a, b, t_1
Par2TT =	A3 + B1	4	$C^*, T_{b1}, T_{b2}, a, b$
Par2Sar =	A3 + B2	5	C^*, T_o, a, b

For every models the date of flowering y occurs when a critical state of forcing units is attained (F^*), that is y such as $S_f(y) = F^*$.

This critical state of forcing (F^*) units is related to the state of chilling as follows also for every model: $F^* = a \exp(b S_c(y))$.

Table 2. *Continued.*

$$C^* = S_c(t_1)$$

A hypotheses 'period of chilling and forcing'

A1:

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

$$S_f(t) = \sum_{t_1}^t R_f(x_t)$$

A2:

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

$$S_f(t) = \sum_{t_1}^t R_f(x_t)$$

A3:

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

$$S_f(t) = \sum_{t_0}^t kR_f(x_t)$$

with $\begin{cases} k = \frac{S_c}{C^*} & S_c < C^* \\ k = 1 & S_c > C^* \end{cases}$

B hypotheses 'forcing and chilling modelling'

B1:

$$R_c(x_t) = \begin{cases} 0 & x_t \geq T_{b_1} \\ 1 & x_t < T_{b_1} \end{cases}$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_{b_2} \\ x_t - T_{b_2} & x_t < T_{b_2} \end{cases}$$

B2:

$$R_f(x_t) = \begin{cases} 0 & x_t \leq 0 \\ \frac{28.4}{1 + e^{-0.185(x_t - 18.4)}} & x_t > 0 \end{cases}$$

$$R_c(x_t) = \begin{cases} 0 & x_t \leq -3.4 \text{ or } x_t \geq 10.4 \\ \frac{x_t + 3.4}{T_o + 3.4} & -3.4 < x_t \leq T_o \\ \frac{x_t - 10.4}{T_o - 10.4} & T_o < x_t < 10.4 \end{cases}$$

Model SeqTT: t_1 such as $(t_1 > 1 \text{ January}) \cap (S_c > 2) \cap (\text{for } i = 1-4, x_{t+i} > T_{b2})$

models, a hypothesis was selected if it was the most accurate for every species or most of them.

The selection of the best predictor model for each species in the Montpellier dataset was carried out by comparison of the external validity of each model. The model explaining the highest percentage of variance on external data was chosen as the best predictor. Models selected using the

Montpellier dataset were fitted with 9 years of the Lyon dataset (1982–90) and tested with the data for the remaining 7 years (1991–97) in order to test if the models of highest external validity in Montpellier were the same in Lyon.

For each species, the estimates of the best predictor model were fitted using 16 years of data in both datasets, as 16 years was the maximum number that could be chosen to

allow comparisons between estimates of the species shared by both localities. The 16 years chosen in Montpellier were 1977–92, so that 11 years were common to both datasets.

Estimate comparisons of the two species in both localities

Estimates of the best predictor model for *P. acerifolia* and *B. sempervirens* were fitted independently using 16 years of both the Lyon and Montpellier datasets. *Platanus acerifolia* Willd. (*Platanus orientalis* L. × *Platanus occidentalis* L.) has been introduced in Europe to be used as a roadside tree essentially. Its propagation is only achieved from cuttings in nurseries (Ricaud *et al.* 1995). Thus, the genetic diversity of *P. acerifolia* is likely to be much less important than the genetic diversity commonly reported in natural population of forest trees. In contrast, *B. sempervirens* is a shrub that is naturally propagated. We expect that the genetic part of phenology of *P. acerifolia* is the same from one population to another whereas it may be different for *B. sempervirens*. The comparison of Montpellier and Lyon estimates of these species permits the estimation of the genetic differences between both populations of each species. Since estimates

cannot be compared independently to each other because of the interdependence of some parameters, the dates predicted by Lyon's estimates and Montpellier's temperatures were compared with the dates observed in Montpellier. In the same way, dates predicted by Montpellier's estimates and Lyon's temperatures were compared with the dates observed in Lyon.

RESULTS

Model selection

Each model has internal validity (i.e. the percentage of variance explained by the model is very high) whatever the species, with the exception of model Par2Sar for *U. minor* (Table 4). The percentage of variance explained ranges from zero to 93%, with a mean of 58% when averaging over species and models.

Models ForcTT, Par1TT, Par2TT showed significant external validity for only two species, and models ForcSar, SeqTT for three species (Tables 3 and 4). Models SeqSar and Par1Sar showed relatively high significant external

d.f.	ForcSar 1	ForcTT 2	TT 3	Seq 4	Par 5	Alt 4
<i>A. hippocastanum</i>	0.23 ns 0.34 *	0.74 *	0.84 ns	0.82 ns	0.48 ns	0.88 *
<i>B. sempervirens</i>	0.36 ns 0.03 ns	0.55 ns 0.46 *	0.58 ns 0.58 **	0.72 ns	0.45 ns	0.66 ns 0.69 ***
<i>O. europaea</i>	0.70 ns 0.80 ***	0.84 ** 0.82 ***	0.90 * 0.64 ***	0.91 * 0.33 *	0.74 ns 0.64 ***	0.78 ns 0.67 ***
<i>P. acerifolia</i>	0.65 ns 0.43 *	0.67 *	0.90 * 0.65 ***	0.79 ns	0.81 *	0.73 ns
<i>U. minor</i>	0.47 ns –	0.72 *	0.75 ns	0.83 ns	0.57 ns	0.76 ns

Significance level: ns, non significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; d.f. = degree of freedom.

Table 3. Percentage of variance explained (R^2) by the Forc models considering the dataset of Montpellier. In the first line R^2_{int} , the percentage of variance explained of the data used to fit the models. In the second line R^2_{ext} , the percentage of variance explained of the external data. Results obtained with the same dataset are recalled for the Thermal Time (TT), Sequential (Seq), Parallel (Par) and Alternating (Alt) models (from Chuine *et al.* 1998)

d.f.	SeqTT 4	SeqSar 4	Par1 TT 5	Par1Sar 4	Par2TT 5	Par2Sar* 5
<i>A. hippocastanum</i>	0.12 ns 0.34 *	0.51 ns 0.24 ns	0.76 ns	0.64 ns 0.28 ns	0.79 ns	0.15 ns 0.38 *
<i>B. sempervirens</i>	0.45 ns 0.03 ns	0.51 ns 0.61 ***	0.61 ns	0.42 ns 0.62 ***	0.54 ns 0.32 *	0.43 ns 0.65 ***
<i>O. europaea</i>	0.76 ns 0.80 ***	0.93 * 0.63 ***	0.86 ns 0.67 ***	0.91 * 0.68 ***	0.47 ns 0.35 *	0.73 ns 0.75 ***
<i>P. acerifolia</i>	0.54 ns 0.43 *	0.89 * 0.69 ***	0.90 ns	0.89 * 0.71 ***	0.62 ns	0.00 ns 0.86 ***
<i>U. minor</i>	0.32 ns –	0.67 ns 0.38 *	0.72 ns	0.64 ns 0.49 *	0.37 ns	–

Significance level as in Table 3. –, means that the model was worse than the mean date of flowering; , values in italic do not take into account the unpredictable years.

Table 4. Percentage of variance explained by the different Seq and Par models using the Montpellier dataset. In the first line R^2_{int} , in the second line R^2_{ext}

validity for almost all the species. On the contrary, the Par2Sar model was unable to predict the date of flowering for some years for every species except *O. europaea*, because the chilling requirements (C^*) could not be fulfilled in those years.

The value of coefficient k (potential of buds to respond to forcing temperature) used in the Par2Sar and Par2TT models was only dependent of a critical state of chilling (C^*) and not of K_m (always fitted to be zero in both models), the minimum potential of unchilled buds to respond to forcing temperatures (Hänninen 1990; Kramer 1994b).

Hypotheses selection

Table 5 shows, for each hypothesis tested, which models were compared and the results of their external validity comparisons. The results can be summarized as follows. (i) Chilling temperatures coupled with forcing temperatures better predicted the timing of flowering than forcing temperatures alone, except for *B. sempervirens*. (ii) The exponential negative relationship between S_f and S_c increased the accuracy of the models. (iii) The action of the temperatures was better supported by chilling and forcing rate function as defined by Hänninen (1990), than by sums of degree-days and number of chilling days. (iv) The period during which chilling temperatures were active on bud growth differed among species. However, chilling temperatures could be active from the onset of dormancy to the onset of quiescence or to the onset of budburst. In contrast, forcing temperatures were only active from the onset of quiescence to the onset of budburst.

Considering these results, two models (SeqSar and Par1Sar) among the eight models tested, could be kept for further investigations to find the most accurate budburst model for any tree species. The Thermal Time and Alternating models could also be kept since they were the best predictor models for *P. acerifolia* and *B. sempervirens*, respectively; as well as the ForcSar model which with only one parameter showed a high explained sum of squares on external data.

Cross validation of the best predictor models

Each of the five best predictor models fitted with 9 years of the Lyon dataset had internal validity, varying from 27 to 98%, with a mean of 77%. The external validity varied from 2 to 97%, when it existed, i.e. in 84% of the cases (Table 6), and had a mean of 58% when averaging over species and models. Considering the species shared by both localities, the best predictor models were not exactly the same in Montpellier and in Lyon according to external validity. The best predictor models of *P. acerifolia* were still the SeqSar and Thermal Time models, plus the Alternating model in Lyon and the Par1Sar model in Montpellier. On the contrary, the best predictor models of *B. sempervirens*, which were the Alternating, SeqSar and Par1Sar models in Montpellier, were the SeqSar and ForcSar models in Lyon.

Table 5. For each hypothesis tested, the models compared, the comparison of the percentage of variance explained on external data (R^2_{ext}) and the result of the comparison are given

	Models compared		R^2_{ext} comparison		Conclusion
	with similar d.f.	with different d.f.	R^2_{ext} values comparison per species	number of significant R^2_{ext} values	
(i)	ForcSar/SeqSar, Par1Sar ForcTT/SeqTT, Par1TT	ForcSar < SeqSar, Par1Sar *A,h Par1TT < ForcTT < SeqTT *B,s	ForcSar < SeqSar, Par1Sar *A,h Par1TT < ForcTT < SeqTT *B,s	ForcSar < SeqSar, Par1Sar Par1TT < ForcSar < SeqTT	Hypothesis selected: chilling coupled with forcing temperatures Hypothesis selected: $F^* = a e^{(b \cdot S)}$
(ii)	SeqSar/Seq	Par2Sar/Par	SeqSar > Seq Par2Sar > Par	SeqSar > Seq Par2Sar = Par	
(iii)	SeqTT/SeqSar	ForcTT/ForcSar Par1TT/Par1Sar Par2TT/Par2Sar	SeqTT < SeqSar *A,h, O,e no trends	SeqTT < SeqSar ForcTT < ForcSar	Sarvas chilling and forcing rate functions more accurate than sums of degree-days and number of chilling days
(iv)	SeqSar/Par1Sar SeqSar/Par1Sar/Par2Sar	SeqTT/Par2TT SeqTT/Par1TT/Par2TT	Par1TT < Par1Sar Par2TT < Par2Sar *B,s SeqSar < Par1Sar SeqTT < Par2TT *B,s	Par1TT < Par1Sar Par2TT > Par2Sar SeqSar = Par1Sar SeqTT > Par2TT Par2Sar < Par1Sar = SeqSar SeqTT > Par2TT > Par1TT	Chilling temperatures active from onset of dormancy to onset of quiescence or to budburst Forcing temperatures active from onset of quiescence to budburst

* = except for; B.s, *B. sempervirens*; A,h, *A. hippocastanum*; U,m, *U. minor*; O,e, *Olea europaea*; d.f., degree of freedom.

	Thermal Time	Alternating	ForcSar	SeqSar	Par1Sar
<i>A. glutinosa</i>	0.82 *	0.82 ns	0.72 **	0.88 *	0.82 ns
	–	0.25 ns	–	–	0.22 ns
<i>B. verrucosa</i>	0.98 ***	0.92 *	0.83 ***	0.98 ***	0.97 ***
	0.94 ***	0.97 ***	0.86 ***	0.95 ***	0.91 ***
<i>B. sempervirens</i>	0.75 ns	0.74 ns	0.54 *	0.84 ns	0.85 ns
	0.54 *	–	0.75 **	0.92 ***	0.48 ns
<i>C. betulus</i>	0.95 ***	0.89 *	0.84 ***	0.94 *	0.93 *
	0.78 ***	0.95 ***	0.90 ***	0.88 **	0.83 ***
<i>C. sativa</i>	0.53 ns	0.73 ns	0.35	0.76 ns	0.60 ns
	0.46 *	0.38 *	0.02	–	0.02 ns
<i>C. avellana</i>	0.88 *	0.70 ns	0.63 *	0.89 **	0.97 **
	0.77 **	–	0.31	0.74 ***	0.67 *
<i>P. acerifolia</i>	0.88 **	0.93 *	0.59 *	0.92 *	0.93 *
	0.86 ***	0.88 ***	0.72 **	0.88 ***	0.81 ***
<i>S. nigra</i>	0.76 *	0.76 ns	0.27	0.87 *	0.87 *
	0.14 ns	–	0.48 *	0.32 ns	0.25 ns
<i>T. baccata</i>	0.96 ***	0.86 ns	0.35	0.59 ns	0.58 ns
	0.76 **	0.03 ns	0.83 ***	0.27 ns	0.40 ns
<i>U. montana</i>	0.74 ns	0.77 ns	0.58 *	0.76 ns	0.60 ns
	–	0.06 ns	0.44	0.24 ns	0.38 ns

Significance level as in Table 3.

Estimates

Comparison between estimates was made for the common best predictor model in both localities, which was the SeqSar model. The estimates of *P. acerifolia* were very similar, whereas *B. sempervirens* estimates were different (Table 7). Since the sets of estimates cannot be easily compared, the Montpellier estimates of both species were used to predict their dates of flowering in Lyon to see if the predictions were similar to the predictions obtained with Lyon estimates. In the same way, Lyon estimates were used to predict their dates of flowering in Montpellier. Figure 1 shows the linear regression of the predicted dates against the observed dates using both kind of estimates. The Lyon estimates provided more accurate predictions in Lyon than were provided by the Montpellier estimates in Montpellier: $R^2 = 0.93$ against 0.81 for *P. acerifolia* and 0.91 against 0.69 for *B. sempervirens*.

Concerning *P. acerifolia*, the regressions show that there was no difference between estimates fitted in Lyon and estimates fitted in Montpellier since the predictions were similar. Moreover, the regression slope was similar to the bisector. It should be noticed that there were about 13 d of difference between flowering in Montpellier and flowering in Lyon for *P. acerifolia*, and about 10 d for *B. sempervirens*. Thus, the predictions of *P. acerifolia* show that the 13 d of difference are solely due to the differences of temperatures between the two localities, situated at a distance of 256 km. In contrast, the Montpellier estimates of *B. sempervirens* did not accurately predict flowering in Lyon and vice versa (Fig. 1). Montpellier estimates predicted flowering 20 d later on average than those observed in Lyon, and Lyon estimates predicted flowering 20 d earlier on average than those observed in Montpellier.

Table 6. Percentage of variance explained for the Lyon dataset. At the first line: R^2_{int} , at the second line: R^2_{ext}

However, the estimates still explain the inter-annual variability of the dates of flowering in both cases.

DISCUSSION

Models comparison

The comparison of the accuracy of the different models for the different species shows that there is no consensus model; i.e. no single model that accurately predicts the dates of flowering of every species. This point was already illustrated by the studies of Hunter & Lechowicz (1992) and Chuine *et al.* (1998) and indicates that all different possible models must be tested for each species. Nevertheless, according to the comparison of the hypotheses performed in this study, the characteristics of the best potential predictor models are: (i) to relate the critical state of forcing to the state of chilling with an exponential negative relationship; (ii) to use forcing and chilling rate functions as defined in Hänninen (1990) rather than sums of degree-days and chilling days to simulate temperature action on buds development; and (iii) to consider forcing temperatures active from the onset of quiescence and not from the onset of dormancy. The better predictions obtained with the logistic forcing rate function than the degree-days had also been shown by Kramer (1994b) on *Fagus sylvatica*.

The choice of the best predictor models from the fits and tests using the Montpellier dataset seems justified since the external validity obtained with the Lyon dataset is very high (Table 6). The internal and external validities varied markedly with the species considered, as in Montpellier. Some of the species had their dates of flowering accurately predicted by all the models. The species concerned are

Table 7. Estimates of the best predictor models, fitted with the Montpellier or the Lyon dataset (16 years). (1) *A. glutinosa* (2) *B. verrucosa* (3) *B. sempervirens* (Lyon) (4) *B. sempervirens* (Montpellier) (5) *C. betulus* (6) *C. sativa* (7) *C. avellana* (8) *P. acerifolia* (Lyon), (9) *P. acerifolia* (Montpellier) (10) *O. europaea* (11) *S. nigra* (12) *T. baccata* (13) *U. montana* (14) *U. minor*

Model	1	2	3	4	5	6	7	8	9	10	11	12	13	14
ForcSar			191		303					1045	700	158	298	
Thermal		2.15				7.8	0.0							
Time		296.6				584	257							
		168				236	100							
Alternating		6.9			7.7			9.9						
		39.4			27.0			86.6						
		80.1			291.6			299.0						
		-0.0158			-0.0100			-0.0131						
SeqSar		-2.7		7.1			10.1	8.1	10.3				10.3	
		256.1		394.6			221.3	365.4	395.9				174	
		-0.0040		-0.0183			-0.0218	-0.0052	0.0063				-0.0051	
		161		167			102	166	164				138	
		-2.9		4.6			11.8	10.3	10.3				-3.4	
ParISar		352.8		227.2			378.4	398.1	398.1				151.4	
		-0.0035		-0.0021			-0.017	-0.0039	-0.0039				-10 ⁻⁸	
		161		167			96	162	162				136	

T_b, *F^{*}*, *C^{*}*, *T₀*, *t₁*, *a*, *b* as defined in Tables 1 and 2. *t₁* = number of days from 1 September.

especially *B. verrucosa*, *C. betulus* and *P. acerifolia* (Table 6) for which the models explain about 90% of the variance of external data, which is almost perfect considering the precision of the data. The Forc models are as accurate as the Seq and Par models and sometimes more accurate despite the fact that they require much fewer parameters. Their selection as best predictor models is then justified in this instance.

The percentages of variance explained (internal validity) of the models presented here are higher than that developed by Andersen (1991) who modelled the beginning of the pollen season of *Alnus* sp., *Ulmus* sp. and *Betula* sp. from airborne pollen data (0.83 against 0.61 for *Ulmus* and 0.98 against 0.83 for *Betula* for the best models) except for *Alnus* (0.88 against 0.99). Andersen's models took chilling and forcing temperatures into account but the forcing and chilling rate functions were totally different from ours. In addition every parameter was fixed in his study which make a more precise comparison impossible.

Conditions for reliable fits and tests

The first condition, after the use of adequate optimization algorithms to fit the models, is to fit models with data of the same locality. Phenology, as a component of the reproductive success, and also the survival of individual trees, are subject to climate-dependent selective pressures. It can therefore be expected that the different populations of a single species are adapted to local climatic conditions if these selection pressures are high compared to gene flow. Local adaptation of tree phenology has never been demonstrated clearly although many experiments and especially transfer experiments have been made for that purpose (Perry & Wang 1960; Kuser & Ching 1980; Billington & Pelham 1991; Beuker 1994; Ducouso *et al.* 1996; Falusi & Calamassi 1996; Li *et al.* 1997a,b) but those experiments have shown that populations of some species were differentiated for their phenology. Although, biological significance cannot be given yet to budburst models parameters, it is very probable that some of them, and in particular the base temperature and the optimal temperature of chilling, can be considered as effective thermal thresholds being under genetic control. As a consequence, if the different populations of a species are differentiated for their phenology, we expect that the estimates will be different from one region to another. Hence the use of data from different populations may lead to wrong model estimates.

A second condition pertains to the choice of the data to fit and test the models. Two datasets from the same locality are needed (or from two localities in similar climate). Valuable tests of external validity should be made with at least as many years as those used to fit the models. In addition, phenological events observed in a population are heterogeneous, which seem to indicate that two individuals of the same population may have a different genetic base to their phenology and thus, that their estimates could be different. In a global change context, where the aim is the phenology modelling of species or populations, data

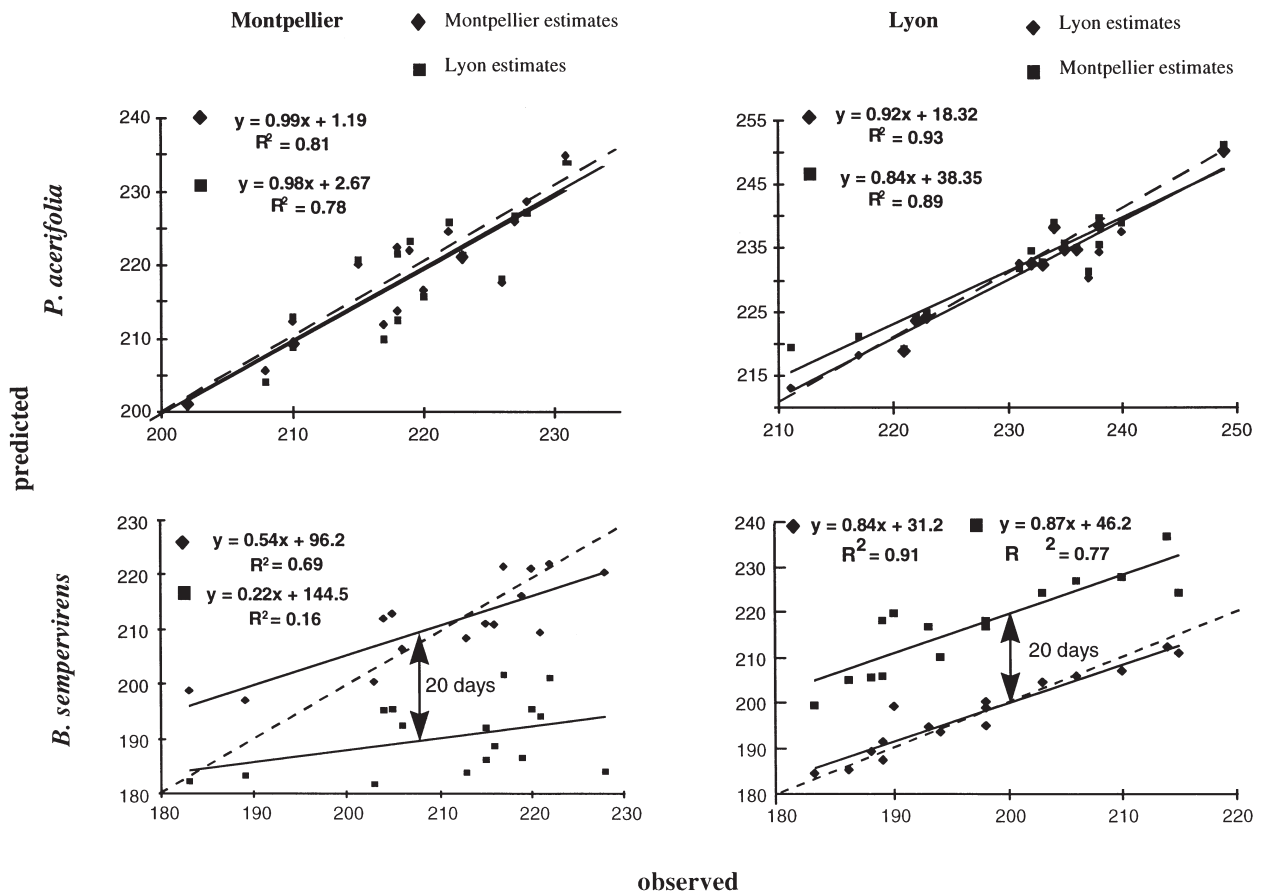


Figure 1. Predictions of the dates of flowering of *P. acerifolia* and *B. sempervirens* by the SeqSar model in Montpellier and in Lyon. Equation of the linear regression of the observed dates against the predicted dates and the R^2 of these regressions are given. Square symbols correspond to the predictions made with the estimates fitted in the locality observed (for example Montpellier) and diamond symbols correspond to the predictions made with the estimates fitted in the other locality (for example Lyon). The dotted slope represents the bisector.

concerning only some individual trees would probably lead to meaningless estimates. Thus, two long time series of data concerning many tree individuals of a population at a single locality are ideally needed to find the reliable predictor models and their estimates.

Estimates significance

Although budburst models are empirical models, the biological significance cannot be given to the estimates, primarily because of the dependence between some of the parameters. This dependence implies that different value sets can be equivalent. This is the case for the T_o , a and b parameters. T_o determines the state of chilling, and a and b determine the state of forcing (F^*) needed to flower. In a single place, F^* does not vary a lot from one year to another, as the accurate results obtained with the Thermal Time and Forc models show. Due to the mathematical relationship between T_o , a and b , similar states of forcing can be obtained with different set of (T_o , a , b) values (Fig. 2). Thus, there is not enough constraint on these parameters if they are fitted in a single place to provide

reliable independent estimates. But we can expect that using populations of different origins, there should be scope for an estimation of the (T_o , a , b) parameter set since the range of C^* and F^* is expanded. We would like to underline that the (a , b) estimates obtained for *C. avellana* and *B. verrucosa* are similar to those measured experimentally by Murray *et al.* (1989) for both of these species and show that they pertain actually to the third group defined by Murray *et al.* (1989). This correspondence provides us with confidence in the estimation of those parameters which is difficult due to the dependence upon other parameters such as the critical state of chilling and the base temperatures.

The range of the T_o parameter is $[-3.4 \text{ } ^\circ\text{C}$ to $10.4 \text{ } ^\circ\text{C}]$. This range has been defined by experiments in both boreal and temperate climate (Sarvas 1974). As Montpellier and Lyon are in south of France in a Mediterranean and temperate climate it could be suggested that this range is not adequate if the populations do not respond to the same temperature from the north to the south of Europe. In addition, some species show very high (*C. avellana*, *P. acerifolia*, *A. glutinosa*, *U. minor*)

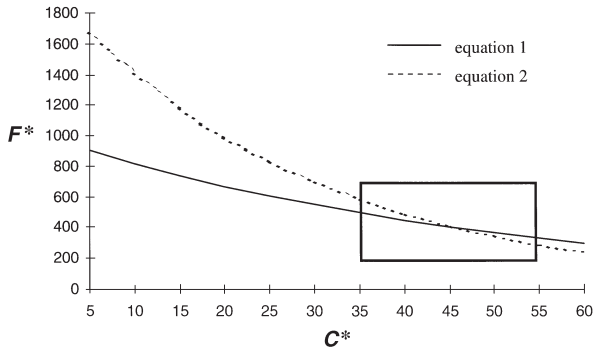


Figure 2. Relationship between C^* and F^* . $F^* = a e^{(b \times C^*)}$. eqn 1: $a = 1000$, $b = -0.02$. eqn 2: $a = 2000$, $b = -0.035$. The quadrant shows the small differences between F^*_1 and F^*_2 in the range $C^* = 35$ to 55 . This magnitude correspond to the magnitude of C^* observed in Montpellier during the period 1974–92.

or very low (*B. verrucosa*, *U. minor*) T_o values which suggest that this range was underestimated. However, if the range is expanded to $[-5\text{ }^\circ\text{C}$ to $15\text{ }^\circ\text{C}]$, some T_o estimates reach the boundaries of the range but the internal and external validities remain approximately constant or decrease (Table 8). Thus, it seems that for some species the rate of chilling is independent of the temperature as has already been shown by Kramer (1994b) for *F. sylvatica*. If T_o estimates do not correspond to the optimal temperature of chilling but are the results of mathematical relationship between T_o , a and b , then any range could be used for T_o as the results obtained for *P. acerifolia* and *U. minor* suggest. This result is also consistent with the fact that for these species models of the Thermal Time type (TT, Forc) are almost as accurate as the others. However, it seems that mixed models (chilling and forcing) make better predictions than the TT or Forc types models suggesting that the duration of the chilling (and not its intensity) is involved.

Estimate comparisons

The Lyon dataset is more appropriate to fit models taking into account chilling temperatures. This is probably due to the fact that winter chilling is usually interrupted by warmer events in Montpellier; effects which are not accounted for in the models. These warm events are

assumed to suppress or decrease the effects of the chilling temperatures.

Platanus acerifolia estimates fitted in a locality accurately predict the dates of flowering in another locality with different climate conditions whereas *B. sempervirens* estimates do not. This result suggests the existence of a local adaptation of the timing of flowering to local climate for *B. sempervirens*, or at least a differentiation between the different populations, and not for *P. acerifolia*.

As previously explained, *P. acerifolia* trees should be genetically more similar than natural tree populations usually are since it is a planted tree, propagated only by cuttings in nurseries, and created by hybridization between a *P. occidentalis* individual and *P. orientalis* individual. This could explain the high similarity between *P. acerifolia* estimates fitted in localities distant by 256 km. On the contrary, populations of *B. sempervirens* are natural, and if the model parameters actually represent the genetic component of phenology, the differences observed between the estimates of the SeqSar model in Lyon and Montpellier suggest strongly that both populations are differentiated for the timing of flowering. Those results indicates that this approach can be useful for studying the local adaptation of phenology of natural populations of widespread tree species. In particular, *P. acerifolia* can be used as a control since the genetic differences between individuals are supposed to be much lower than for other natural tree populations. Such an approach may in particular help to explain the numerous clinal trends observed for the response of phenology to climate.

Accurate budburst models that are able to predict internal data as well as external data are now available. It would, however, be worthwhile to test these models with other kinds of phenological data, especially data based on observations of natural populations. We expect that with adequate data such models could help in the study of local adaptation of phenology to climate, which can now be taken into account to obtain reliable predictions under future climatic scenarios.

ACKNOWLEDGMENTS

The authors are particularly grateful to T. Lenormand and T. Bataillon for constructive criticisms, and to J. D. Thompson for revising the English language of this paper. We are also very grateful to I. Leinonen and an anonymous referee for

Table 8. Estimates of the SeqSar model, range of T_o extending to $[-5\text{ }^\circ\text{C}$ to $15\text{ }^\circ\text{C}]$

	T_o	a	b	t_1	R^2_{int}	R^2_{ext}	R^2_{int}	R^2_{ext}
<i>A. hippocastanum</i>	9.2	930.2	-0.0006	20	–	–	0.51 ns†	0.24 ns†
<i>B. sempervirens</i>	-4.9	236.4	-1×10^{-7}	157	0.60 ns	0.29 ns	0.51 ns†	0.61 ***†
<i>O. europaea</i>	10.7	1223.4	-0.00278	144	0.84 *	0.61 ***	0.93 *†	0.63 ***†
<i>P. acerifolia</i>	-2.2	358.7	-0.00487	155	0.67 ns	0.38 *	0.89 *†	0.69 ***†
<i>U. minor</i>	14.8	496.8	-0.01896	123	0.90 *	–	0.67 ns†	0.38 *†

Significance level as in Table 3. † R^2 values refer to the SeqSar model with range of T_o of $[-3.4\text{ }^\circ\text{C}$ to $10.4\text{ }^\circ\text{C}]$.

their useful comments which have improved the manuscript. We thank also D. Duzer, J. Ferrier, L. Quet, G. Sare and D. Vernier for the pollen analyses. Palynological analyses of Montpellier and Lyon were financed by the 'Centre hospitalier Universitaire de Montpellier', and the AFEDA "Association Française d'Etude des Ambrosia", respectively. This study was financially supported by the CNRS. This is ISEM contribution 98-088.

REFERENCES

- Andersen T.B. (1991) A model to predict the beginning of the pollen season. *Grana* **30**, 269–275.
- Beuker E. (1994) Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. & *Picea abies* (L.) Karst. *Tree Physiology* **14**, 961–970.
- Billington H.L. & Pelham J. (1991) Genetic variation in the date of budburst in Scottish birch population: implications for climate change. *Functional Ecology* **5**, 403–409.
- Boyer W.D. (1973) Air temperature, heat sums, and pollen shedding phenology of longleaf pine. *Ecology* **54**, 421–425.
- Cannell M.G.R. & Smith R.I. (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of Applied Ecology* **20**, 951–963.
- Cecich R.A., Kang H. & Chalupka W. (1994) Regulation of early flowering in *Pinus Banksiana*. *Tree Physiology* **14**, 275–284.
- Chuine I., Cour P. & Rousseau D.D. (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant, Cell and Environment* **21**, 455–466.
- Cour P. (1974) Nouvelles techniques de détection des flux et des retombées polliniques. Etude de la sédimentation des pollens et des spores à la surface du sol. *Pollen et Spores* **16**, 103–141.
- Cour P. & Villemur P. (1985) Fluctuations des émissions polliniques atmosphériques et prévisions des récoltes des fruits. In *V^e Colloque sur les recherches fruitières*, INRA-CITFL, Bordeaux.
- Dominguez C.A. & Dirzo R. (1995) Rainfall and flowering synchrony in a tropical shrub: variable selection on the flowering time of *Erythroxylum Havanense*. *Evolutionary Ecology* **9**, 204–216.
- Ducouso A., Guyon J. & Krémer A. (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl). *Annual Science of Forest* **53**, 775–782.
- Falusi M. & Calamassi R. (1996) Geographic and bud dormancy in beech seedlings (*Fagus sylvatica* L). *Annales Des Sciences Forestières* **53**, 967–979.
- Fox G.A. (1989) Consequences of flowering-time variation in a desert annual: adaptation and history. *Ecology* **70**, 1294–1306.
- Frenguelli G., Bricchi E., Romano B., Ferranti M.F. & Antognozzi E. (1992) The role of air temperature in determining dormancy release and flowering of *Corylus avellana* L. *Aerobiologia* **8**, 415–418.
- Häkkinen R., Linkosalo T. & Hari P. (1995) Methods for combining phenological time series: application to bud burst in birch (*Betula pendula*) in Central Finland for the period 1896–1955. *Tree Physiology* **15**, 721–736.
- Hänninen H. (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica* **213**, 1–47.
- Hänninen H. (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell and Environment* **14**, 449–454.
- Hänninen H. (1995) Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of budburst phenology. *Canadian Journal of Botany* **73**, 183–199.
- Hänninen H. (1996) Effects of climatic warming on northern trees: testing the frost damage hypothesis with meteorological data from provenance transfer experiments. *Scandinavian Journal of Forestry Research* **11**, 17–25.
- Hänninen H., Kellomäki S., Laitinen K., Pajari B. & Repo T. (1993) Effect of increased winter temperature on the onset of height growth of Scots pine: a field test of a phenological model. *Silva Fennica* **27**, 251–257.
- Hänninen H., Leinonen I., Repo T. & Kellomäki S. (1996) Overwintering and productivity of Scots Pine in a changing climate. *Silva Fennica* **30**, 2–3.
- Heide O.M. (1993) Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* **88**, 531–540.
- Hunter A.F. & Lechowicz M.J. (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology* **29**, 597–604.
- Kramer K. (1994a) A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. *Plant, Cell and Environment* **17**, 367–377.
- Kramer K. (1994b) Selecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology* **31**, 172–181.
- Kramer K. (1995) Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant, Cell and Environment* **18**, 93–104.
- Kramer K., Friend A. & Leinonen I. (1996) Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. *Climate Research* **7**, 31–41.
- Kramer K. & Mohren G.M.J. (1996) Sensitivity of FORGRO to climatic change scenarios: a case study on *Betula pubescens*, *Fagus sylvatica* and *Quercus robur* in the Netherlands. *Climatic Change* **34**, 231–237.
- Kuser J.E. & Ching K.K. (1980) Provenance variation in phenology and cold hardiness of Western Hemlock seedlings. *Forest Science* **26**, 463–470.
- Landsberg J.J. (1974) Apple fruit bud development and growth; analysis and an empirical model. *Annals of Botany* **38**, 1013–1023.
- Lebreton J.-D., Burnham K.P., Clobert J. & Anderson D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.
- Li P., Beaulieu J. & Bousquet J. (1997a) Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*). *Canadian Journal of Forest Research* **27**, 189–198.
- Li P., Beaulieu J., Daoust G. & Plourde A. (1997b) Patterns of adaptive genetic variation in eastern white pine (*Pinus strobus*) from Quebec. *Canadian Journal of Forest Research* **27**, 199–206.
- Lieth H. (1971) The phenological viewpoint in Productivity studies. In *Productivity of forest ecosystems* (ed. UNESCO) pp. 71–83. UNESCO, Paris.
- Mauget J.-C. (1983) Etude de la levée de dormance et du débourrement des bourgeons de noyer (*Juglans regia* L., cv. 'Franquette') soumis à des températures supérieures à 15°C au cours de leur période de repos apparent. *Agronomie* **3**, 745–750.
- Mergen F. (1963) Ecotypic variation in *Pinus strobus* L. *Ecology* **44**, 716–727.
- Murray M.B., Cannell M.G.R. & Smith R.I. (1989) Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology* **26**, 693–700.
- Myking T. & Heide O.M. (1995) Dormancy release and chilling requirements of buds of latitudinal ecotypes of *Betula pendula* and *B. Pubescens*. *Tree Physiology* **15**, 697–704.
- Nelson E.A. & Lavender D.P. (1979) The chilling requirement of western hemlock seedlings. *Forest Science* **25**, 485–490.

- Nizinski J.J. & Saugier B. (1988) A model of leaf budding and development for a mature *Quercus* forest. *Journal of Applied Ecology* **25**, 643–652.
- Perry T.O. & Wang L.W. (1960) Genetic variation in the winter chilling requirement for date of dormancy break for *Acer robur*. *Ecology* **41**, 790–794.
- Reinartz J.A. (1984) Life history variation, of common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. *Journal of Ecology* **72**, 897–912.
- Ricaud S., Alaoui-Sossé B., Crabbé J. & Barnola P. (1995) Dormance et croissance des bourgeons du platane hybride (*Platanus acerifolia*) en milieu urbain. *Canadian Journal of Botany* **73**, 130–140.
- Richard P. (1985) Contribution aéropalynologique à l'étude de l'action des facteurs climatiques sur la floraison de l'Orme (*Ulmus campestris*) et de l'If (*Taxus baccata*). *Pollen and Spores* **27**, 53–94.
- Rohlf F.J. & Sokal R.R. (1969) *Statistical Tables*, p. 350. W. H. Freeman and Co., San Francisco, CA.
- Sarvas R. (1974) Investigations on the annual cycle of development of forest trees. Autumn dormancy and winter dormancy. *Communicationes Instituti Forestalis Fenniae* **84**, 101.
- Schnelle F. & Volkert E. (1974) International phenological observations. In *Phenology and Seasonality Modelling* (ed. H. Lieth), pp. 383–387. Springer Verlag, New York.
- Sedgley M. & Griffin A.R. (1989) *Sexual Reproduction of Tree Crops*, p. 325. Harcourt, Brace and Jovanovich, Academic Press, London.

Received 20 June 1998; received in revised form 11 September 1998; accepted for publication 11 September 1998