Selecting a model to predict the onset of growth of *Fagus sylvatica*

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Summary

1. To evaluate the impacts of climate change on the primary production of temperate deciduous tree species, the onset and cessation of the growth must be accurately described. The aim of this study is to find a model which predicts the onset of growth of *Fagus sylvatica* (European beech) accurately.

2. Several models have been proposed for the prediction of the timing of budburst of woody plants. Most of these models have been evaluated for species other than *Fagus sylvatica*, and in some cases for flower buds. Six models were fitted to data on leaf unfolding of *Fagus sylvatica*, collected in the Netherlands over 57 years (1901–68).

3. All models require only temperature as input. For *Fagus sylvatica*, however, photoperiod may influence the timing of the onset of growth. Therefore, photosensitivity was incorporated in these models. This reduced the predictive power compared to models that do not incorporate photosensitivity.

4. The model proposed by Sarvas (1974), in which the development of rest and quiescence is strictly separated in time, resulted in the best predictions of the average date of leaf unfolding in *Fagus sylvatica*.

Key-words: chilling, dormancy release, photosensitivity, quiescence, rest, temperature.

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Notation

See Appendix 1.

Introduction

The developmental processes in the bud that release dormancy and thus trigger the onset of growth of temperate zone trees are mainly regulated by temperature (Romberger 1963). This regulation is such that a period with chilling temperature (-5 to $+10\,°C$) followed by a period with forcing temperature ($>0\,°C$) induces budburst (Samish 1954; Vegis 1964; Wareing 1969; Nienstaedt 1974; Richardson, Seeley & Walker 1974; Lavender 1981).

Generally, the influence of photoperiod on trees requiring chilling is that a long photoperiod substitutes for a lack of chilling (Vegis 1964; Flint 1974; Nienstaedt 1974; Lavender 1981; Cannell & Smith 1983). However, for *Fagus sylvatica* the experimental evidence on the role of photoperiod in the timing of budburst is conflicting (Wareing 1953; Vegis 1964; Falusi & Calamassi 1990). Wareing (1953) found that budburst in *Fagus sylvatica* is induced when an

absolute length of the dark period is achieved, even after a prolonged period of chilling. On the other hand, Falusi & Calamassi (1990) found that chilling completely eliminates dormancy, with very slight interaction between day length and chilling.

The aim of this study was to examine models presented in the literature and select the model that most accurately predicts the timing of the start of the growing period of *Fagus sylvatica* L. Models that incorporate photoperiod as a substitute for chilling were compared with models that do not. In later studies this model could be coupled with a model describing primary production in order to evaluate the impact of climate change on growth and development.

Material and methods

MODELS

The definitions of the different phases during dormancy, which where introduced by Sarvas (1974), have been adopted here. **Rest** is defined as the period in which buds remain dormant due to growth-

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arresting physiological conditions in the bud itself. The growth-arresting conditions are removed when buds are exposed to chilling temperature for a certain period. The subsequent stage of dormancy is called quiescence. **Quiescence** is defined as the period in which the buds remain dormant due to unfavourable environmental conditions. Budburst takes place when the buds are exposed to forcing temperatures for a prolonged period.

Taking a system-analytical approach, Hänninen (1990) formalized four models on dormancy release presented in the literature and introduced a **competence function** which is defined as the bud's potential to respond to forcing temperature. The values of the competence function range between zero and unity, so it indicates to what degree a bud responds to a forcing temperature relative to the potential response at that temperature.

The notation used is presented in Appendix 1, while the equations characterizing the models are presented in Appendix 2.

The four models which Hänninen (1990) described have the following in common: (i) the competence function depends on the state of chilling; (ii) the rate of chilling during rest is assumed to have an optimum between minimum and maximum temperature thresholds (equation 1, Fig. 1); (iii) the rate of forcing during quiescence is assumed to be logistically related to temperature (equation 2, Fig. 2). Two models with other functions for the rate of
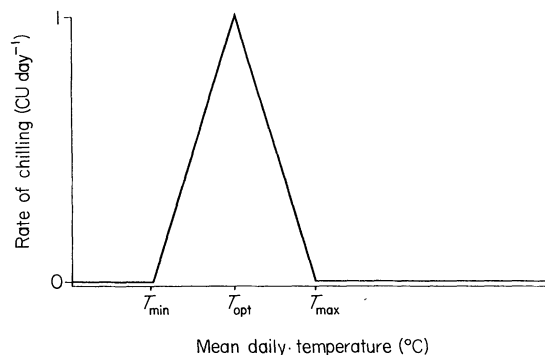
Fig. 1. Rate of chilling for the parallel, sequential, deepening rest and four phase model.
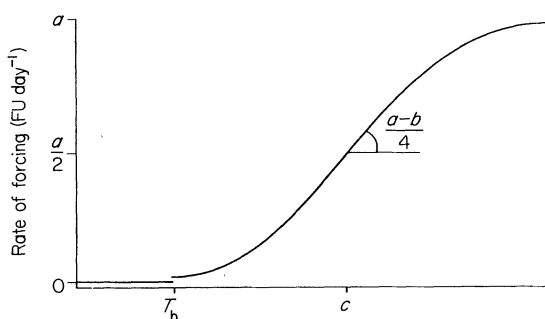
chilling and forcing and with a competence function independent of the state of chilling, were characterized using Hänninen's terminology. In all models the state of chilling and the state of forcing are the summation of the rate of chilling and forcing, respectively, using a variable time-step with a maximum of 1 day (equations 3 and 4).

Sequential model

Sarvas (1974) considered rest and quiescence as two strictly separate phases. On this basis, there will be no transition from rest to quiescence unless the critical state of chilling is attained (equation 5). Similarly, there will be no transition from quiescence to the active phase unless the critical state of forcing is attained. This model was called the sequential model, because the state of chilling and the state of forcing increase sequentially in time (Model I of Hänninen 1990).

Parallel model

Landsberg (1974) proposed a model for the development of apple fruit buds. He stated that for dormancy release it is essential that, even when the critical state of chilling has not yet been attained, response to forcing temperature must be possible. The bud's potential to respond to forcing temperature increases concomitantly with the time spent in chilling conditions (equation 6, Fig. 3). After attaining full chilling, the rate of development is logistically related to temperature (equation 2, Fig. 2). This model was called the parallel model, because the state of chilling and the state of forcing increase together in time (Model II of Hänninen 1990).

Deepening rest model

Kobayashi, Fuchigami & English (1982) suggested a model for rest development in red-osier dogwood (*Cornus sericea*) based on the work of Fuchigami *et al.* (1982). During rest they discerned a phase of deepening rest and a phase of decreasing rest (equation 7, Fig. 4). After the end of rest a quiesc-
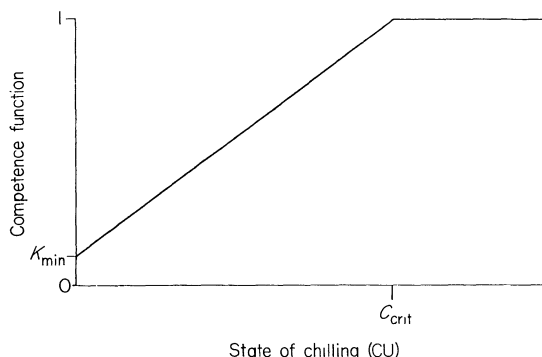
Fig. 2. Rate of forcing for the parallel, sequential, deepening rest and four phase model.

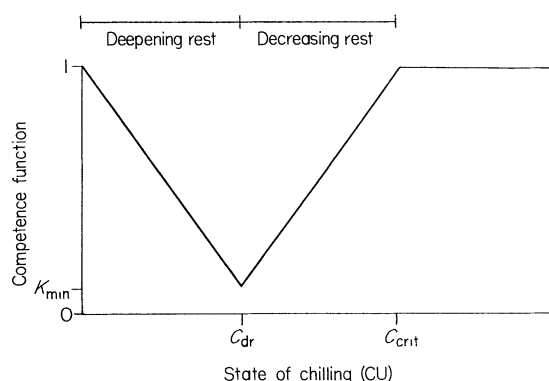**Fig. 3.** Competence function for the parallel model.

Fig. 4. Competence function for the deepening rest model.

ence phase is defined (Kobayashi & Fuchigami 1983). During quiescence, developmental rates increase logistically with temperature (equation 2, Fig. 2). This model was called the deepening rest model, because the other models consider decreasing rest only (Model III of Hänninen 1990).

Four phase model

Vegis (1964) concluded that the range of external conditions in which development is possible narrows and widens during the annual cycle. Based on this idea he defined three different phases during rest (rephrased in Hänninen's terminology): (i) pre-rest, development is still possible but only at a narrower range of external conditions than at the time of full growth activity: (ii) true rest, development has stopped and cannot be resumed whatever the external conditions may be; and (iii) post-rest, the range over which growth is possible widens again. Post-rest is followed by quiescence in which buds respond fully to forcing temperatures.

Hänninen formalized this mechanism by proposing an increasing temperature threshold during pre-rest and a decreasing threshold during post-rest (equation 8, Fig. 5). During true rest buds cannot respond to forcing temperatures. During pre-rest such a response is very unlikely because the temperature threshold increases while the temperature decreases.
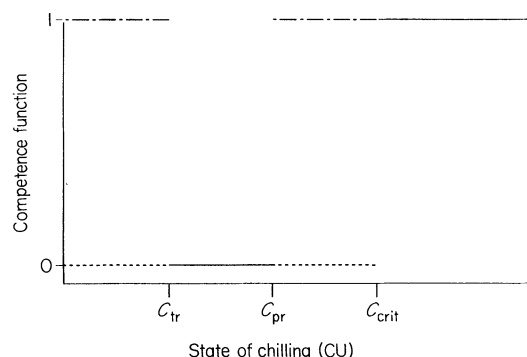
During post-rest, many more forcing units are accumulated per day because the temperature threshold decreases and the temperature possibly increases again. Transition from pre-rest to true rest, and from the true rest to post-rest occurs when the state of chilling attains critical values (equation 9, Fig. 6). This model was called the four phase model, because the other models do not consider three phases during rest (Model IV of Hänninen 1990).

Thermal time model

This model has been used frequently since Reaumur introduced it in 1735 (Robertson 1968). It was observed that the rate at which plants develop increases proportionally with temperature above a base temperature (equation 10, Fig. 7). Forcing units are accumulated after a given starting date, i.e. the onset of quiescence, so the duration of rest is assumed to be constant. This is equivalent to accumulating one chilling unit per day (equation 11) from the onset of rest up to the onset of quiescence. The model is similar to the sequential model, with time equivalent to the rate of chilling, and the fixed onset of quiescence equivalent to the critical state of chilling. This model reflects the findings of Wareing (1953) that an absolute photoperiod is required to break rest. Because in natural situations this absolute photoperiod is reached every year at the same date, the onset of quiescence is fixed. This model was

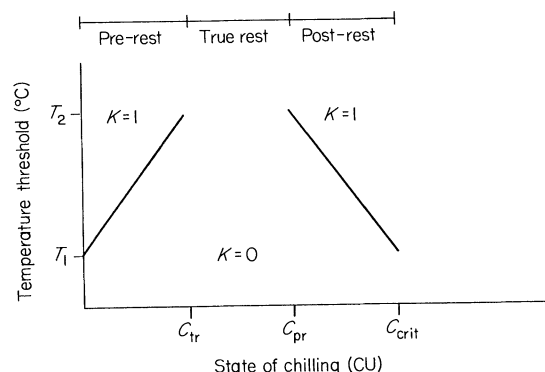**Fig. 6.** Temperature threshold for the four phase model.

Fig. 5. Competence function for the four phase model: $T > T_{trh}$ (— — — — — —); $T \leq T_{trh}$ (-------); all values of T (———).
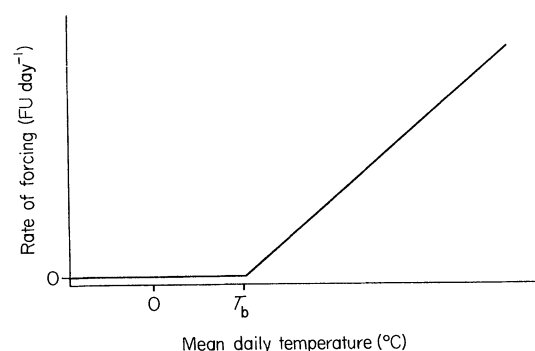

Fig. 7. Rate of forcing for the thermal time model.

called the thermal time model by Cannell & Smith (1983).

Alternating model

Murray, Cannell & Smith (1989) used thermal time (equations 10–12) as the state of forcing and the number of chilling days as the state of chilling to predict budburst among other species, of *Fagus sylvatica*. Days with an average temperature below the base temperature are regarded as chilling days (equation 13). As was found by Cannell & Smith (1983), the critical thermal time required for budburst is not a constant, but declines exponentially with the state of chilling (equation 14, Fig. 8). This model differs from the other models in relating forcing to chilling. The rate of forcing is not increased when more chilling units are accumulated, but the critical state of forcing required for budburst is lowered when the state of chilling increases. It was called the alternating model because from the onset of quiescence on, either the state of chilling increases, when the temperature is below the base temperature, or the state of forcing is increased, when above.

Photosensitivity

The most basic model relating the timing of budburst to photoperiod, proposes an absolute day length to induce budburst. This model was considered as the null model since it predicts budburst to occur each year at the same date.

Photoperiod was included additively to the rate of chilling in the models (equation 15). With this formulation, photosensitivity guarantees that the chilling requirement is attained even when little chilling is accumulated due to high winter temperatures. Because the thermal time model does not consider the rate of chilling, photoperiod was not included in this model.

PARAMETER ESTIMATION

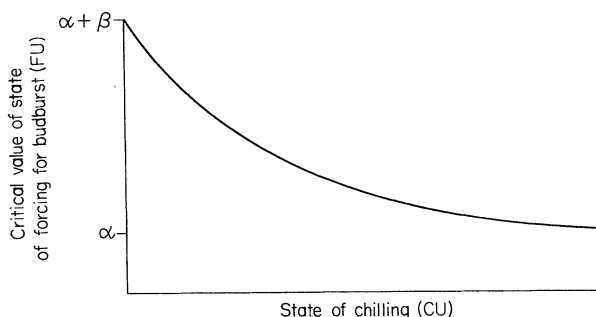The minimum sum of squares of the residuals (absolute differences between predicted and ob-

Fig. 8. Critical state of forcing for the alternating model.

served dates of leaf unfolding) was used as the criterion to identify the optimal set of parameter values for each of the models. Several searching methods were used to inspect the parameter space.

The parameter values of the models formalized by Hänninen were estimated with 'SENECA', a Simulation ENvironment for ECological Applications (Scholten, de Hoop & Herman 1990). Here the parameters are constrained within user-defined limits. This guarantees that biologically realistic values are obtained. Using a 'controlled random search' (Price 1979) for all parameters simultaneously, the parameter range was reduced. Initial values for the parameter ranges were derived from the literature (Hänninen 1990) or set subjectively, but adjusted when the method found a boundary value to be optimal.

The critical state of forcing for the thermal time model was found by varying the starting day of accumulating thermal time from 1 November to 1 May using a step size of 1 day, and the base temperature from −5 to 10 °C with a step size of 0·1C°. The parameters of equation 14 of the alternating model were fitted with GENSTAT using the directive FITNONLINEAR, because the same method was applied by Murray *et al.* (1989). This was done repeatedly, by varying the onset of quiescence between 1 December and 1 February with a step size of 14 days, and the base temperature from 0 to 10 °C with a step size of 1C°.

DATA

The models were fitted using phenological observations gathered in the time-span 1901–68 from many locations throughout the Netherlands. Data for 1931–39, 1945 and 1954 are lacking. The models were tested using data gathered at three phenological stations in Germany in the period 1951–90.

The average of the daily minimum and maximum temperatures was used. The temperature series from De Bilt (52·06°N, 5·20°E), which is located in the centre of the Netherlands, was available for the Dutch observations. For the German observations the temperature series of Celle (52·36°N, 10·02°E) was used.

The phenological stage considered is called 'leaf unfolding'. Leaf unfolding is defined by the Hoffman-Ihne instruction for observers (Bos 1893) as follows: at two or three places in the tree a normal, unwrinkled, leaf surface should be visible, but full leaf size has not yet been attained (Fig. 9d). The observations should be done on free-standing individuals, not standing in especially favoured or unfavoured sites (south side of wall, very wet or dry soils, etc.). Particularly early or late individuals should be excluded. The average date of leaf unfolding should preferably be taken from several individuals standing near each other. In the Dutch
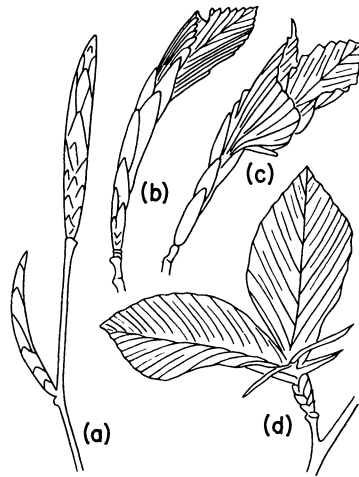
Fig. 9. Budburst of *Fagus sylvatica*: (a) buds still closed; (b) and (c) leaves protruding, but not yet unfolded; (d) first leaves have emerged to leaf base, and have unfolded: leaf unfolding (DWD 1962).

observations before 1930 the observer was allowed to make observations on different groups of *Fagus sylvatica* in subsequent years (Bos 1893). Since 1940 it has been mandatory to observe the same group every year (KNMI 1950). The observers are urged to inspect their trees daily because in a warm spring the stages depicted in Fig. 1 can occur within a week.

The advantage of the Dutch data set is that it covers a relatively long period. It contains 1964 individual observations covering 57 years. Its disadvantages are that the provenance of the observed trees is unknown and that the sites of observation as well as the number of observations vary between years. Yearly averages were taken because only one temperature series covering the full time-span of phenological observations was available. From the south to the north of the Netherlands the date of leaf unfolding is delayed by 2·8 days per degree latitude, which coincides with a difference in average yearly temperature of about 1C° (1950−87). From east to west the delay in the day of leaf unfolding is 0·6 days per degree longitude.

The four German phenological stations are all located within 0·5 °N and 0·5 °E of the meteorological station at Celle; 160 individual observations were available, covering 40 years. For testing the models, yearly averages were taken. For the German observations yearly averages were taken of the results from the four phenological stations.

Results

Table 1 presents the parameter sets of each model yielding lowest sum of squares of the residuals, SS_{res}, found. For the four phase model without day length no results are presented because, for this model, the parameter set with the best result predicted the date of leaf unfolding in only 10 of the 57 years. In the other years the state of forcing did not reach the critical state required for leaf unfolding. The SS_{res} of the thermal time model and the alternating model varied very little when the onset of quiescence was varied between 1 December and 1 February, and the base temperature was adjusted

Table 1. Parameter values yielding the lowest SS_{res}. See Appendix 1 for an explanation of the parameter names. Abbreviation of the models are: s, sequential; p, parallel; dr, deepening rest; 4p, four phase; tt, thermal time; a, alternating; s − i, improved sequential. + L indicates a model including day length

	s	s + L	p	p + L	dr	dr + L	4p + L	tt	a	a + L	s − i
t_1[a]	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov		1 Nov	1 Nov	1 Nov
t_2[a]								1 Jan	1 Jan	1 Jan	
C_{crit}	57·40	59·11	117·18	105·96	95·71	74·91	170·90				117·83
F_{crit}	262·53	264·44	224·30	191·50	166·51	164·96	302·76	206·40			9·66
T_{min}	−3·80	−4·58	−3·87	−4·01	−0·96	−2·65	−3·23				−17·02
T_{opt}	0·41	2·38	1·47	4·95	2·57	1·67	2·58				−1·34
T_{max}	12·43	12·02	10·33	13·68	8·73	10·86	8·87				92·15
T_b	0·00[b]	0·00[b]	0·00[b]	0·00[b]	0·00[b]	0·00[b]	0·00[b]	4·50[a]	5·00[a]	5·00[a]	0·00[b]
a	26·49	27·75	31·33	29·95	29·10	31·38	20·41				1·00[b]
b	0·19	−0·23	−0·15	−0·17	−0·17	−0·20	−0·30				−0·12
c	−17·07	−18·52	−23·34	−24·99	−19·50	−23·18	−14·08				−20·54
d		94·21			95·59	93·22	2·12			58·51	
K_{min}			0·26	0·11	0·11	0·24					
C_{dr}					31·69	31·29					
C_{tr}							56·97				
C_{dr}							113·93				
T_1							10·82				
T_2							17·47				
α									66·00	72·83	
β									511·00	546·58	
γ									0·017	0·016	

[a] Fixed after initial testing.
[b] Fixed.

accordingly. Therefore, for both models the onset of quiescence was fixed at 1 January.

It was found that SS_{res} for the fit of the models exceeded the SS_{res} for the fit of the null model, i.e. the mean (Table 2). Including day length as a substitute for chilling decreased the SS_{res} of each of the models. With the parameter values presented in Table 1, the date of leaf unfolding of the German data was predicted. Again it was found that the SS_{res} of the predictions exceeded the SS_{res} of the null model, and that including day length decreased the SS_{res} of a model (Table 2).

IMPROVING THE FIT OF THE MODEL

Because all models performed worse than the null model, an attempt was made to develop a model with a higher accuracy of prediction than the current models. The sequential model without day length appeared the most promising model to improve. Therefore, this model was adapted in two ways. Firstly, the constraint on the parameter range was released, so the parameters were allowed to take biologically unrealistic values. Secondly, the temperature asymptote of the logistic function of forcing, a, was set at unity, reducing the number of parameters to estimate. This model was called the sequential-i model. Mathematically the sequential-i model is equivalent to the sequential model. However, the biological interpretation of the rate of forcing changes. The rate of forcing is now expressed relative to the maximal rate of forcing at the optimal forcing temperature.

The sequential-i model was fitted using Newton's method of a directed search in the parameter space (Gill & Murray 1978). This was done with the subroutine E04FCF of the NAG FORTRAN library. The parameter values of the sequential-i model are presented in Table 1. The criterion for this method of a global minimum of SS_{res}, however, was not attained. The SS_{res} of the fit and predictions are presented in Table 2. It was found that the SS_{res} for both the fit of the Dutch data and the prediction of the German data were reduced considerably, compared both to the other models and to the null model. However, the sequential-i model overestimated the date of leaf unfolding systematically, especially for the German data.

Discussion and conclusion

Models

The underlying physiological mechanisms leading to dormancy release are largely unknown, but cannot be related simply to an increase of a growth-promoting substance or to a decrease of a growth-inhibiting substance (e.g. Powell 1969; Wareing 1969). It is known that temperate-zone tree species require a certain period with chilling temperature, followed by a period with a higher temperature, forcing a bud to burst. Based on this very simple empirical model the average date of the onset of growth of *Fagus sylvatica* can be predicted with considerable accuracy.

In the model with the lowest SS_{res}, the sequential-i model, chilling was allowed to occur at a very wide range of temperatures (Table 1). This means that the rate of chilling is virtually independent of temperature, because the curve in Fig. 1 then shows a very broad plateau close to unity in the range of actual winter temperatures (about -10 to $+10$ °C. Consequently, the onset of quiescence varies little between years (11 March $\pm$ 5·4 days). So the sequential-i model nearly reduces to the thermal time model with a logistic rate of forcing instead of a

Table 2. Statistics for the fit and predictions of the models. SS_{res}, sum of squares of the residuals; MAX_{res}, maximum residual; LU_{avg}, average date of leaf unfolding. $+ L$ indicates a model including day length. N_{par}, number of parameters in the model

Model	Fit (The Netherlands, $n = 57$)			Prediction (Germany, $n = 40$)			N_{par}
	SS_{res}	MAX_{res}	LU_{avg}	SS_{res}	MAX_{res}	LU_{avg}	
Null	1622	11	1 May	2494	21	1 May	0
Sequential	1624	11	1 May	3108	15	7 May	10
Parallel	2623	19	3 May	6256	25	10 May	11
Deepening rest	3352	17	27 Apr	9461	32	12 May	12
Sequential $+ L$	3882	25	1 May	4837	26	9 May	11
Parallel $+ L$	4117	24	29 Apr	5516	27	9 May	12
Deepening rest $+ L$	13351	40	16 Apr	3923	24	7 May	13
Four phase $+ L$	5209	27	25 Apr	4817	24	9 May	15
Thermal time	4602	24	2 May	5810	41	24 May	3
Alternating	2034	18	28 Apr	6797	32	19 Apr	6
Alternating $+ L$	5190	14	29 Apr	9879	47	11 Apr	7
Sequential-i	488	9	2 May	885	12	6 May	9
Data			1 May			1 May	

linear one. However, the SS_{res} of the sequential-i model was found to increase when the model was simplified by using a linear rate of forcing instead of the logistic function.

Photosensitivity

The experimental evidence that photoperiod can substitute for a lack of chilling (Vegis 1964; Flint 1974; Nienstaedt 1974; Lavender 1981; Cannell & Smith 1983) suggests an additive model. Photosensitivity then guarantees that the chilling requirement is attained when, in a warm winter, little chilling is accumulated. A similar formulation was used by Primault (in Robertson 1973), and by Hänninen *et al.* (1990) for the joint factor model on growth cessation of trees.

Multiplicative models and polynomials of the rate of chilling and photoperiod are also frequently used (Nuttonson 1948; Robertson 1968; Caprio 1974; Campbell & Sugano 1975). However, when photoperiod is multiplicatively coupled to the rate of chilling, photoperiod has no effect when the rate of chilling equals zero, i.e. due to high temperature. So this model does not represent photoperiod as a substitute for chilling.

Fitting an additive model of the state of chilling and an absolute photoperiod was not possible. For such a model, finding both the best photoperiod and the best critical state of chilling entails increasing the critical state of chilling by an amount equal to that added to the state of chilling. Thus, there is an infinite number of parameter sets for this model yielding the same result. So the effects of photoperiod cannot be evaluated using this type of model. A similar reasoning holds true for a multiplicative model of the state of chilling and an absolute photoperiod. Therefore, it was concluded that the additive model of the rate of chilling and photoperiod is a simple and realistic way to incorporate photoperiod. Nevertheless, the result of this way of introducing photoperiod was that the SS_{res} of the model increases, thus making the model more complex as well as a worse predictor for the date of leaf unfolding.

Parameter estimation

The models have in common that state variables must attain one or more thresholds for which no data are available. Finding optimal parameter values for such a model is particularly difficult because the same result can be obtained either by lowering the threshold, or by tuning the rate parameters so that the threshold is attained earlier. There is little hope that, even when constrained parameter ranges are used, a fitting procedure will find biologically realistic parameter values as long as no direct measurements of the parameters are available. The reason that

the deepening rest and the four phase model perform poorly may be the introduction of additional thresholds during rest. Due to the correlation between these thresholds, many different thresholds yield the same prediction. Consequently, a poor fit does not necessarily indicate that the structure of the models is inappropriate.

Conclusion

The modified version of the sequential model performs better than the other models considered, including the null model. The aim of this study was to select the model that most accurately predicts the onset of growth of *Fagus sylvatica*. It appears that the sequential-i model could be used for further study of impacts of climatic warming on primary production of *Fagus sylvatica*.

Acknowledgements

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Appendix 1. Notation

Symbol		Units
Arbitrary units		
CU	Chilling units	
FU	Forcing units	
Variables		
R_{chl}	Rate of chilling	CU day^{-1}
R_{frc}	Rate of forcing	FU day^{-1}
S_{chl}	State of chilling, integral of rate of chilling	CU
S_{frc}	State of forcing, integral of rate of forcing	FU
K	Competence function: bud's potential to respond to forcing temperature [0–1]	—
T	Mean daily temperature	°C
L	Day length	h day^{-1}
t	Time	day
Parameters		
C_{crit}	Critical value of state of chilling for the transition form rest to quiescence	CU
F_{crit}	Critical values of state of forcing for the transition from quiescence to the active period, i.e. budburst	FU
K_{min}	Minimum potential of unchilled bud to respond to forcing temperature	—
C_{dr}	Critical state of chilling for transition from deepening rest to decreasing rest	CU
C_{tr}	Critical value of state of chilling for transition from pre-rest to true rest	CU
C_{pr}	Critical value of state of chilling for transition from true rest to post-rest	CU
T_{mn}	Minimum temperature for rate of chilling	°C
T_{opt}	Optimal temperature for rate of chilling	°C
T_{max}	Maximum temperature for rate of chilling	°C
T_b	Base temperature	°C
T_1	Lower value of temperature range for which development is possible	°C
T_2	Upper value of temperature range for which development is possible	°C
T_{trh}	Temperature threshold above which development is possible and below which development is impossible	°C
t_1	Date of onset of rest	day
t_2	Date of onset of quiescence	day
$a, b, c, \alpha, \beta, \gamma, \delta$	Constants	

Appendix 2. Equations

Rate of chilling for the parallel, sequential, deepening rest and four phase model

$$R_{chl} = \begin{cases} 0 & T \leq T_{min} \\ \dfrac{T - T_{min}}{T_{opt} - T_{min}} & T_{min} < T \leq T_{opt} \\ \dfrac{T - T_{max}}{T_{opt} - T_{max}} & T_{opt} < T < T_{max} \\ 0 & T \geq T_{max} \end{cases} \qquad \text{eqn 1}$$

Rate of forcing for the parallel, sequential, deepening rest and four phase model

$$R_{frc} = \begin{cases} 0 & T \leq T_b \\ K\dfrac{a}{1 + e^{b(T+c)}} & T > T_b \end{cases} \qquad \text{eqn 2}$$

State of chilling (all models)

$$S_{chl} = \sum_{t_1}^{t} R_{chl} \qquad \text{eqn 3}$$

State of forcing (all models)

$$S_{frc} = \sum_{t_2}^{t} R_{frc} \qquad \text{eqn 4}$$

Sequential model

$$K = \begin{cases} 0 & S_{chl} < C_{crit} \\ 1 & S_{chl} \geq C_{crit} \end{cases}$$

eqn 5

Parallel model

$$K = \begin{cases} K_{min} + \dfrac{1 - K_{min}}{C_{crit}} S_{chl} & S_{chl} < C_{crit} \\ 1 & S_{chl} \geq C_{crit} \end{cases}$$

eqn 6

Deepening rest model

$$K = \begin{cases} 1 - \dfrac{1 - K_{min}}{C_{dr}} S_{chl} & S_{chl} < C_{dr} \\ K_{min} + \dfrac{(1 - K_{min})(S_{chl} - C_{dr})}{C_{crit} - C_{dr}} & C_{dr} \leq S_{chl} < C_{crit} \\ 1 & S_{chl} > C_{crit} \end{cases}$$

eqn 7

Four phase model

$$K = \begin{cases} 1 & S_{chl} < C_{tr}, \ T > T_{trh} \\ 0 & S_{chl} < C_{tr}, \ T \leq T_{trh} \\ 0 & C_{tr} \leq S_{chl} < C_{pr} \\ 0 & C_{pr} \leq S_{chl} < C_{crit}, \ T \leq T_{trh} \\ 1 & C_{pr} \leq S_{chl} < C_{crit}, \ T > T_{trh} \\ 1 & S_{chl} \geq C_{crit} \end{cases}$$

eqn 8

$$T_{trh} = \begin{cases} T_1 + \dfrac{T_2 - T_1}{C_{tr}} S_{chl} & S_{chl} < C_{tr} \\ T_1 + \dfrac{(T_1 - T_2)(S_{chl} - C_{crit})}{C_{crit} - C_{pr}} & C_{pr} \leq S_{chl} < C_{crit} \end{cases}$$

eqn 9

Thermal time model

$$R_{frc} = \begin{cases} 0 & T \leq T_b \\ K(T - T_b) & T > T_b \end{cases}$$

eqn 10

$$R_{chl} = 1$$

eqn 11

$$K = \begin{cases} 0 & t < t_2 \\ 1 & t \geq t_2 \end{cases}$$

eqn 12

Alternating model

$$R_{chl} = \begin{cases} 1 & T \leq T_b \\ 0 & T > T_b \end{cases}$$

eqn 13

$$F_{crit} = \alpha + \beta e^{-\gamma S_{chl}}$$

eqn 14

Photosensitivity

$$R_{chl} = R_{chl} + \delta L$$

eqn 15