

Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology¹

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Abstract: A framework is presented for modelling bud burst phenology of trees from the cool and temperate regions. Three ecophysiological aspects affecting the timing of bud burst are considered: (i) effects of environmental factors on the rest status of the bud, (ii) effect of rest status on the ability for bud burst, and (iii) direct effect of air temperature on the rate of development towards bud burst. Any model for bud burst phenology can be presented within the framework with three submodels, each of them addressing one of the corresponding three ecophysiological aspects. A total of 96 hypothetical models were synthesized by combining submodels presented in the literature. The models were tested in two experiments with saplings of *Pinus sylvestris* L. growing in experimental chambers at their natural site in eastern Finland. In the first experiment, air temperature and (or) concentration of atmospheric CO₂ was elevated. Elevation of the air temperature hastened bud burst, whereas elevation of the concentration of CO₂ did not affect it. Several models accurately predicted the timing of bud burst for natural conditions but too early for bud burst at the elevated temperatures. This finding suggests that (i) the risk of a premature bud burst with subsequent frost damage, as a result of climatic warming, was overestimated in a recent simulation study, and (ii) bud burst observations in natural conditions alone are not sufficient for the testing of these mechanistic models. Several models did predict the timing of bud burst accurately for all treatments, but none of them obtained sufficiently strong support from the findings to stand out as superior or uniquely correct. In the second experiment a photoperiod submodel for rest break was tested by exposing the saplings to short-day conditions. The short-day treatment had only a minor effect on the timing of bud burst. These results demonstrated the importance of the concept of model realism: the accuracy of a model can be lost in new conditions (e.g., global warming), unless the model correctly addresses the essential ecophysiological aspects of the regulation of timing of bud burst.

Key words: annual cycle of development, chilling, dormancy, field test, photoperiod, rest break.

Résumé : L'auteur présente un cadre de travail pour la modélisation de la phénologie du débournement des bourgeons chez les arbres de régions froides à tempérées. Il considère trois paramètres écophysologiques qui affectent la chronologie de l'ouverture des bourgeons : (i) les effets des facteurs environnementaux sur l'état de repos du bourgeon, (ii) l'effet de l'état de repos sur la capacité de bourgeon à débourrer, et (iii) l'effet direct de la température de l'air sur le taux de développement conduisant à l'ouverture des bourgeons. Tout modèle proposé pour la phénologie du débournement peut être présenté selon le cadre de travail en utilisant trois sous-modèles chacun impliquant un des trois paramètres écophysologiques. En combinant les modèles hypothétiques présentés dans la littérature, l'auteur a pu synthétiser 96 modèles hypothétiques. Les modèles ont été vérifiés dans deux expériences avec des plantules de *Pinus sylvestris* L. cultivées en compartiments expérimentaux sur leurs sites naturels, dans l'est de la Finlande. Dans la première expérience, la température de l'air et (ou) la teneur en CO₂ atmosphérique étaient élevées. Une augmentation de la température de l'air accélère l'ouverture du bourgeon, alors qu'une augmentation de la teneur en CO₂ demeure sans effet. Plusieurs modèles ont permis de prédire correctement le moment de l'ouverture du bourgeon sous des conditions naturelles mais prédisent un débournement trop hâtif pour des conditions de température élevées. Cette constatation suggère que (i) le risque d'une ouverture prématurée suivie de dommages par le gel, suite à un réchauffement climatique, a été surestimé dans une récente étude de simulation, et (ii) les

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observations sur le débournement des bourgeons effectuées seulement sous les conditions naturelles ne sont pas suffisantes pour vérifier ces modèles mécanistes. Plusieurs modèles ont permis de prédire le moment du débournement avec précision pour tous les traitements, mais aucun d'entre eux n'a reçu suffisamment de support pour se distinguer comme supérieur ou comme le seul valable. Dans la deuxième expérience, l'auteur a étudié un sous-modèle impliquant la photopériode dans l'ouverture des bourgeons en exposant les plantules à des conditions de jours courts. Le traitement en jours courts n'a montré que des effets mineurs sur le moment de l'ouverture des bourgeons. Ces résultats démontrent l'importance du concept de réalisme des modèles : l'exactitude d'un modèle peut disparaître sous de nouvelles conditions (e.g., réchauffement global), à moins que le modèle ne tienne compte des paramètres écophysologiques essentiels impliqués dans la régulation du moment d'ouverture des bourgeons.

Mots clés : cycle annuel du développement, traitement par le froid, dormance, essais sur le terrain, photopériode, bris de repos.

[Traduit par la rédaction]

Introduction

Levins (1968) established three concepts for assessing the validity of biological models: reality, accuracy (or precision), and generality. A model has high reality, if it represents causal relationships and if its structure accounts for all essential aspects in the study object. A model of low reality, on the contrary, is based on noncausal correlations or it is lacking in some essential aspects. A model has high accuracy if its predictions correspond closely to observations and high generality if it can be applied to a wide range of cases, in terms of number of species or locations. According to Levins (1968) it is not possible to maximize all three aspects of validity in one model, so one aspect has to be sacrificed for the other two.

Modelling of plant phenology has a long tradition, starting from the early work of Reamur during the 18th century (Wang 1960). The main emphasis historically in plant phenology has been in model accuracy, and model realism has received much less attention. This is indicated in the structure of most plant phenological models: they correlate the timing of various developmental events (vegetative bud burst, flowering) as accurately as possible with climatic indices (degree-days, chilling units) but do not consider explicitly the ecophysiological interpretation of the model variables (for reviews, see Wang 1960; Sarvas 1972, 1974; Cannell 1989, 1990; Fuchigami et al. 1982; Hänninen 1990a).

Emphasizing the concept of realism, Hänninen (1990a) analysed the prevailing models developed for bud burst phenology of trees from cool and temperate regions. Bud burst is a result of ontogenetic development, i.e., a sequence of morphological changes inside the bud (Romberger 1963; Sarvas 1972, 1974). The rate of ontogenetic development is either implicitly or explicitly considered in models of bud burst phenology: the higher the rate, the earlier bud burst occurs. In modelling the rate of ontogenetic development, Hänninen (1990a) presented a general framework in which any model for bud burst can be presented using three submodels, each submodel addressing one of three essential ecophysiological aspects of bud burst: the rest break, the shift to growth competence, and the course of bud development to bursting (Fig. 1).

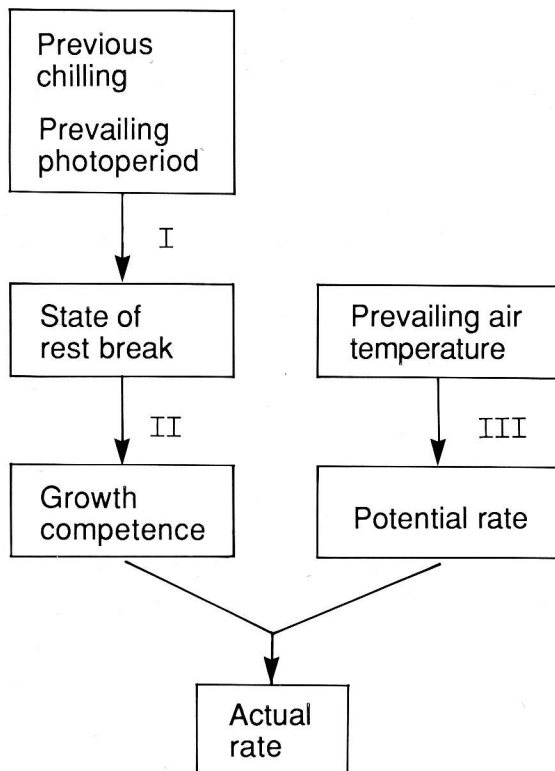
After growth cessation and bud set, the buds are in a state of rest, i.e., they have no or limited ability for ontogenetic development towards bud burst (Doorenbos 1953; Samish

1954). Rest break refers to the invisible physiological changes in the dormant bud that lead to full ability for ontogenetic development, i.e., the attainment of the state of quiescence (Romberger 1963; Weiser 1970; Kobayashi and Fuchigami 1983a; Hänninen 1990a). The first submodel, rest break, considers the effects of either chilling or photoperiod on the process of rest break (Fig. 1). The second submodel, growth competence, considers the effect of rest break on the growth competence of the buds, i.e., on their ability for ontogenetic development. This submodel links the effects of rest-breaking environmental factors on the prevailing rate of ontogenetic development. The third submodel, ontogenetic development, considers the direct effect of prevailing air temperature on the rate of bud development towards bursting (Fig. 1).

When ecophysiological realistic models are sought, a repeated process of model formulation and testing is needed. In the framework of Hänninen (1990a), any published model for tree bud burst is a special case in a three-dimensional space of submodels, each submodel specifying the ecophysiological assumptions implied in the existing model (Fig. 1). There is also no a priori reason why the assumed mechanisms (submodels) could not exist in previously unrecognized combinations. Thus this general framework (Hänninen 1990a) can also be used for synthesizing and exploring novel models for experimental testing. Identifying mechanistically correct models of bud burst, either novel or published, is critical to evaluating the impact of global change on tree phenology. Cannell and Smith (1983, 1986) and Murray et al. (1989) developed a simulation approach for examining the effects of the predicted climatic warming on bud burst phenology and risk of frost damage in trees. For conditions simulating possible future climates in Scotland they found several patterns of change in bud burst phenology, some indicating increased risk of frost damage. Hänninen (1991) applied a similar modelling approach to Finnish conditions. In his simulations premature bud burst sometimes took place during midwinter warm spells that were followed by periods of frost reaching -25°C . According to these simulations, climatic warming would cause heavy frost damage to trees in Finland.

The general aim of the present study was to facilitate the development of ecophysiological realistic models for tree bud burst, with special reference to assessing the consequences of the predicted climatic change. The specific aims

Fig. 1. Schematic presentation of ecophysiological factors affecting the rate of ontogenetic development towards bud burst. Submodels: I, rest break; II, growth competence; III, ontogenetic development.



were (i) to develop the framework of Hänninen (1990a) further, (ii) to use the framework for formulating hypothetical models for experimental testing, (iii) to test the formulated models with *Pinus sylvestris* L. saplings growing in semi-controlled field conditions corresponding to climatic change, and (iv) to test with the *Pinus* saplings the hypothesis that climatic change would cause a premature bud burst and subsequent frost damage to trees.

Modelling framework

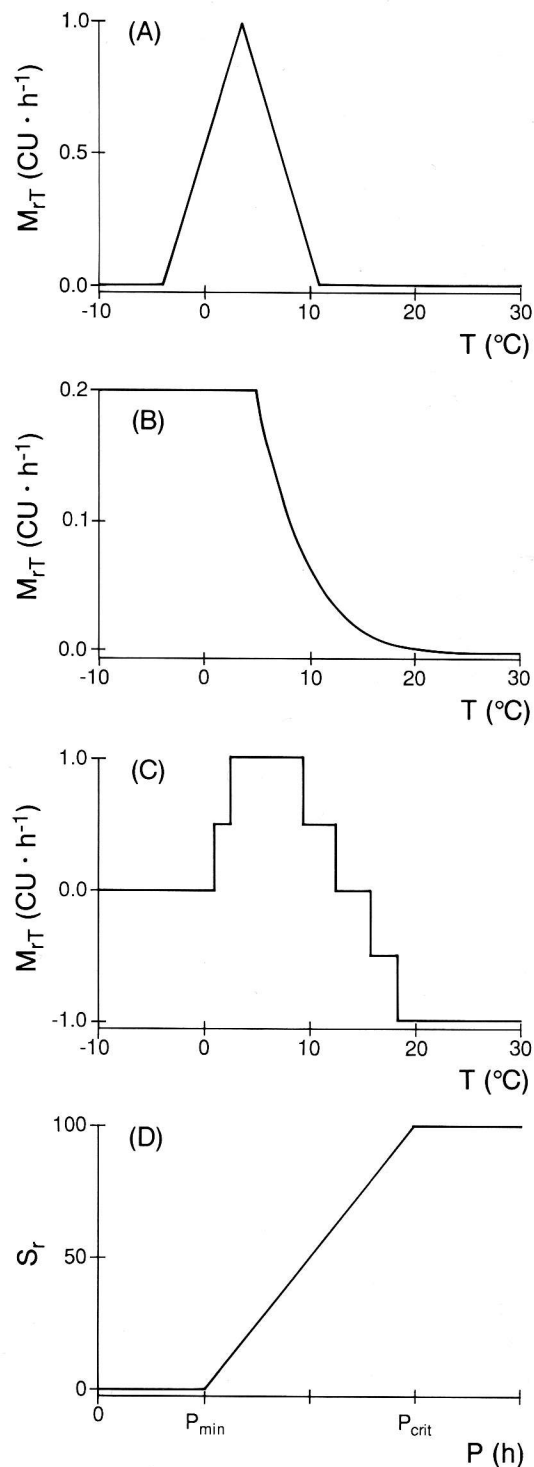
Analysis of the models

The developmental status of the bud at any given moment t is described with the values of three state variables, i.e., state of rest break $S_r(t)$; growth competence, $C(t)$; and state of ontogenetic development, $S_o(t)$. When calculating the values of the three state variables, general and specific equations are used. The general equations determine the basic model structure but leave the assumptions concerning rest break, growth competence, and ontogenetic development unspecified. These assumptions are specified with additional equations, referred to later as submodels. The general equations are provided in the text, whereas the equations for submodels are located in Tables 1–3.

State of rest break $S_r(t)$

According to the prevailing view, the process of rest break consists of a sequence of changes in the balance between growth promoters and growth inhibitors in the bud, but the exact nature of these changes still remains unknown (Smith and Kefford 1964; Perry 1971; Wareing and Phillips 1978,

Fig. 2. Submodels for rest break. (A–C) Submodels for the air temperature response of rate of rest break, M_{rT} . CU, arbitrary chilling unit. (D) A submodel for the dependency of state of rest break, S_r , on the prevailing photoperiod, P . P_{\min} , minimum photoperiod prevailing at winter solstice; P_{crit} , photoperiod requirement of rest completion. For the equations and references, see Table 1.



pp. 269–275; Hanover 1980; Dennis 1987; Powell 1987; Rinne et al. 1994a, 1994b). The state of rest break $S_r(t)$ indicates how a large proportion of these changes has taken place up to the moment t . The state of rest break is modelled

Table 1. Submodels for rest break.

(i) Submodel in Fig. 2A (Sarvas 1974; Hänninen 1990b)

$$0 \text{ CU h}^{-1}, \quad T(t) \leq -3.4^\circ\text{C}$$

$$M_{rr}(t) = \begin{cases} a_1 \cdot T(t) + a_2, & -3.4^\circ\text{C} < T(t) \leq 3.5^\circ\text{C} \\ a_3 \cdot T(t) + a_4, & 3.5^\circ\text{C} < T(t) \leq 10.4^\circ\text{C} \end{cases}$$

$$0 \text{ CU h}^{-1}, \quad T(t) > 10.4$$

$$a_1 = 0.159 \text{ CU h}^{-1} \text{ }^\circ\text{C}^{-1} \text{ (CU = arbitrary chilling unit),}$$

$$a_2 = 0.506 \text{ CU h}^{-1}, a_3 = -0.159 \text{ CU h}^{-1} \text{ }^\circ\text{C}^{-1},$$

$$\text{and } a_4 = 1.621 \text{ CU h}^{-1}$$

(ii) Submodel in Fig. 2B (Landsberg 1974)

$$0.2 \text{ CU h}^{-1}, \quad T(t) < 5^\circ\text{C}$$

$$M_{rr}(t) = \frac{1 \text{ CU h}^{-1} \text{ }^\circ\text{C}}{T(t)}, \quad T(t) \geq 5^\circ\text{C}$$

(iii) Submodel in Fig. 2C (Richardson et al. 1974)

$$0.0 \text{ CU h}^{-1}, \quad T(t) < 1.4^\circ\text{C}$$

$$0.5 \text{ CU h}^{-1}, \quad 1.4^\circ\text{C} \leq T(t) < 2.4^\circ\text{C}$$

$$1.0 \text{ CU h}^{-1}, \quad 2.4^\circ\text{C} < T(t) \leq 9.1^\circ\text{C}$$

$$M_{rr}(t) = 0.5 \text{ CU h}^{-1}, \quad 9.1^\circ\text{C} < T(t) \leq 12.4^\circ\text{C}$$

$$0.0 \text{ CU h}^{-1}, \quad 12.4^\circ\text{C} < T(t) \leq 15.9^\circ\text{C}$$

$$-0.5 \text{ CU h}^{-1}, \quad 15.9^\circ\text{C} < T(t) \leq 18.0^\circ\text{C}$$

$$-1.0 \text{ CU h}^{-1}, \quad T(t) > 18.0^\circ\text{C}$$

(iv) Submodel in Fig. 2D

$$0, \quad \text{before Dec. 21}$$

$$S_r(t) = 100 \cdot \frac{P(t) - P_{\min}}{P_{\text{crit}} - P_{\min}}, \quad \text{after Dec. 21}$$

P_{\min} is the minimum photoperiod prevailing at winter solstice, and P_{crit} is the photoperiod requirement of rest completion.

NOTE: $M_{rr}(t)$ is the air temperature response of rate of rest break, $T(t)$ is the air temperature, $S_r(t)$ is the state of rest break, and $P(t)$ is the prevailing photoperiod.

with a dimensionless relative scale from zero (rest initiation, none of the required biochemical changes have occurred) to 100 (rest completion, biochemical changes completed).

The effect of chilling on the state of rest break $S_r(t)$ is modelled by calculating the rate of rest break $M_r(t)$, i.e., the momentary change in the value of $S_r(t)$ (cf. Hari 1968). The general equation for $M_r(t)$ is

$$[1] \quad M_r(t) = 100 \frac{M_{rr}(t)}{C_{\text{crit}}}$$

Table 2. Submodels for growth competence, $C(t)$.

(i) Submodel in Fig. 3A (Sarvas 1972, 1974; Richardson et al. 1974; Hänninen 1990a)

$$C(t) = \begin{cases} 0, & S_r(t) < 100 \\ 1, & S_r(t) = 100 \end{cases}$$

(ii) Submodel in Fig. 3B (Landsberg 1974; Campbell 1978; Hänninen 1990a)

$$C(t) = \begin{cases} C_{\min 1} + \left(\frac{1 - C_{\min 1}}{100}\right) \cdot S_r(t), & S_r(t) < 100 \\ 1, & S_r(t) = 100 \end{cases}$$

$C_{\min 1}$ is the initial minimum growth competence.

(iii) Submodel in Fig. 3C (Cannell and Smith 1983)

$$0, \quad \text{before Feb. 1}$$

$$C(t) = C_{\min 2} + \left(\frac{1 - C_{\min 2}}{100}\right) \cdot S_r(t), \quad \text{after Feb. 1 } S_r(t) < 100$$

$$1, \quad \text{after Feb. 1 } S_r(t) = 100$$

$C_{\min 2}$ is the initial minimum growth competence.

(iv) Submodel in Fig. 3D (Fuchigami et al. 1982; Hänninen 1990a)

$$1 - \left(\frac{1 - C_{\min 3}}{S_{r1}}\right) \cdot S_r(t), \quad S_r(t) < S_{r1}$$

$$C(t) = C_{\min 3} + \left(\frac{1 - C_{\min 3}}{100 - S_{r1}}\right) \cdot (S_r(t) - S_{r1}), \quad S_{r1} \leq S_r(t) < 100$$

$$1, \quad S_r(t) = 100$$

$C_{\min 3}$ is the minimum growth competence, and S_{r1} is the state of rest break, both at the beginning of the period of increasing growth competence.

(v) Submodel in Fig. 3E (Hänninen 1990a)

$$0, \quad S_r(t) < S_{r2}$$

$$C(t) = \frac{S_r(t) - S_{r2}}{100 - S_{r2}}, \quad S_{r2} \leq S_r(t) < 100$$

$$1, \quad S_r(t) = 100$$

S_{r2} is the state of rest break required for increase in growth competence to begin.

(vi) Submodel in Fig. 3F (Hänninen 1990a; see also Vegis 1964)

$$0, \quad S_r(t) < S_{r3}$$

$$C(t) = \frac{(1 - C_{\min 4} - \Delta C(t)) \cdot (S_r(t) - S_{r3}) + C_{\min 4} + \Delta C(t)}{100 - \Delta S_r - S_{r3}}$$

$$S_{r3} < S_r(t) \leq (100 - \Delta S_r(t))$$

$$1, \quad S_r(t) = (100 - \Delta S_r(t))$$

Table 2 (concluded).

where (Fig. 3G)

$$0, \quad T(t) < T_1$$

$$\Delta C(t) = \left(\frac{\Delta C_{\max}}{T_2 - T_1} \right) \cdot (T(t) - T_1), \quad T_1 \leq T(t) < T_2$$

$$\Delta C_{\max}, \quad T(t) \geq T_2$$

and (Fig. 3H)

$$0, \quad T(t) < T_1$$

$$\Delta S_r(t) = \left(\frac{\Delta S_{r\max}}{T_2 - T_1} \right) \cdot (T(t) - T_1), \quad T_1 \leq T(t) < T_2$$

$$\Delta S_{r\max}, \quad T(t) \geq T_2$$

S_{r3} is the state of rest break required for increase in growth competence to begin, $C_{\min4}$ is the minimum growth competence after the attainment of S_{r3} , $\Delta C(t)$ is the increase in the growth competence due to prevailing air temperature at the time of attainment of S_{r3} , ΔS_r is the decrease in the value of S_r required for attainment of full growth competence due to prevailing air temperature, ΔC_{\max} and $\Delta S_{r\max}$ are maximum value of ΔC and ΔS_r , respectively, and T_1 and T_2 are the lower and higher limits of the temperature range, where the prevailing air temperature increases the growth competence, respectively.

NOTE: $S_r(t)$ is the state of rest break.

where $M_{rT}(t)$ is the air temperature response of rate of rest break (to be specified with a submodel; Figs. 2A–2C), and C_{crit} is the genotype-specific time integral of M_{rT} at the time of rest completion, referred to later as the chilling requirement of rest completion. The variable $M_{rT}(t)$ is expressed in arbitrary chilling units (CU) per unit of time, the parameter C_{crit} in the corresponding chilling units, and the variable $M_r(t)$ in the dimensionless units of state of rest break, per unit of time.

By definition, the state of rest break at a given moment t , $S_r(t)$, is calculated by integrating the rate of rest break (eq. 1) from the beginning of the rest period, t_{ri} , up to the moment t :

$$[2] \quad S_r(t) = \int_{t_{ri}}^t M_r(\tau) d\tau$$

When $S_r(t)$ attains the value of 100, then the model predicts that rest completion, i.e., attainment of quiescence, will occur. After that the value of $S_r(t)$ is 100 until the time of next rest initiation, when the value is set at zero.

Contrary to the chilling models, the effect of photoperiod on the state of rest break is modelled directly with a submodel (Fig. 2D), without the rate–state approach (cf. Nizinski and Saugier 1988). Thus in the case of the photoperiod models, no general equations for rate and state of rest break are used.

Growth competence $C(t)$

Growth competence describes the physiological ability of the

Table 3. Submodels for ontogenetic development.

(i) Submodel in Fig. 4A (Sarvas 1972; Hänninen 1990b)

$$0 \text{ HU h}^{-1}, \quad T(t) \leq 0^\circ\text{C}$$

$$m_{oT}(t) = \frac{a_5}{1 + e^{a_6 \cdot (T(t) - a_7)}}, \quad T(t) > 0^\circ\text{C}$$

$a_5 = 28.4 \text{ HU h}^{-1}$ (HU = arbitrary high temperature unit),

$a_6 = -0.185^\circ\text{C}$, and $a_7 = 18.4^\circ\text{C}$.

(ii) Submodels in Fig. 4B

$$0 \text{ HU h}^{-1}, \quad T(t) < T_{\text{thr}}$$

$$m_{oT}(t) = 1 \text{ HU h}^{-1} \text{ }^\circ\text{C}^{-1} \cdot (T(t) - T_{\text{thr}}), \quad T(t) \geq T_{\text{thr}}$$

The threshold temperature T_{thr} applied in the three submodels is $+2^\circ\text{C}$, $+5^\circ\text{C}$, and $+8^\circ\text{C}$, respectively.

NOTE: $m_{oT}(t)$ is the air temperature response of potential rate of ontogenetic development and $T(t)$ is the air temperature.

bud for ontogenetic development. Growth competence is modelled with a dimensionless relative scale from zero (no ontogenetic development in any prevailing environmental conditions) to 1 (ontogenetic development at the potential rate determined by prevailing air temperature) (Figs. 1 and 3) (cf. Hari et al. 1970).

State of ontogenetic development $S_o(t)$

The ontogenetic development towards bud burst is a sequence of morphological changes in the bud (Romberger 1963; Sarvas 1972, 1974). The variable state of ontogenetic development, $S_o(t)$, indicates how large a proportion of the sequence has occurred up to the moment t . The state of ontogenetic development is modelled with a dimensionless relative scale from zero (formation of bud completed, no ontogenetic development towards bud burst) to 100 (stage of bud burst attained).

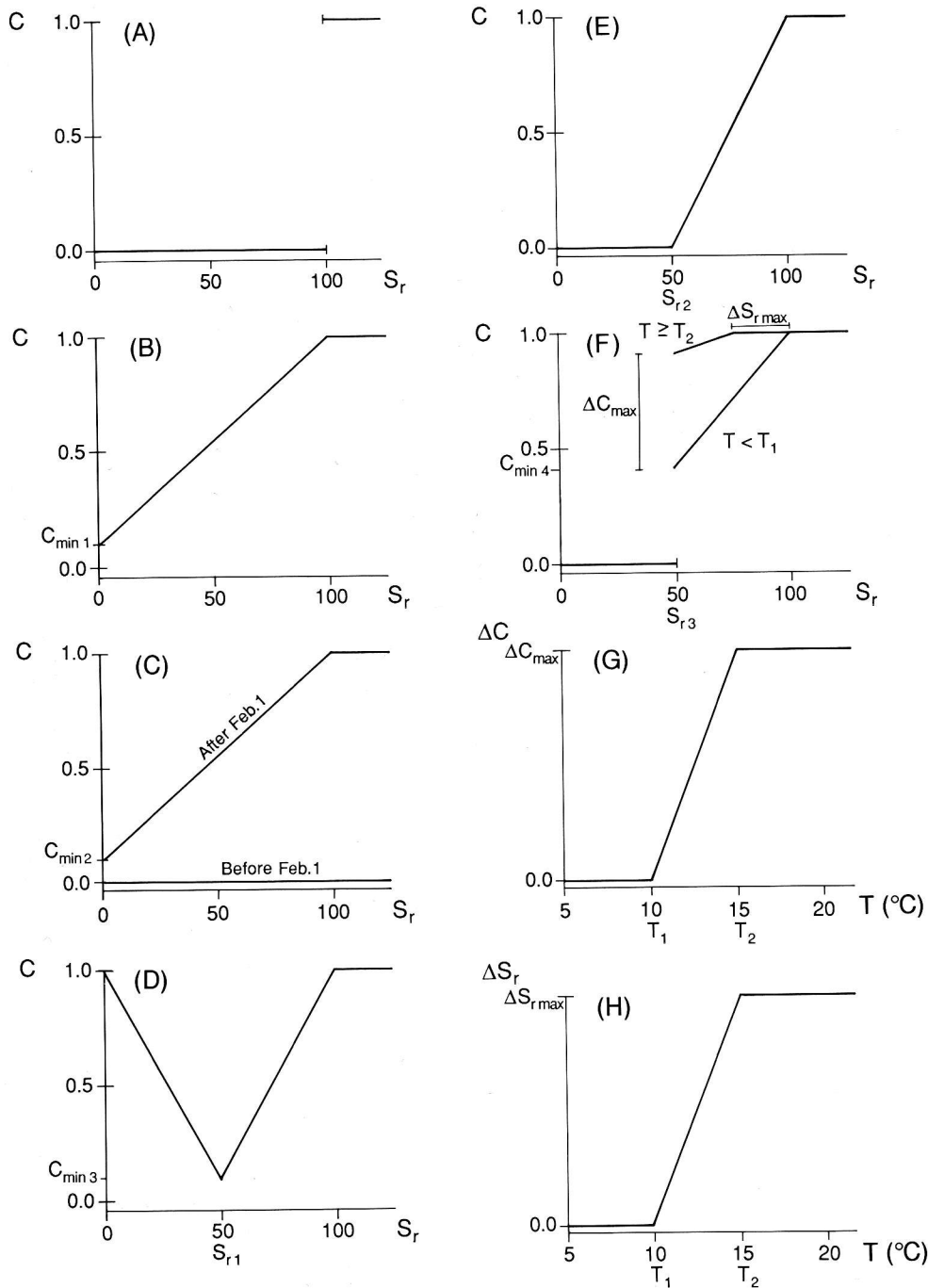
The state of ontogenetic development, $S_o(t)$, is calculated via the rate of ontogenetic development, $M_o(t)$, basically in a similar manner as the state of rest break is calculated in the case of chilling models via the rate of rest break (eqs. 1 and 2) (cf. Hari 1968). In the case of the state of ontogenetic development, however, an additional general equation (eq. 4) is needed because the rate of ontogenetic development depends on the growth competence and on the prevailing air temperature (Fig. 1).

The potential rate of ontogenetic development, $m_o(t)$, describes the direct effect of air temperature on the rate of ontogenetic development:

$$[3] \quad m_o(t) = 100 \frac{m_{oT}(t)}{H_{\text{crit}}}$$

where $m_{oT}(t)$ is the air temperature response of potential rate of ontogenetic development (to be specified with a submodel, Fig. 4), and H_{crit} is the genotype-specific time integral of m_{oT} at the time of bud burst, referred to later as the high-

Fig. 3. Submodels for growth competence. (A–F) Submodels for the dependency of the growth competence, C , on the state of rest break, S_r . The prevailing date in (C) and the prevailing air temperature in (F) are additional factors affecting the growth competence. (G and H) The effect of air temperature on the growth competence in (F). The lower line in (F) represents the case when $T < T_1$ ($\Delta C = 0$; $\Delta S_r = 0$). When $T \geq T_1$, then the ordinate of the point (S_{r3} , $C_{\min 4}$) is increased by ΔC obtained from (G), and the abscissa of the point (100, 1) is decreased by ΔS_r obtained from (H). The upper line represents the case when $T \geq T_2$ ($\Delta C = \Delta C_{\max}$; $\Delta S_r = \Delta S_{r\max}$). For the equations and references, see Table 2.



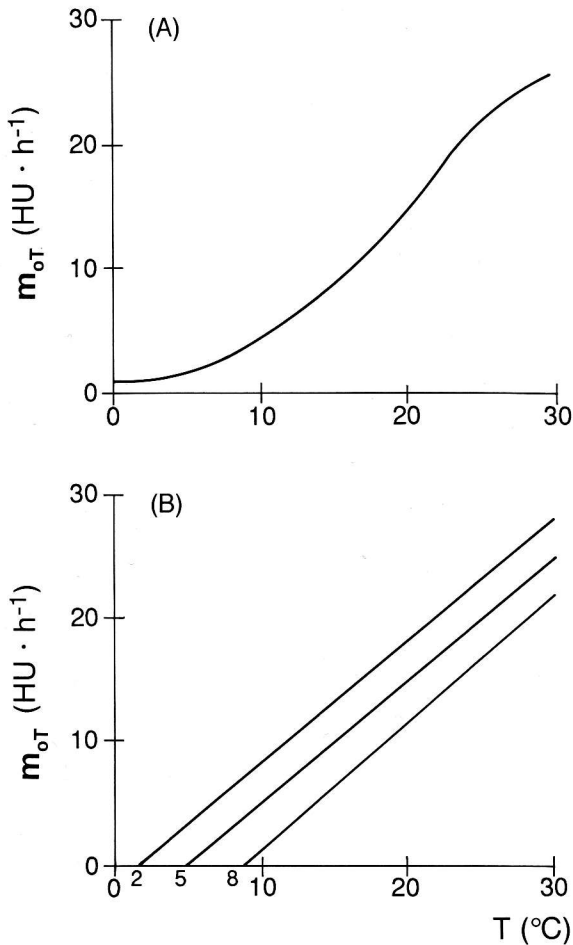
temperature requirement of bud burst. The variable $m_{o7}(t)$ is expressed in arbitrary high-temperature units (HU) per unit of time, and the parameter H_{crit} is expressed in the corresponding arbitrary high-temperature units. The variable $m_o(t)$ is expressed in the dimensionless units of the state of ontogenetic development, per unit of time.

The actual rate of ontogenetic development, $M_o(t)$, is calculated as (Fig. 1) (cf. Hari et al. 1970)

$$[4] \quad M_o(t) = C(t) m_o(t)$$

where $C(t)$ is the prevailing growth competence, and $m_o(t)$ is the prevailing potential rate of ontogenetic development.

Fig. 4. Submodels for ontogenetic development. (A and B) The air temperature response of potential rate of ontogenetic development, m_{oT} . HU, an arbitrary high temperature unit. The numbers 2, 5, and 8 along the x-axis in (B) denote the threshold temperature, T_{thr} . For the equations and references, see Table 3.



$M_o(t)$ is expressed in dimensionless units of the state of ontogenetic development, per unit of time.

By definition, the state of ontogenetic development at time t , $S_o(t)$, is obtained by integrating the actual rate of ontogenetic development (eq. 4) from the beginning of the rest period, t_{ri} , up to the moment t :

$$[5] \quad S_o(t) = \int_{t_n}^t M_o(\tau) d\tau$$

When $S_o(t)$ attains the value of 100, then the model predicts that bud burst will occur (Fig. 5). The value of $S_o(t)$ is set at zero at the next rest initiation.

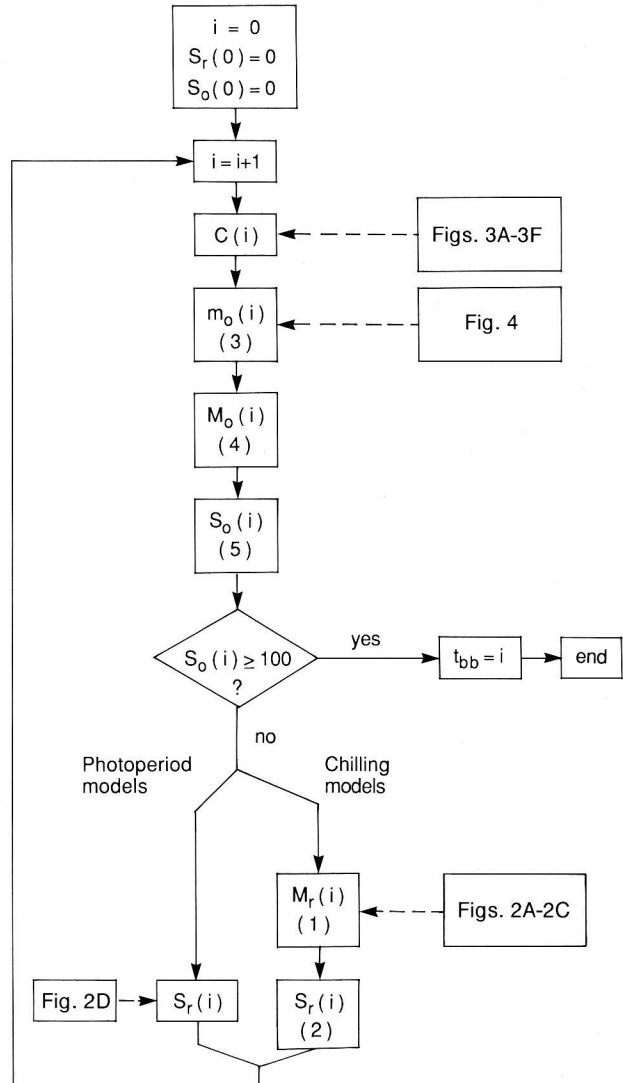
Submodels

Rest break

In the present study, three chilling submodels and one photoperiod submodel were considered for rest break (Fig. 2; Table 1).

The first chilling submodel assumes that the rate of rest break has its maximum at 3.5°C and decreases towards both higher and lower temperatures. No rest break takes place in

Fig. 5. Calculation algorithm used with all of the 96 models developed in the study. Arrows indicate sequence of the calculations; arrows with broken lines indicate selection of an optional submodel for each of the three submodel categories. Figure 4 includes threshold temperatures +2, +5, and +8°C. Numbers in parentheses refer to equations in the text. i , time step applied (1 hour, 1 day); $C(i)$, growth competence; $m_o(i)$, potential rate of ontogenetic development; $M_o(i)$, actual rate of ontogenetic development; $S_o(i)$, state of ontogenetic development; t_{bb} , time of bud burst; $M_r(i)$, rate of rest break; $S_r(i)$, state of rest break.

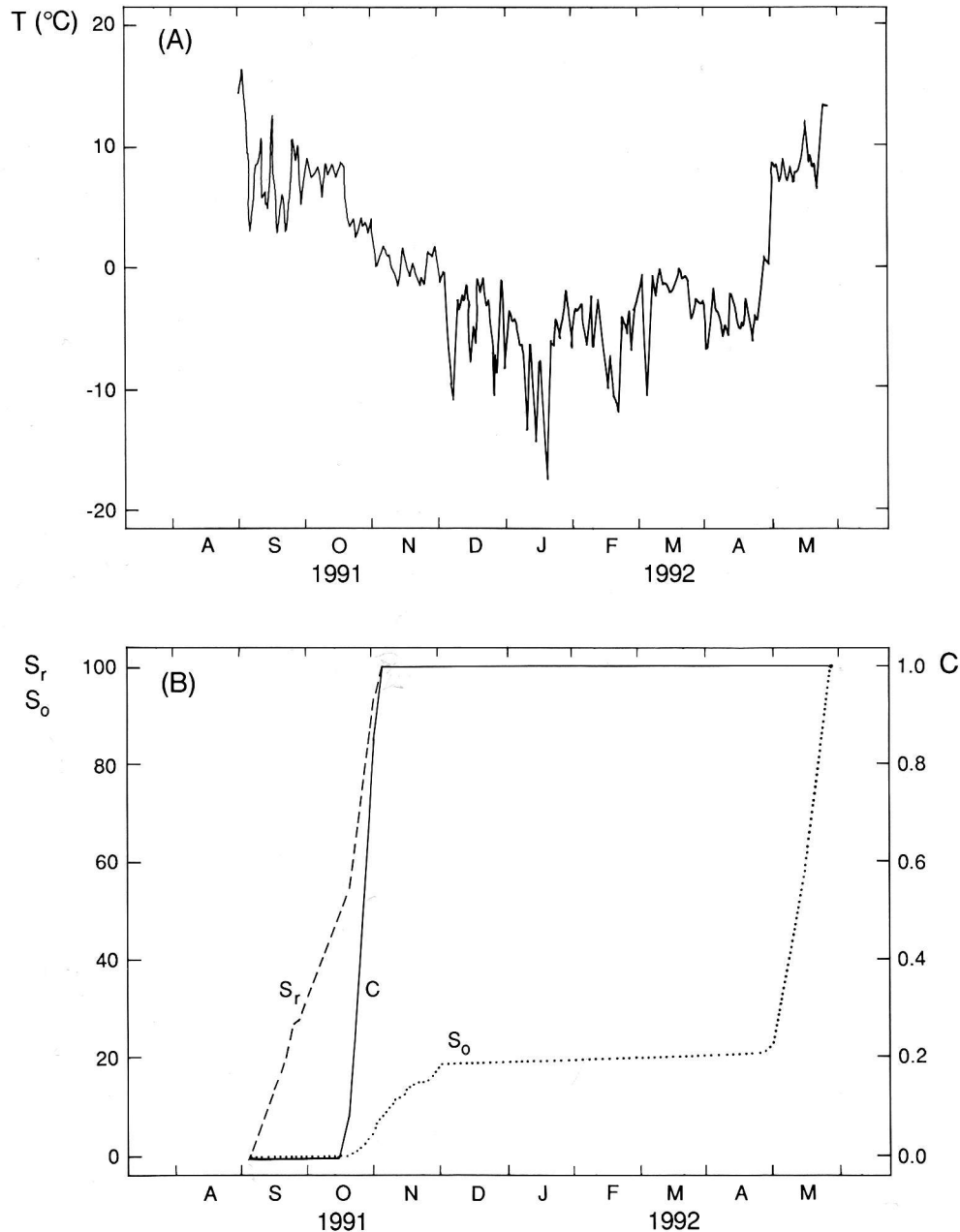


temperatures below -3.4°C or above 10.4°C (Fig. 2A; Table 1).

The second chilling submodel assumes that rest break takes place at the maximum rate in all temperatures equal to or below +5°C. In temperatures higher than +5°C the rate of rest break decreases exponentially (Fig. 2B; Table 1).

The third chilling submodel assumes that the maximum rate of rest break is obtained in any temperature between +2.4 and +9.1°C. The rate of rest break decreases towards both lower and higher temperatures, and no rest break takes place in temperatures below 1.4°C. Temperatures above 15.9°C cause a negation of the rest-breaking effect of previ-

Fig. 6. (A) Daily mean temperatures in treatment 3 of the scenario experiment (Table 4). (B) Simulated development of the bud for the temperature conditions of (A). The model used in the simulation was specified by selecting the submodels represented by Figs. 2A, 3E, and 4A for rest break, growth competence, and ontogenetic development, respectively. S_r , state of rest break; S_o , state of ontogenetic development; C , growth competence.



ous chilling, i.e., the rate of rest break is negative (Fig. 2C; Table 1).

In the photoperiod model it was assumed that the state of rest break is zero until the winter solstice (Dec. 21), after which it increases linearly with increasing photoperiod until a critical photoperiod value is attained (Fig. 2D; Table 1).

Growth competence

In the present study, six submodels for growth competence were considered (Fig. 3; Table 2).

The first submodel assumes that the bud has no growth competence before rest completion. At the time of rest com-

pletion the bud abruptly attains full growth competence (Fig. 3A; Table 2).

In the second submodel, a gradual increase in growth competence during the rest period from an initial minimum value was assumed (Fig. 3B; Table 2).

The third submodel was identical to the second but involved an additional assumption that the growth competence is zero before February 1, regardless of the state of rest break (Fig. 3C; Table 2).

In the fourth submodel, subsequent periods of decreasing and increasing growth competence during the rest period were assumed (Fig. 3D; Table 2).

The fifth submodel for growth competence is intermediate between the first two. It assumes that the bud has no growth competence during the initial phases of rest. The growth competence starts to increase gradually with increasing state of rest break after the state of rest break has attained a critical value (Fig. 3E; Table 2).

The sixth submodel for growth competence is identical to the fifth, but involves an additional assumption that at a given range of state of rest break, high air temperatures increase the growth competence (Figs. 3F–3H; Table 2).

Ontogenetic development

In the present study, four submodels for the air-temperature response of potential rate of ontogenetic development ($m_{oT}(t)$ in eq. 3) were considered (Fig. 4; Table 3).

The first submodel for $m_{oT}(t)$ assumes a sigmoidal response and no ontogenetic development below 0°C (Fig. 4A; Table 3).

In the second, third, and fourth submodels for $m_{oT}(t)$ it is assumed that no ontogenetic development takes place below a threshold temperature and that the rate of ontogenetic development increases linearly with increasing temperature above the threshold. The threshold temperatures applied in the three submodels are +2, +5, and +8°C, respectively (Fig. 4B; Table 3).

Synthesis of the models

In the present study, four, six, and four submodels were considered for rest break, growth competence, and ontogenetic development, respectively (Figs. 2–4; Tables 1–3). By combining these 14 submodels in all possible permutations, a total of $4 \times 6 \times 4 = 96$ models were obtained for experimental testing. Regardless of which submodel is specified for each of the three submodels, the sequence of calculations is always the same, reflecting the assumed causal connections between the modelled phenomena (Figs. 1, 5).

Simulation example

To illustrate how the development of the buds is simulated with this approach, a model was synthesized by selecting the submodels represented by Figs. 2A, 3E, and 4A for rest break, growth competence, and ontogenetic development, respectively. Temperature data from treatment 3 of the scenario experiment described later (cf. Table 4) were used as input for the calculations. The values $C_{crit} = 30$ CU and $H_{crit} = 150$ HU were used for the chilling requirement of rest completion and high-temperature requirement of bud burst, respectively (Hänninen 1991). Otherwise the calculations were carried out as described in Materials and methods, specifications for the calculations.

Air temperatures dropped below +10°C in the beginning of September (Fig. 6A). As these temperatures belong to the rest breaking range (Fig. 2A), the rest break was initiated (increasing S_r , Fig. 6B). Despite the ongoing process of rest break, the buds had no growth competence during the first weeks of the simulation ($C = 0$, Fig. 6B) because the submodel for growth competence requires that $S_r = 50$ before growth competence starts to increase (Fig. 3E).

Since the bud had no growth competence, no ontogenetic development took place during the first weeks of the simulation ($S_o = 0$, Fig. 6B) despite the air temperatures being well above 0°C (Fig. 6A), i.e., in the range promoting

Table 4. Experimental treatments of the study.

Treatment code	Description	<i>n</i>
Scenario experiment		
1990–1991		
1	Open air control	2
2	Elevated air temp. 1	4
1991–1992		
3	Open air control	4
4	Chamber control	4
5	Elevated CO ₂	4
6	Elevated air temp. 2	4
7	Elevated CO ₂ + elevated air temp. 2	4
8	Elevated air temp. 3	4
Photoperiod experiment		
	Open air control	15
	Chamber control	15
	Short day (5 h)	15

NOTE: See Figs. 6A and 7 for the temperature treatments of the scenario experiment. *n*, number of experimental saplings, nine buds in each sapling observed.

ontogenetic development (Fig. 4A). Ontogenetic development started when growth competence began to increase (increasing C and S_o , Fig. 6B). Due to the low growth competence, however, the rate of ontogenetic development was low. The rate of ontogenetic development did not increase with increasing growth competence because the increase in growth competence (Fig. 6B) was paralleled by a simultaneous decrease in temperature (Fig. 6A). S_o attained the value of about 20 during autumn, indicating the occurrence of approximately 20% of the ontogenetic sequence towards bud burst. During winter a slight increase in S_o (Fig. 6B) took place as air temperature rose temporarily above 0°C even though the daily mean temperature remained below 0°C (Fig. 6A). During spring rapid ontogenetic development took place (rapidly increasing S_o , Fig. 6B), as comparatively high temperatures were accompanied by the maximal growth competence of the bud. The simulated bud burst took place on May 27 ($S_o = 100$, Fig. 6B).

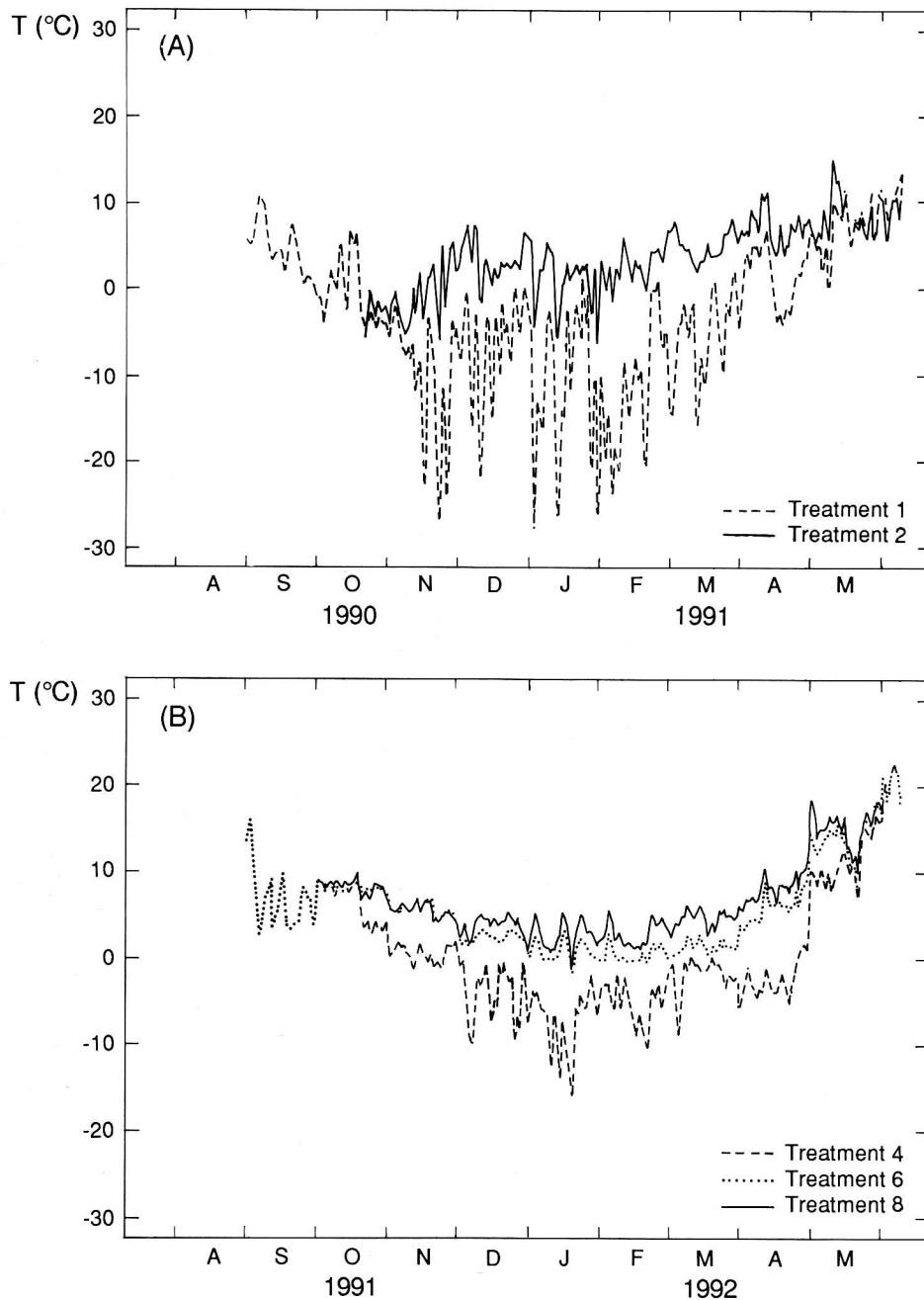
Materials and methods

Scenario experiment

In this experiment the models of bud burst phenology were tested with *P. sylvestris* saplings growing in semicontrolled conditions at their natural site. The experimental treatments were designed to describe the future conditions predicted for the site due to climatic change (Table 4). The experiment was carried out in a naturally regenerated 20- to 30-year-old *P. sylvestris* stand in eastern Finland near the Mekrijärvi Research Station (62°47'N, 30°58'E, 144 m asl). The trees are growing on sandy soil of low fertility. The mean annual temperature and rainfall at the site are +2.0°C and 600 mm, respectively. No management practices have been carried out at the site.

Each of the experimental saplings (height 2–3 m) was surrounded by a chamber (2.5 × 2.5 × 3.5 m). Four

Fig. 7. Daily mean temperatures in the scenario experiment. The temperatures in treatments 5 and 7 were similar to those in treatments 4 and 6, respectively. For treatment 3, see Fig. 6A.



saplings were used for each treatment. The south and west walls of the chambers were constructed of radiative heating glass, and the north and east walls of greenhouse plastic. Below ground level, the walls were constructed by placing styrofoam plates (50 mm in thickness) about half a metre into the soil. A clear shutter 1.5 m square was constructed on top of the chambers. The chamber shutters for control saplings were kept open all the time; those on other chambers were kept closed during the treatments. During sunny weather in spring and summer, however, the shutters were opened to avoid excess heating of the saplings. During winter, snow was shovelled into the chambers with closed shutters to keep precipitation similar to that for chambers with open shutters.

The temperature was elevated during autumn, winter, and

spring (Fig. 7). Summertime warming was not included, since most of the climatic scenarios for Finland involve drastic warming for wintertime and only moderate warming for summertime (e.g., 6 and 2°C, respectively; Bach 1987; Kettunen et al. 1987). However, incoming solar radiation slightly raised the temperatures in the chambers over the open air during summer.

The warming treatments were designed to correspond to the warmest winters predicted for the site after doubling of the atmospheric carbon dioxide concentration. This was because a premature bud burst with subsequent frost damage occurred in the simulations of Hänninen (1991) only during these winters. The temperature treatments were designed in two steps. (i) Temperature data for 73 years were created by

elevating the mean daily temperatures in a temperature record over a 73-year period according to the climatic scenario corresponding to doubling of the atmospheric carbon dioxide concentration. Depending on the month, the daily elevation was from 3.2 to 6.2°C (Bach 1987; Kettunen et al. 1987; Hänninen 1991). (ii) Three winters among the warmest in the scenario temperature data were then selected for the warming treatments. Among the warming treatments of 1991–1992, treatments 6 and 7 had the same temperature elevation, but in treatment 8 the temperature was elevated more (Fig. 7; Table 4). Contrary to the scenario data, heavy frosts were not allowed in the elevated temperature treatments. The minimum temperature in treatments 6–8 was -5.3°C . In treatment 2, however, the minimum temperature dropped during heavy frost to -14.0°C .

The concentration of atmospheric carbon dioxide was elevated on average to 700 ppm in treatments 5 and 7 (Table 4). Due to economic constraints, the elevation of the concentration was carried out only during daytime and only between April 15 and September 15, 1992.

During 1990–1991, the air temperature was monitored by thermohydrographs in standard meteorological screens. One screen was located in the open air and another in one of the four chambers. The hourly temperature readings from these two thermohydrographs represented temperatures for treatments 1 and 2 in the calculations (Table 4). During 1991–1992 the air temperature was monitored automatically in the chambers and in the open air at hourly intervals. Two temperature sensors were located in each of the 20 chambers and beside each of the four open-air control saplings (one sensor in the lower and one in the upper part of the crown). The mean of the corresponding 2 (sensors per sapling) \times 4 (saplings) = 8 temperature readings represented the hourly temperature for each of treatments 3–8 (Table 4).

The height growth of nine buds in each of the saplings was observed during the experiment: the terminal bud of the sapling and the terminal buds of two twigs in each of the four uppermost whorls. A small needle was pushed through the stem approximately 2 cm below the bud, and the distance between the tip of the bud and the needle was measured manually twice a week. The height growth values for days without a measured value were determined by linear interpolation. The time for onset of height growth in each of the nine buds was determined as the day when elongation exceeded 2 mm. The day of onset of height growth for a given treatment was calculated as the mean of the 18 buds (2 saplings \times 9 buds per sapling, treatment 1; Table 4) or 36 buds (4 saplings \times 9 buds per sapling, other treatments; Table 4). To keep the terminology of the present study consistent with the literature, the day of onset of height growth will be referred to as day of bud burst.

Photoperiod experiment

The photoperiod experiment was carried out to test the photoperiod submodel for state of rest break (Fig. 2D; Table 1) with 45 saplings of *P. sylvestris* growing in semicontrolled conditions at their natural site (Table 4). The experiment was located near the scenario experiment on sandy soil with low fertility. The age and height of the experimental saplings were 10–15 years and 1.5–2 m, respectively.

The saplings of the short-day treatment were covered with opaque chambers (inside black, outside white). The cham-

bers were removed daily from 10:00 to 15:00, providing a 5-h photoperiod, which is approximately the minimum natural photoperiod at the site. The saplings of the chamber control were treated similarly, but the chambers were constructed of transparent plastic. Furthermore, saplings of open air control were included in the experiment. The experimental treatments were initiated on January 2, 1992. Determination of day of bud burst was carried out as in the scenario experiment.

Testing of the models

Outline

Each of the 96 synthesized models was tested with data from the scenario experiment. The 14 submodels were taken as they were presented in the literature (Tables 1–3), i.e., their parameter values were not varied. The values of parameters C_{crit} (chilling requirement of rest completion; eq. 1) and P_{crit} (photoperiod requirement of rest completion; Fig. 2D; Table 1) were estimated to give the best fit to the bud burst observations in all eight treatments of the scenario experiment (Table 4). The value of parameter H_{crit} (high-temperature requirement of bud burst; eq. 3) was fixed by fitting the model to the bud burst observations in one treatment, and the observations from the seven other treatments were subsequently used as an independent test of the model.

Ranges of parameters C_{crit} and P_{crit}

To estimate the value of parameter C_{crit} for each of the 72 models involving a chilling submodel for rest break (Figs. 2A–2C), or the value of parameter P_{crit} for each of the 24 models involving the photoperiod submodel for rest break (Fig. 2D), 10 sets of calculations described in Comparison of the models were carried out with each of the 96 models. The value of C_{crit} (or P_{crit}) was varied as 10, 20, . . . , 100% of the maximum value of the parameter. The maximum values were determined by assuming that rest completion took place in all treatments before observed bud burst. To determine the maximum value, consider the first chilling submodel (Fig. 2A; Table 1) as an example. The accumulation of chilling units for the time period from September 1 to the day of bud burst was calculated for each treatment by integrating the function $M_c(t)$ for the submodel (Table 1) for that time period, i.e., by summing the hourly values obtained for the function. As this was done for all eight treatments, the maximum value of C_{crit} for the submodel was calculated as 80% of the minimum accumulation of the chilling units, among the eight treatments. With this procedure, the maximum value of $C_{\text{crit}} = 49.7$ CU was attained for the first chilling submodel (Fig. 2A). With a similar procedure, the maximum values of $C_{\text{crit}} = 29.4$ 41.7 CU were obtained for the second (Fig. 2B) and third (Fig. 2C) chilling submodels, respectively. The maximum value of P_{crit} was obtained for the photoperiod submodel (Fig. 2D) in a similar way, but the accumulation of chilling units until the day of bud burst was replaced by the photoperiod prevailing at the day of bud burst in the procedure. In this way, the maximum value of $P_{\text{crit}} = 9.92$ h for the photoperiod submodel was attained.

Comparison of the models

Assume first a fixed value of C_{crit} for a specific model involving a chilling submodel for rest break (or a fixed value

of P_{crit} for a specific model involving a photoperiod submodel for rest break). The value of H_{crit} for the specific model was determined by fitting the model to the open-air control of 1991–1992 (treatment 3, Table 4). By definition, at the date of bud burst, t_{bb} holds (cf. eqs. 3–5) as follows:

$$[6] \quad S_o(t_{bb}) = \int_{t_{ri}}^{t_{bb}} M_o(\tau) d\tau = 100 \int_{t_{ri}}^{t_{bb}} C(\tau) \frac{m_{oT}(\tau)}{H_{crit}} d\tau = 100$$

thus

$$[7] \quad H_{crit} = \int_{t_{ri}}^{t_{bb}} C(\tau) m_{oT}(\tau) d\tau$$

Subsequently, the model prediction for the day of bud burst was calculated for the other seven treatments by eqs. 1–5 (Fig. 5), using the value of H_{crit} obtained from fitting the model to treatment 3 with eqn. 7. The accuracy of the model was determined by calculating the mean square root error (MSRE) between the predicted and observed date of bud burst for the seven treatments. These calculations were repeated with the 10 values of C_{crit} (or P_{crit}) determined earlier (see Ranges of parameters C_{crit} and P_{crit}). Finally, the 96 models were ranked on the basis of their MSRE. Out of the 10 calculations carried out with a given model, the calculation minimizing the MSRE for the model was selected (i.e., the value of parameter C_{crit} (or P_{crit}) was estimated separately for each of the 96 models).

Specifications for the calculations

The beginning of rest period t_{ri} in eqs. 2, 5, and 7 was set arbitrarily as September 1 (Hänninen 1991). To avoid the integration error inherent in averaging environmental data for nonlinear response functions (Smolander 1984), the air temperature responses of rate of rest break (Figs. 2A–2C; Table 1) and air temperature responses of potential rate of ontogenetic development (Fig. 4; Table 3) were calculated with a time step of 1 h. To facilitate the simulations, the value of growth competence (Fig. 3; Table 2) and the actual rate of ontogenetic development (eq. 4) were calculated with a time step of 1 day. The following parameter values for the submodels were used in the tests of the models: $P_{min} = 4.8$ h, $C_{min1} = 0.1$, $C_{min2} = 0.1$, $C_{min3} = 0.1$, $S_{r1} = 50$, $S_{r2} = 50$, $C_{min4} = 0.4$, $S_{r3} = 50$, $\Delta C_{max} = 0.5$, $\Delta S_{max} = 20$, $T_1 = 10^\circ\text{C}$, and $T_2 = 15^\circ\text{C}$ (Hänninen 1990a).

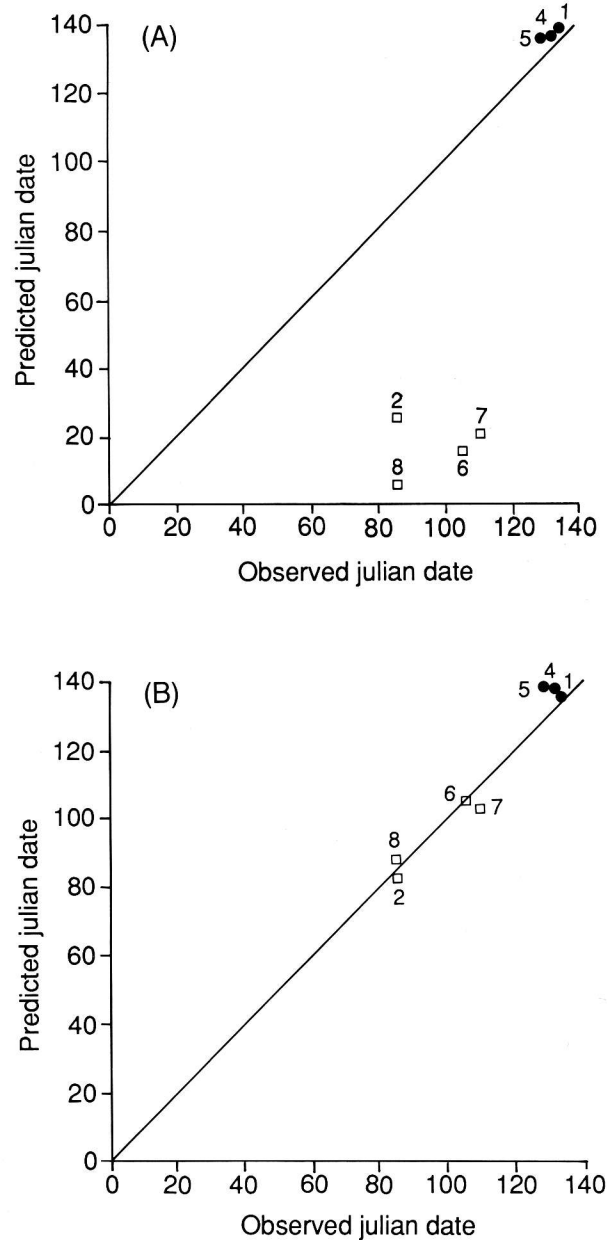
Results of the photoperiod experiment were used for testing the photoperiod submodel for state of rest break (Fig. 2D; Table 1). If the photoperiod has substantial impact on the rest break, then depending on the submodel for growth competence, the saplings of the short-day treatment should show bud burst either not at all (e.g., Fig. 3A) or considerably later than the saplings of the other treatments (e.g., several weeks later, Fig. 3B).

Results

Scenario experiment

Bud burst took place in the natural temperature conditions between May 11 and 14 and in the elevated temperature conditions between March 25 and April 19 (Fig. 8A). Several of the 96 models tested predicted quite accurately the timing of bud burst for natural temperature conditions, but the

Fig. 8. Predicted and observed timing of bud burst of *Pinus sylvestris* saplings in the scenario experiment. (A) Predictions by a model developed for Finnish tree species (Sarvas 1972, 1974; Hänninen 1990b), specified with submodels represented in Figs. 2A, 3A, and 4A. (B) Predictions by the most accurate model of the test, specified with the submodels represented in Figs. 2D, 3C, and 4A. Numbers refer to the treatment code in Table 4. ●, natural temperature conditions; □, elevated temperature conditions. The observed timing of bud burst is the mean of 36 observations (nine buds in each of four saplings), except in treatment 1, where it is the mean of 18 observations (nine buds in each of two saplings).



predicted bud burst was too early for elevated temperature conditions (Fig. 8A). The most accurate models, however, predicted the timing for all treatments with a MSRE of a few days (Fig. 8B; Table 5).

None of the submodels considered did outstandingly better than the others, since almost all of the submodels appear

Table 5. Ranking of the 20 most accurate models for timing of bud burst.

Rank	Submodel													MSRE (days)		
	Rest break				Growth competence						Ontogenetic development					
	Fig. 2A	Fig. 2B	Fig. 2C	Fig. 2D	Fig. 3A	Fig. 3B	Fig. 3C	Fig. 3D	Fig. 3E	Fig. 3F	Fig. 4A	Fig. 4B ^a	Fig. 4B ^b		Fig. 4B ^c	
1				×					×			×				4.1
2				×						×		×				4.2
3				×	×							×				4.3
4				×								×				4.3
5		×										×				4.8
6	×											×				4.8
7			×									×				4.8
8		×			×							×				6.4
9				×		×						×				6.4
10	×													×		7.0
11				×		×							×			7.3
12				×						×			×			8.1
13				×	×								×			8.2
14				×						×			×			8.3
15	×				×										×	8.4
16		×					×							×		8.6
17	×										×				×	8.6
18	×							×					×			8.7
19		×						×					×			8.7
20			×					×					×			8.7

NOTE: Each of the 20 models comprised the three submodels indicated by ×. MSRE, mean square root error between the observed and predicted time of bud burst.

^a $T_{thr} = +2^{\circ}\text{C}$.

^b $T_{thr} = +5^{\circ}\text{C}$.

^c $T_{thr} = +8^{\circ}\text{C}$.

among the most accurate models (a model is a combination of three submodels; Table 5). As an example, the photoperiod submodel (Fig. 2D) seems to be the best among the four submodels for rest break, as it is involved in the four most accurate models. This is, however, not any indication of the superiority of the photoperiod submodel, because the three chilling submodels appear in the models ranked 5–7, and the difference in MSRE between the first and seventh models is only 0.7 days (Table 5). The results for the submodels for ontogenetic development were a little more clear-cut, as the sigmoidal submodel (Fig. 4A) was involved in the nine most accurate models, and the difference between the 1st and 10th models in MSRE is 3.3 days (Table 5).

The saplings of the treatments with elevated concentrations of atmospheric carbon dioxide (treatments 5 and 7) burst bud at approximately the same time as the saplings in the corresponding treatments without the elevated concentrations (treatments 4 and 6, Fig. 8A). Thus, elevating the concentration of atmospheric carbon dioxide during the daytime between April 15 and September 15 did not affect the timing of bud burst during the following spring.

Photoperiod experiment

Bud burst took place in the saplings of the short-day treatment on average 2 and 4 days later than in the saplings of the open-air and chamber controls, respectively (Fig. 9). Larger differences were expected on the basis of the photoperiod submodel for state of rest break. Thus, these results suggest

a falsification of the photoperiod submodel for state of rest break (Fig. 2D; Table 1).

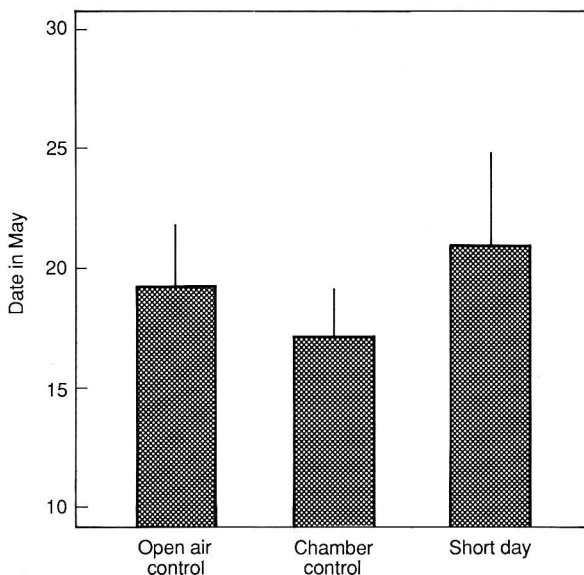
Discussion

Modelling framework

The main purpose for developing the modelling framework in the present study was to facilitate the development of ecophysiological based and realistic models for bud burst phenology in the trees from cool and temperate regions. This purpose implied the need for developing new ecophysiological concepts that link together previous models, which were mainly presented in terms of different climatic concepts. As an example, consider the concepts of rate and state of rest break, $M_r(t)$ and $S_r(t)$, respectively (eqs. 1 and 2; Fig. 6). The concept of state of rest break in the present study has largely the same role as the concepts of chill unit accumulation (e.g., Richardson et al. 1974) or accumulation of chilling unit sum (e.g., Hänninen 1990b) in earlier studies. Temperature response of rate of rest break, M_{rT} in eq. 1, is analogous to the temperature response of hourly or daily accumulation rate of chilling units (Figs. 2A–2C), and the integration in eq. 2 is analogous to summing of hourly or daily rates in previous studies. The new concepts and terminology were introduced for the following three reasons.

First, it is a biological process, not a climatic process that is being modelled. Second, if the purpose is to obtain information about the developmental stage of the bud, the chilling

Fig. 9. Observed timing of bud burst of *Pinus sylvestris* saplings in the photoperiod experiment (Table 4). The vertical bars indicate the standard deviations. $n = 135$ (nine buds in each of 15 saplings).



requirement has to be taken into account, as well as the number of chilling units accumulated. In the present study the accumulation rate of chilling units (as expressed with the old terminology) was divided by C_{crit} in eq. 1, hence providing a relative physiological scale common to all genotypes with different chilling requirements. Third, the framework also has to be able to address species where chilling is not the driving force of rest break, or at least not the only driving force. The variable state of rest break fulfils this requirement: it has essentially the same physiological interpretation, regardless of the environmental factors that are assumed to affect it (Fig. 1).

The concept of growth competence, $C(t)$, facilitates the consideration of different models within the same framework (eq. 4; Figs. 1 and 3) (Hänninen 1990a; Kramer 1994a). The concept is closely related to the concept of state of rest break, $S_r(t)$, but has a completely different meaning. $S_r(t)$ indicates how a large proportion of the rest breaking biochemical changes has taken place in the bud but does not contain any information on growth competence. Sarvas (1972, 1974), for instance, assumed that the process of rest break has no influence on the growth competence until rest completion, when full growth competence is attained abruptly (Fig. 3A), whereas Landsberg (1974) assumed that growth competence increases gradually during the process of rest break (Fig. 3B).

In the present study, 96 hypothetical models were synthesized for experimental testing by combining the original 14 submodels considered. Some of the synthesized models were reformulations of previous models, but most of them appear here for the first time. Still other models can be synthesized within the framework by considering new versions for the submodels. As an example, the detailed model of Fishman et al. (1987a, 1987b), addressing the effects of temperature fluctuation on rest break, could be introduced to the framework as the fifth alternative for the submodel of rest break. The essence of the modelling framework is that it points out

the three ecophysiological aspects to be addressed and provides the general equations [1]–[5] for the formulation of the models.

Testing of the models

The model developed for Finnish forest trees (Sarvas 1972, 1974; Hänninen 1990b) predicted accurately the timing of bud burst for natural conditions, but its prediction for elevated temperature conditions in the future was about 70 days earlier than the experimental observations (Fig. 8A). Even though the overall model was falsified in this way, its submodel for air temperature response of potential rate of ontogenetic development (Fig. 4A) obtained slight support (Table 5). This fits well with the fact that this submodel was based on more comprehensive empirical evidence than the other two submodels involved in the overall model (Figs. 2A and 3A) (Sarvas 1972, 1974).

Several models, developed mainly as new combinations of previous models, predicted accurately the timing of bud burst for all treatments of the scenario experiment. The results, however, did not provide strong support for any of the models, since models with substantially different assumptions were almost equally accurate in their predictions (Table 5). A falsification of the photoperiod model for rest break was suggested in an experiment designed specifically for testing it (Fig. 9), even though the photoperiod submodel appeared in the four most accurate models in the test with the scenario experiment (Table 5).

These experimental results demonstrate the importance of the concept of model realism (Levins 1968). A model of high accuracy can have low realism and because of its low realism is vulnerable to loss of accuracy in any situation where its realism is not sufficient. This trade-off has several essential methodological implications.

The models for bud burst phenology of trees have been traditionally tested and developed with long-term observations from natural conditions (Boyer 1973; Cannell and Smith 1983; Hari and Häkkinen 1991; Hunter and Lechowicz 1992; Kramer 1994a, 1994b). The results of the present study show that this approach is, even though necessary, not sufficient for model testing. An unrealistic model, i.e., a model that is missing some essential part of the regulation mechanism for timing of bud burst, was accurate for predicting the timing of bud burst for natural conditions (Fig. 8A). This conclusion is in agreement with the findings of Hunter and Lechowicz (1992), who generated artificial data sets of timing of bud burst for natural conditions by calculating the timing of bud burst with models and found that several other models, besides the one used in the data generation, were able to predict the generated timing of bud burst. Both the findings of the present study and those of Hunter and Lechowicz (1992) call for an experimental approach, if the purpose is to develop realistic phenological models.

The seven most accurate models in the scenario experiment had quite high accuracy, as their values of MSRE were less than 5 days (Table 5), despite the fact that the experiment involved quite drastic manipulation of environmental conditions. Ideally only one of the models should have high realism, as the trees belonging to the same population obviously cannot obey several regulation systems. The main problem was that approximately the same accuracy was obtained with any model that prevented or slowed onto-

genetic development (increase in $S_0(t)$) during autumn and winter (results not shown). This condition was fulfilled with very different models, because the natural correlations between the environmental factors (accumulation of chilling and changes in photoperiod) were not removed enough in the scenario experiment. To get any further in testing the realism of the bud burst models, the natural correlations among environmental factors would have to be altered more drastically.

In the photoperiod experiment the natural correlation between photoperiod and temperature conditions was completely broken (Table 4) and a clear-cut result was obtained: the photoperiod had only a minor effect on the timing of bud burst (Fig. 9). Thus, even though several models involving the photoperiod submodel for rest break were accurate in the scenario experiment (Fig. 8B; Table 2), the findings of the photoperiod experiment suggest that photoperiod does not regulate the rest break of the trees, or if it does, then its effect can be compensated with some other environmental cues.

Another factor causing problems is that models describing long-term biological processes are only tested with the timing of the end-point event of the process, i.e., timing of bud burst (Fig. 6B). Testing of the models would be improved considerably if observations for the preceding point-events were available (Fuchigami et al. 1982). In the case of ontogenetic development, direct observations on the point-events can be made with the aid of microscopy (Sarvas 1972, 1974) and indirect observations with the aid of forcing experiments (Kobayashi and Fuchigami 1983b). For growth competence only indirect observations are available (Sarvas 1974; Kobayashi et al. 1982; Kobayashi and Fuchigami 1983a; Hänninen 1990a; Hänninen and Backman 1994). Several biochemical observations are available for rest break, but they still have limited value for modelling because the biochemical mechanism of rest break is not exactly known (Smith and Kefford 1964; Perry 1971; Wareing and Phillips 1978, pp. 269–275; Hanover 1980; Dennis 1987; Powell 1987; Rinne et al. 1994a, 1994b).

Besides the approach using long-term observations from natural conditions, models for bud burst also have been developed and tested in phytotron and greenhouse experiments. These studies have generally acknowledged chilling temperature as the major environmental factor regulating rest break, even though long photoperiods have been found to compensate for lack of chilling (Perry and Wang 1960; Kriebel and Wang 1962; Jensen and Gatherum 1965; Nienstaedt 1966, 1967; Hoffman and Lyr 1967; Worrall and Mergen 1967; Farmer 1968; Sarvas 1974; Campbell and Sugano 1975, 1979; Nelson and Lavender 1979; Hinesley 1982; Garber 1983; Hänninen 1990a; Heide 1993a). In *Fagus sylvatica* L., however, the photoperiod has a more profound effect on the rest break (Wareing 1953; Falusi and Calamassi 1990; Heide 1993b). Phytotron and greenhouse studies are practically limited to the seedling stage or to the use of twig material. Thus, results cannot be applied without further testing on intact older trees. This is one of the main reasons for establishing the present experimental approach using older saplings in semicontrolled field conditions.

The original models considered in the present study were presented for a wide variety of tree taxa. Part of the models were developed for vegetative bud burst and part for flowering. Despite this diversity in original scope, similar biologi-

cal assumptions appear throughout the models. However, no a priori generalizations can be drawn on the environmental regulation of foliar bud burst or flowering. The regulation of foliar bud burst and flowering can vary, not only according to species of the tree and type of the bud (Lechowicz 1995), but also according to the age of the tree (Ununger et al. 1988).

Consequences of climatic warming

The warming treatments hastened bud burst in the scenario experiment, but the hastening was about 70 days less than predicted by the model developed earlier for Finnish forest trees (Fig. 8A). This finding suggests that climatic warming will not increase the risk of frost damage in *P. sylvestris* saplings as much as was predicted earlier on the basis of computer simulations (Hänninen 1991).

Concluding remarks

The results of the present study demonstrate the importance of the concept of realism (Levins 1968) for modelling bud burst phenology of trees. A model of low realism is always vulnerable to loss of accuracy in any further critical test, no matter how accurate it has been in previous tests. A model of high realism, on the contrary, addresses the essential environmental responses in the physiological phenomena related to the regulation of timing of bud burst. That is why the model of high realism is able to produce reasonably accurate predictions also for unusual or extreme conditions. The concept of realism is also crucial from the practical point of view: if predictions concerning climatic change are realized, then the realism of phenological models will be tested on a global scale.

To obtain ecophysiologically realistic models for the bud burst phenology of the trees, three steps should be taken. (i) The physiological phenomena affecting the timing of bud burst should be distinguished. (ii) Hypothetical models about the environmental regulation of the physiological phenomena should be collected from the literature or new ones developed. (iii) The hypothetical models should be tested experimentally with the species and provenances of interest. In the present study, an attempt was made to follow this approach, but the main experiment mimicking climatic change was not sufficient in itself to identify the most realistic phenological model. In further studies, the natural correlations of the climatic factors should be altered to a greater degree to reveal the critical cues driving phenological responses. Furthermore, the present whole-tree physiological approach should be supplemented with more basic physiological studies (microscopy, biochemical analyses, forcing experiments). In this way, models of high realism can be developed for assessing the effects of predicted climatic change on bud burst phenology and subsequent risk of frost damage in trees. The empirical results of the present study suggest that the risk of frost damage was recently overestimated in a simulation study, because the available information did not allow the formulation of a model with sufficient realism (Hänninen 1991).

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References

- Bach, W. 1987. Development of climatic scenarios: A. From general circulation models. *In* The impact of climatic variations on agriculture. Vol. 1: Assessment in cool temperate and cold regions. *Edited by* M.L. Parry, T.R. Carter and N.T. Konijn. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 125–157.
- Boyer, W.D. 1973. Air temperature, heat sums, and pollen shedding phenology of longleaf pine. *Ecology*, **54**: 420–426.
- Campbell, R.K. 1978. Regulation of bud-burst timing by temperature and photoperiod during dormancy. *In* Proceedings: Fifth North American Forest Biology Workshop. *Edited by* C.A. Hollis and A.E. Squillace. Forestry Department, University of Florida, Gainesville, Fla. pp. 19–33.
- Campbell, R.K., and Sugano, A.I. 1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Bot. Gaz.* **136**: 290–298.
- Campbell, R.K., and Sugano, A.I. 1979. Genecology of bud-burst phenology in Douglas-fir: response to flushing temperature and chilling. *Bot. Gaz.* **140**: 223–231.
- Cannell, M.G.R. 1989. Chilling, thermal time and the date of flowering of trees. *In* Manipulation of fruiting. *Edited by* C.J. Wright. Butterworths, London. pp. 99–113.
- Cannell, M.G.R. 1990. Modelling the phenology of trees. *In* Modelling to understand forest functions. *Edited by* H. Jozefek. University of Joensuu, Joensuu, Finland. pp. 11–27.
- Cannell, M.G.R., and Smith, R.I. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* **20**: 951–963.
- Cannell, M.G.R., and Smith, R.I. 1986. Climatic warming, spring budburst and frost damage on trees. *J. Appl. Ecol.* **23**: 177–191.
- Dennis, F.G., Jr. 1987. Two methods of studying rest: temperature alternation and genetic analysis. *HortScience*, **22**: 820–824.
- Doorenbos, J. 1953. Review of the literature on dormancy in buds of woody plants. *Meded. Landbouwhogeschool Wageningen*, **53**: 1–23.
- Falusi, M., and Calamassi, R. 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree Physiol.* **6**: 429–438.
- Farmer, R.E., Jr. 1968. Sweetgum dormancy release: effects of chilling, photoperiod, and genotype. *Physiol. Plant.* **21**: 1241–1248.
- Fishman, S., Erez, A., and Couvillon, G.A. 1987a. The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. *J. Theor. Biol.* **124**: 473–483.
- Fishman, S., Erez, A., and Couvillon, G.A. 1987b. The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. *J. Theor. Biol.* **126**: 309–321.
- Fuchigami, L.H., Weiser, C.J., Kobayashi, K., Timmis, R., and Gusta, L.V. 1982. A degree growth stage ($^{\circ}\text{GS}$) model and cold acclimation in temperate woody plants. *In* Plant cold hardiness and freezing stress. Mechanisms and crop implications. Vol. 2. *Edited by* P.H. Li and A. Sakai. Academic Press, New York. pp. 93–116.
- Garber, M.P. 1983. Effects of chilling and photoperiod on dormancy release of container-grown loblolly pine seedlings. *Can. J. For. Res.* **13**: 1265–1270.
- Hänninen, H. 1990a. Modeling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn.* **213**: 1–47.
- Hänninen, H. 1990b. Modeling dormancy release in trees from cool and temperate regions. *In* Process modelling of forest growth: responses to environmental stress. *Edited by* R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren. Timber Press, Portland, Ore. pp. 159–165.
- Hänninen, H. 1991. Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ.* **14**: 449–454.
- Hänninen, H., and Backman, R. 1994. Rest break in Norway spruce seedlings: test of a dynamic temperature response hypothesis. *Can. J. For. Res.* **24**: 558–563.
- Hanover, J.W. 1980. Control of tree growth. *BioScience*, **30**: 756–762.
- Hari, P. 1968. A growth model for a biological population, applied to a stand of pine. *Commun. Inst. For. Fenn.* **66**(7): 1–16.
- Hari, P., and Häkkinen, R. 1991. The utilization of old phenological time series of budburst to compare models describing annual cycles of plants. *Tree Physiol.* **8**: 281–287.
- Hari, P., Leikola, M., and Räsänen, P. 1970. A dynamic model of the daily height increment of plants. *Ann. Bot. Fenn.* **7**: 375–378.
- Heide, O.M. 1993a. Daylength and thermal responses of bud burst during dormancy release in some northern deciduous trees. *Physiol. Plant.* **88**: 531–540.
- Heide, O.M. 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiol. Plant.* **89**: 187–191.
- Hinesley, L.E. 1982. Dormancy in *Abies fraseri* seedlings at the end of the first growth cycle. *Can. J. For. Res.* **12**: 374–383.
- Hoffmann, G., and Lyr, H. 1967. Über die Wirkung der winterlichen Thermoperiode auf das Wurzel- und Sprowwachstum von *Pinus sylvestris* L. *Flora (Jena)*, **158**: 373–383.
- Hunter, A.F., and Lechowicz, M.J. 1992. Predicting the

- timing of bud burst in temperate trees. *J. Appl. Ecol.* **29**: 597–604.
- Jensen, K.F., and Gatherum, G.E. 1965. Effects of temperature, photoperiod, and provenance on growth and development of Scots pine seedlings. *For. Sci.* **11**: 189–199.
- Kettenen, L., Mukula, J., Pohjonen, V., Rantanen, O., and Varjo, U. 1987. The effects of climatic variations on agriculture in Finland. In *The impact of climatic variations on agriculture*. Vol. 1. Assessment in cool temperate and cold regions. Edited by M.L. Parry, T.R. Carter, and N.T. Konijn. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 513–614.
- Kobayashi, K.D., and Fuchigami, L.H. 1983a. Modeling temperature effects in breaking rest in red-osier dogwood (*Cornus sericea* L.). *Ann. Bot. (London)*, **52**: 205–215.
- Kobayashi, K.D., and Fuchigami, L.H. 1983b. Modeling bud development during the quiescent phase in red-osier dogwood (*Cornus sericea* L.). *Agric. Meteorol.* **28**: 75–84.
- Kobayashi, K.D., Fuchigami, L.H., and English, M.J. 1982. Modeling temperature requirements for rest development in *Cornus sericea*. *J. Am. Soc. Hortic. Sci.* **107**: 914–918.
- Kramer, K. 1994a. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* **31**: 172–181.
- Kramer, K. 1994b. 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 Environ.* **17**: 367–377.
- Kriebel, H.B., and Wang, C.W. 1962. The interaction between provenance and degree of chilling in bud-break of Sugar maple. *Silvae Genet.* **11**: 125–130.
- Landsberg, J.J. 1974. Apple fruit bud development and growth; analysis and an empirical model. *Ann. Bot. (London)*, **38**: 1013–1023.
- Lechowicz, M.J. 1995. Seasonality of flowering and fruiting in temperate forest trees. *Can. J. Bot.* **73**: 175–182.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- Murray, M.B., Cannell, M.G.R., and Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* **26**: 693–700.
- Nelson, E.A., and Lavender, D.P. 1979. The chilling requirement of western hemlock seedlings. *For. Sci.* **25**: 485–490.
- Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. *For. Sci.* **12**: 374–384.
- Nienstaedt, H. 1967. Chilling requirements in seven *Picea* species. *Silvae Genet.* **16**: 65–68.
- Nizinski, J.J., and Saugier, B. 1988. A model of leaf budding and development for a mature *Quercus* forest. *J. Appl. Ecol.* **25**: 643–652.
- Perry, T.O. 1971. Dormancy of trees in winter. *Science (Washington, D.C.)*, **171**: 29–36.
- Perry, T.O., and Wang, C.W. 1960. Genetic variation in the winter chilling requirement for date of dormancy break for *Acer rubrum*. *Ecology*, **41**: 790–794.
- Powell, L.E. 1987. Hormonal aspects of bud and seed dormancy in temperate-zone woody plants. *HortScience*, **22**: 845–850.
- Richardson, E.A., Seeley, S.D., and Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience*, **9**: 331–332.
- Rinne, P., Saarelainen, A., and Junttila, O. 1994a. Growth cessation and bud dormancy in relation to ABA level in seedlings and coppice shoots of *Betula pubescens* as affected by a short photoperiod, water stress and chilling. *Physiol. Plant.* **90**: 451–458.
- Rinne, P., Tuominen, H., and Junttila, O. 1994b. Seasonal changes in bud dormancy in relation to bud morphology, water and starch content, and abscisic acid concentration in adult trees of *Betula pubescens*. *Tree Physiol.* **14**: 549–561.
- Romberger, J.A. 1963. Meristems, growth, and development in woody plants. USDA For. Serv. Tech. Bull. No. 1293.
- Samish, R.M. 1954. Dormancy in woody plants. *Annu. Rev. Plant Physiol.* **5**: 183–204.
- Sarvas, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. *Commun. Inst. For. Fenn.* **76**(3): 1–110.
- Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Commun. Inst. For. Fenn.* **84**(1): 1–101.
- Smith, H., and Kefford, N.P. 1964. The chemical regulation of the dormancy phases of bud development. *Am. J. Bot.* **51**: 1002–1012.
- Smolander, H. 1984. Measurement of fluctuating irradiance in field studies of photosynthesis. *Acta For. Fenn.* **187**: 1–56.
- Ununger, J., Ekberg, I., and Kang, H. 1988. Genetic control and age-related changes of juvenile growth characters in *Picea abies*. *Scand. J. For. Res.* **3**: 55–66.
- Vegis, A. 1964. Dormancy in higher plants. *Annu. Rev. Plant Physiol.* **15**: 185–224.
- Wang, J.Y. 1960. A critique of the heat unit approach to plant response studies. *Ecology*, **41**: 785–790.
- Wareing, P.F. 1953. Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiol. Plant.* **6**: 692–706.
- Wareing, P.F., and Phillips, I.D. 1978. *The control of growth and differentiation in plants*. 2nd ed. Pergamon Press, Oxford, U.K.
- Weiser, C.J. 1970. Cold resistance and injury in woody plants. *Science (Washington, D.C.)*, **171**: 1269–1278.
- Worrall, J., and Mergen, F. 1967. Environmental and genetic control of dormancy in *Picea abies*. *Physiol. Plant.* **20**: 733–745.