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213

HEIKKI HÄNNINEN

MODELLING BUD DORMANCY RELEASE IN TREES FROM COOL AND TEMPERATE REGIONS

VIILEÄN JA LAUHKEAN VYÖHYKKEEN PUIDEN SILMUDORMANSSIN PURKAUTUMISEN MALLITTAMINEN

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MODELLING BUD DORMANCY RELEASE IN TREES FROM COOL AND TEMPERATE REGIONS

Viileän ja lauhkean vyöhykkeen puiden silmudormanssin purkautumisen mallittaminen

Heikki Hänninen

The premises of several models obtained from literature on bud dormancy release in trees from cool and temperate regions differed from each other with respect to responses to air temperature during the rest period of the buds. The predicted timing of bud burst in natural conditions varied among the models, as did the prediction of the models for the outcome of a chilling experiment. Experimental results with two-year-old seedlings of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) did not agree with any of the models. The experimental results also deviated from abundant earlier findings, which also disagreed with any of the models. This finding suggests that Finnish provenances of Scots pine and Norway spruce differ from more southern provenances with respect to temperature regulation of bud dormancy release. A synthesis model for the effects of air temperature on bud dormancy release in trees was developed on the basis of the previous models and the experimental results of both the present and previous studies. The synthesis model contains part of the original models as special cases. The parameters of the synthesis model represent several aspects of the bud dormancy release of trees that should be addressed separately with each species and provenance in experimental studies. Further aspects of dormancy release were discussed, in order to facilitate further development of the models.

Kirjallisuudessa esitettyjen viileän ja lauhkean vyöhykkeen puulajien silmudormanssin purkautumista kuvaavien mallien oletukset olivat keskenään erilaisia silmulevon aikaisten lämpötilavasteiden osalta. Mallien ennusteet silmun puhkeamisen ajoittumisesta luontaisissa olosuhteissa olivat erilaisia, samoinkuin mallien ennusteet kylmäkäsittelykokeen tuloksista. Kaksivuotiailla männyn (*Pinus sylvestris* L.) ja kuusen (*Picea abies* (L.) Karst.) taimilla saadut koetulokset eivät olleet minkään mallin ennusteen mukaisia. Koetulokset poikkesivat myös useiden aikaisempien tutkimusten koetuloksista, jotka nekään eivät sopineet yhteen minkään mallin kanssa. Havaitut erot tämän ja aikaisempien tutkimusten välillä viittaavat siihen, että ilman lämpötila säätelee puiden silmudormanssin purkautumista eri tavoin männyn ja kuusen eri proveniensseilla. Tutkimuksessa kehitettiin ilman lämpötilan vaikutusta puiden silmudormanssin purkautumiseen kuvaava synteesimalli, joka perustuu aikaisempiin malleihin sekä tässä ja aikaisemmissa tutkimuksissa saatuihin koetuloksiin. Osa aikaisemmista malleista voidaan tulkita synteesimallin erikoistapauksiksi. Synteesimallin parametrit kuvastavat silmudormanssin purkautumisen piirteitä, jotka tulee selvittää kokeellisesti kunkin puulajin ja proveniessin osalta erikseen. Näiden piirteiden lisäksi tutkimuksessa tarkasteltiin muita silmudormanssin purkautumisen piirteitä, jotka tulee ottaa mallien jatkokehittelyssä huomioon.

Keywords: annual cycle, climatic adaptation, growth competence, quiescence, rest.
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Contents

Preface

This study was carried out in the Faculty of Forestry at the University of Joensuu between years 1985 and 90, with the kind permission of Seppo Kellomäki and Paavo Pelkonen. The study constitutes part of the research projects "Frost hardiness of forest trees" (1985—1988) and "Dormancy release of forest trees" (1989—1991). The projects have been facilitated and financed by the Academy of Finland, The Finnish Forest Research Institute, The Foundation for Research of Natural Resources in Finland, and the University of Joensuu.

I have been privileged to carry out my studies in a research community where only joy of life and laughter have overriden scientific enthusiasm. Here it is possible to mention only those members of the community who have played the most important supporting roles. My main supervisors, Veikko Koski and Paavo Pelkonen, mediated the Finnish tradition of research on the annual cycle of forest trees. Their eagerness to see this study completed has given me all the necessary arguments for considering them extortionists, but their humanity has prevented this consideration. Pertti Hari, Seppo Kellomäki, and Heikki Smolander have all been splendid guides in introducing me to the field of forest ecophysiology. Tapani Repo and Marja-Liisa Sutinen have taught me a lot about the frost hardiness of trees, a subject especially closely related to my own research. Pentti K. Räsänen and Pasi Puttonen have motivated my work by demonstrating the potential that an ecophysiological understanding of trees has in practical forestry. Juha Lappi provided me with valuable information on several methodological questions.

Various versions of the manuscript have been read by several persons mentioned above. Seppo Kellomäki in particular made great efforts to help me to make my ideas clearer to myself and to the reader.

Pekka Piironen provided the greenhouse facilities at the Botanical Garden of the University of Joensuu. The following people provided various kinds of technical assistance: Anja Aaltonen, Risto Häkkinen, Marja-Leena Jalkanen, Päivi Kokki, Jari Kokkola, Arja Kontkanen, Jukka Matero, Eija Mustonen, Merja Mäkelä, Tapio Mäkelä, Tuija Pekkola, Helen Ruhkala, Juha-Pekka Salmi and Marja-Leena Valkonen. John Stotesbury checked the English language of the manuscript, and Riitta Honkanen and Mika Smolander produced the figures of the study.

Juhani Häggman provided an inspiring place for the writing of the study at the traditional Punkaharju Research Station during the Spring of 1990.

My mother and other members of my family in Varjola gave me valuable support during my studies. My friends in Joensuu, Laukaa, and elsewhere have also greatly encouraged me.

I am grateful to everyone, both those mentioned and those not mentioned above, for the various kinds of support provided. Neither this study, nor real life in general, could have been possible without them.

This study is dedicated to the memory of my father.

Joensuu, August 1990

Heikki Hänninen

Symbols

Symbol	Dimension	Concept
C	—	Competence function
C_{min}	—	Minimum growth competence (model types II, III, synthesis model)
ΔC	—	Increase in minimum growth competence caused by forcing temperature (synthesis model)
ΔC_{max}	—	Maximal increase in minimum growth competence caused by forcing temperature (synthesis model)
CU	—	Chilling unit
CU_{abs}	CU	Absolute chilling requirement for growth competence
CU_{crit}	CU	Chilling requirement for rest completion
CU_{dr}	CU	Chilling requirement for attaining decreasing rest period (model type III)
CU_{tr}	CU	Chilling requirement for attaining true rest period (model type IV)
CU_{pr}	CU	Chilling requirement for attaining postrest period (model type IV)
ΔCU	CU	Decrease in chilling requirement for attaining full growth competence, caused by forcing temperature (synthesis model)
ΔCU_{max}	CU	Maximal decrease in chilling requirement for attaining full growth competence, caused by forcing temperature (synthesis model)
DBB	day	Mean days to bud burst
DRR	—	Dormancy release ratio

Symbol	Dimension	Concept
e	—	Environmental factors
FU	—	Forcing unit
FU_{crit}	FU	Forcing requirement of bud burst
M	—	Rate of development
M_{chl}	$CU\ day^{-1}$	Rate of chilling
M_{frc}	$FU\ day^{-1}$	Rate of forcing
m_{frc}	$FU\ day^{-1}$	Potential rate of forcing
S	—	State of development
S_{crit}	—	Critical state of development
S_{chl}	CU	State of chilling
S_{frc}	FU	State of forcing
T_1	°C	Lower limit for temperature range, where growth competence varies according to temperature during prerest and postrest periods (model type IV)
T_2	°C	Upper limit for temperature range, where growth competence varies according to temperature during prerest and postrest periods (model type IV)
T_3	°C	Lower limit for temperature range, where growth competence increases with increasing temperature (synthesis model)
T_4	°C	Upper limit for temperature range, where growth competence increases with increasing temperature (synthesis model)
t_{BB}	day	Mean day of bud burst
T_{trh}	°C	Threshold temperature for full growth competence (model type IV)

1. Introduction

11. Annual development of trees

Climatic adaptation of trees

The morphological and physiological state of trees from the cool and temperate regions varies according to the season of the year. During summer, trees are in an active growth state, i.e. the processes that are related to utilization of the growth resources of the site are predominant. During winter, trees are in a frosthardy dormant state, and growth processes are slow. Synchronization of this annual development with the annual temperature cycle of the growing site is essential in the climatic adaptation of the trees (Weiser 1970, Sarvas 1972, 1974, Sakai and Larcher 1987, p. 100—102). Early growth onset and late growth cessation cause frequent frost damage, i.e. poor *survival adaptation* (Heide 1985). Late growth onset and early growth cessation in turn cause loss of growth resources of the site, i.e. poor *capacity adaptation* (Heide 1985).

The annual development of native tree populations growing at their natural sites is usually synchronized closely with the annual temperature cycle of the growing site (Campbell and Sugano 1975, 1979). In practical forestry and horticulture, however, both the genetic properties and the growing environment of trees are often manipulated. Furthermore, the natural growing environment of trees will also probably change during the coming decades as a result of climatic warming (e.g. Crane 1985). For these reasons, an understanding of the interaction of genetic and environmental factors in the regulation of the annual development of trees is of great value in practical forestry and horticulture.

Modelling of annual development of trees

The modelling of the annual development of trees is based on the concepts of annual cycle, annual rhythm and the regulation of annual rhythm (Hänninen 1990a, see Sarvas 1972, 1974, Fuchigami et al. 1982). *Annual cycle* denotes the sequence of all developmental events, i.e. changes in the morphological and physiological state of a tree that are repeated under natural conditions each year in a basically similar way. For instance the alternation of periods of growth and dormancy in apical meristems (Sarvas 1972, 1974), the annual course of frost hardiness (Proebsting 1963, 1970, Cannell and Sheppard 1982, Repo et al. 1990), the annual course of photosynthetic capacity (Pelkonen 1980, 1981), and the annual course of translation capacity of ribosomes (Häggman 1986, Kupila-Ahvenniemi et al. 1987), are phenomena in the annual cycle. *Annual rhythm* denotes the timing of the events in the annual cycle. *Regulation of annual rhythm* denotes the interaction of genetic and environmental factors in determining the timing of events in the annual cycle.

In the modelling of the annual development of trees, the regulation of annual rhythm is generally of special interest. Thus, the logical structure of the model and the values of the model parameters describe the tree genotype's response to environmental factors in the determination of the timing of the events in the annual cycle. Models of the annual development of trees are generally based on the two following concepts (Hari 1968, 1972, Sarvas 1972, 1974, Fuchigami et al. 1982):

(i) The momentary developmental status of a tree is described by the value of a variable referred to as *state of development*, S. Each developmental event in the annual cycle of the tree is matched in the model by a value of S specific to the event.

(ii) *Rate of development*, M, i.e. the rate of change in the state of development S, depends on the prevailing environmental factors e, and in some models also on the prevailing state of development, S.

The concepts (i) and (ii) are formulated in three steps. The momentary value of the rate of development M is calculated on the basis of the momentary values of the environ-

mental factors e, and in some models, also on the basis of the momentary value of the state of development S:

$$M(t) = f(e(t), S(t)) \qquad (1)$$

where f is a function indicating the dependence of the rate of development on environmental factors and on the state of development.

The momentary value of the state of development S is obtained by integrating the rate of development M from the beginning of the developmental period until the moment under consideration:

$$S(t) = \int_{0}^{t} M(\tau)\, d\tau \qquad (2)$$

A given developmental event appears when S attains a value S_{crit} that is critical to the event:

$$S(t) \geq S_{crit} \qquad (3)$$

It is assumed in the model structure represented by Eqns. (1) — (3) that environment continuously affects the rate of development of trees. In practical calculations, however, this continuous effect is approximated in a discontinuous numerical way. Instead of the momentary rate of development, the mean rate of development for a short time step (one hour, one day) is calculated using the mean values of the environmental factors for the time step as arguments in the function f in Eqn. (1). Subsequently, the value of the state of development S prevailing at the beginning of a given time step is obtained by summing the mean values of M calculated for the previous time steps. A basically similar approach has been applied for a long period of time in simulating the development of various organisms by accumulating various temperature sums, sums of heat units, or sums of photothermal units (Arnold 1959, Wang 1960, Robertson 1968, 1973, Caprio 1974).

12. Bud dormancy of trees

The alternation of periods of growth and dormancy in apical meristems is a readily observable manifestation of the annual de-velopment of trees from the cool and temperate regions. The role of the prevailing night length is emphasized in the regulation of growth cessation (Vaartaja 1959, Ekberg et al. 1979, Koski and Selkäinaho 1982, Koski and Sievänen 1985), even though temperature conditions prevailing during the growing period have also been shown to affect growth cessation (Koski and Selkäinaho 1982, Koski and Sievänen 1985). During the dormant period, the air temperature is the most important factor regulating the annual development of trees. Dormancy is generally released and bud burst takes place when buds are exposed first to chilling temperatures (e.g. $-5\,°C < T < 10\,°C$) and then to forcing temperatures (e.g. $T > 0\,°C$) thereafter (Chap. 21).

After the general recognition of the effects of air temperature on bud dormancy release in trees, various more specific models of these effects were developed. The earliest models were conceptual (Vegis 1964), while more recently mathematical simulation models for a wide variety of species have also been presented (Sarvas 1972, 1974, Landsberg 1974, Richardson et al. 1974, Campbell 1978, Fuchigami et al. 1982, Kobayashi et al. 1982, Cannell and Smith 1983, Kobayashi and Fuchigami 1983a, b). The simulation models describe the effects of air temperature on bud dormancy release in a quantitative way, thus facilitating prediction of the timing of vegetative bud burst or flowering, on the basis of temperature data from the growing site. Fuchigami et al. (1982), Hänninen (1987) and Cannell (1989, 1990) have reviewed some of the models, and Hänninen and Pelkonen (1988a, b, 1989) have tested some of them. No comprehensive comparison and testing of the models, however, has been carried out.

13. Aims of the study

The aims of the present study are

1) to analyse and compare the premises of prevailing models of the effects of air temperature on bud dormancy release in trees from cool and temperate regions (Chap. 2),
2) to deduce some of the implications of the models for experimental testing (Chap. 3),
3) to test the models experimentally with seedlings of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) (Chap. 4),

4) to develop a synthesis model on the basis of the previous models and the experimental results of previous and present studies (Chap. 5), and
5) in order to facilitate further model develop-ment, to discuss other aspects of bud dormancy release, additional to the aspects examined experimentally in the study (Chap. 6).

2. Premises of models of bud dormancy release

21. Basic concepts

In the present study the concept of *bud dormancy* (or *dormancy*) is defined as the state of any bud when there exists no visible growth (Doorenbos 1953, Romberger 1963, p. 75, Lang et al. 1987). The start of visible growth is referred to as *bud burst*. All morphological and physiological processes during the period of dormancy that lead to bud burst are referred to as *dormancy release* (Table 1).

The bud dormancy of trees is usually classified into three main categories according to the factor that prevents growth. Different nomenclatures for the categories have been used by different authors. Two of the three categories belong to the scope of the present study, i.e. the concepts of *rest* (Romberger 1963, p. 75, Weiser 1970, Fuchigami et al. 1982; synonymous with Doorenbos' (1953) "winter dormancy", with Samish's (1954) "rest in narrow sense", with Sarvas' (1974) "autumn dormancy" and "dormancy I", and with Lang et al.'s (1987) "endodormancy"); and the concept of *quiescence* (Samish 1954, Romberger 1963, p. 75, Weiser 1970, Fuchigami et al. 1982; synonymous with Doorenbos' (1953) "imposed dormancy", with Sarvas' (1974) "winter dormancy" and "dormancy II", and with Lang et al.'s (1987) "ecodormancy").

During the rest period buds remain dormant due to growth arresting physiological conditions in the bud itself. Under natural conditions, buds are usually in a state of rest

Table 1. Terminology of bud dormancy in trees used in the study.

State of bud, name of period	Definition	Process	End of period
Dormancy, bud dormancy	No visible growth	Dormancy release	Bud burst
Rest	No visible growth, and	Rest break	Rest completion
	1) no or reduced growth competence, or	(Ontogenetic development)	(Bud burst)
	2) no growth competence at low forcing temperatures and full growth competence at high forcing temperatures		
Quiescence	No visible growth, and	Ontogenetic development	Bud burst
	full growth competence at all forcing temperatures		

during the autumn. The growth arresting physiological conditions are removed when buds are exposed to chilling temperatures (e.g. $-5\,°C < T < 10\,°C$) for some weeks (Coville 1920, Smith and Kefford 1964, Perry 1971, Flint 1974, Fuchigami et al. 1982). Thereafter, during the quiescence period, buds remain dormant due to environmental conditions unfavourable for growth, i.e. due to low air temperature. Bud burst takes place when the buds are exposed for a prolonged period to forcing temperatures (e.g. $T > 0\,°C$) (Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982).

In the present study the concept of *ontogenetic development* is defined to denote all morphological changes in a dormant bud that lead to bud burst. The concept of *growth competence* is used to describe the bud's potential to respond to forcing temperatures by displaying ontogenetic development (see Landsberg 1977). The bud may have 1) no growth competence (no ontogenetic development in any forcing temperature), 2) reduced growth competence (ontogenetic development at a rate lower than the maximum rate determined by the forcing temperature), or 3) full growth competence (ontogenetic development at a maximum rate determined by the forcing temperature).

The concepts of rest and quiescence are redefined in the present study with the concept of growth competence, in order to facilitate quantitative modelling of bud dormancy release. The concept of rest is redefined as the state of a dormant bud when 1) it has no or reduced growth competence, or 2) when it has no growth competence in low forcing temperatures (e.g. $T < 15\,°C$), and full growth competence in high forcing temperatures (e.g. $T > 15\,°C$). The concept of quiescence is redefined as the state of the dormant

bud when it has full growth competence in all forcing temperatures (Table 1). The attainment of quiescence is referred to as *rest completion* (Richardson et al. 1974, Erez and Couvillon 1987). All physiological processes during the rest period leading to rest completion are referred to as *rest break* (Romberger 1963, p. 75) (Table 1).

22. Modelling principle

The modelling of dormancy release is a special case of modelling of the annual development of trees (Eqns. (1)—(3), Chap. 11). In models of dormancy release, however, two processes of trees, i.e. the rest break and ontogenetic development, are described simultaneously. Thus, models of dormancy release involve two variables for both the rate of development and the state of development, i.e. the *rate and state of chilling* (M_{ch1}, S_{ch1}) for the rest break, and the *rate and state of forcing* (M_{frc}, S_{frc}) for the ontogenetic development. For a complete description of the developmental status of a dormant bud, both the values of the state of chilling S_{ch1} and the state of forcing S_{frc} have to be known.

Rest break

Various temperature response curves have been presented for the rate of chilling (Landsberg 1974, Richardson et al. 1974, Sarvas 1974). In the present study, the rate of chilling is calculated according to the following equation, which has been developed for Finnish forest tree species (*chilling unit model*, Fig. 1a, Sarvas 1974, Hänninen 1990b):

$$M_{ch1}(t) = \begin{cases} 0\ \text{CU day}^{-1}, & T(t) \le -3.4\,°C \\ 0.159\ \text{CU day}^{-1}\,°C^{-1} \cdot T(t) + 0.506\ \text{CU day}^{-1}, & -3.4\,°C < T(t) \le 3.5\,°C \\ -0.159\ \text{CU day}^{-1}\,°C^{-1} \cdot T(t) + 1.621\ \text{CU day}^{-1}, & 3.5\,°C < T(t) \le 10.4\,°C \\ 0\ \text{CU day}^{-1}, & T(t) > 10.4\,°C \end{cases} \quad (4)$$

where $T(t)$ is the prevailing air temperature, °C. In the case of one model (Chap. 232), however, the chilling unit model (4) is

modified in the temperature range above 10.4 °C as follows (Fig. 1b):

$$M_{ch1}(t) = \begin{cases} 0\ \text{CU day}^{-1}, & T(t) \le -3.4\,°C \\ 0.159\ \text{CU day}^{-1}\,°C^{-1} \cdot T(t) + 0.506\ \text{CU day}^{-1}, & -3.4\,°C < T(t) \le 3.5\,°C \\ -0.159\ \text{CU day}^{-1}\,°C^{-1} \cdot T(t) + 1.621\ \text{CU day}^{-1}, & T(t) > 3.5\,°C \end{cases} \quad (5)$$

The state of chilling S_{ch1} is calculated by integrating the rate of chilling M_{ch1} from the beginning of the rest period until the moment under consideration:

$$S_{ch1}(t) = \int_0^t M_{ch1}(\tau)\,d\tau \quad (6)$$

Rest completion takes place when the state of chilling attains a genotype-specific critical value CU_{crit}, i.e. the chilling requirement of rest completion (Sarvas 1974):

$$S_{ch1}(t) \ge CU_{crit} \quad (7)$$
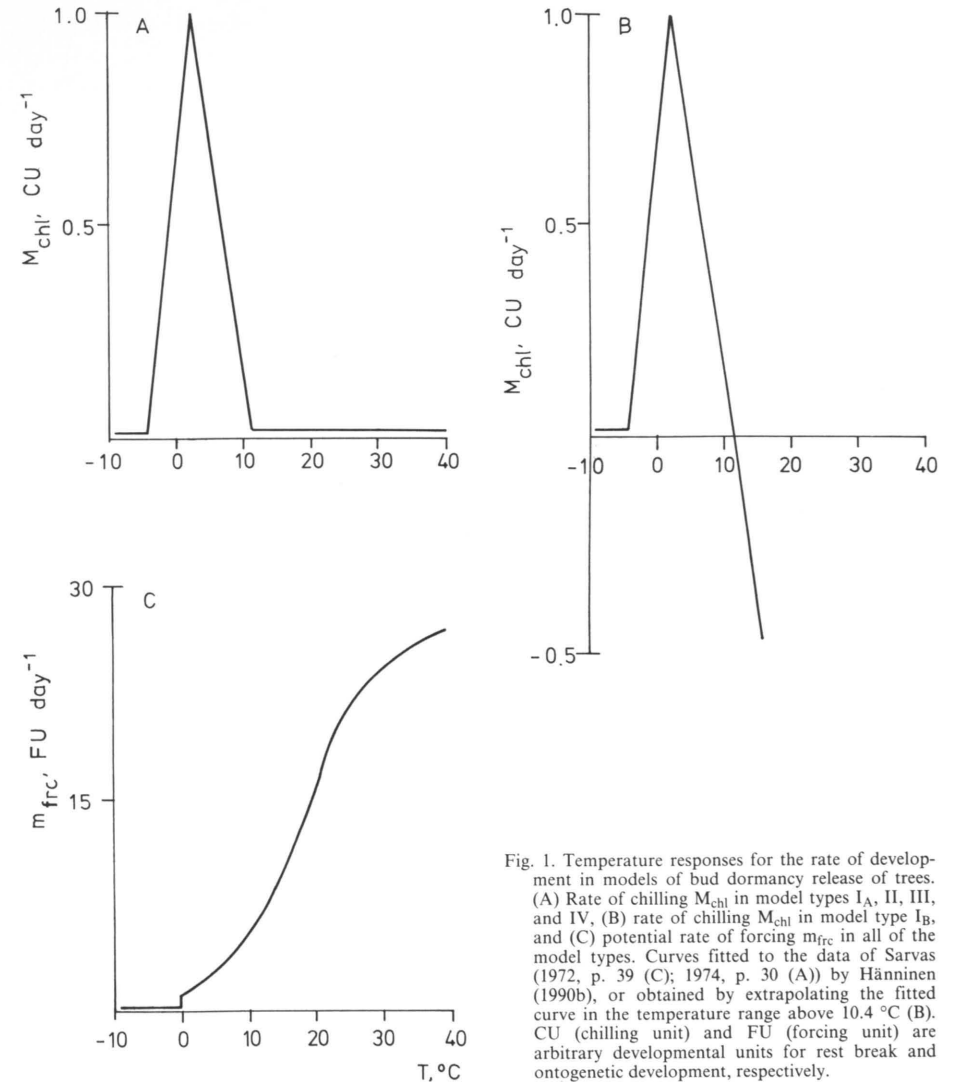
Fig. 1. Temperature responses for the rate of development in models of bud dormancy release of trees. (A) Rate of chilling M_{ch1} in model types I_A, II, III, and IV, (B) rate of chilling M_{ch1} in model type I_B, and (C) potential rate of forcing m_{frc} in all of the model types. Curves fitted to the data of Sarvas (1972, p. 39 (C); 1974, p. 30 (A)) by Hänninen (1990b), or obtained by extrapolating the fitted curve in the temperature range above 10.4 °C (B). CU (chilling unit) and FU (forcing unit) are arbitrary developmental units for rest break and ontogenetic development, respectively.

Ontogenetic development

The rate of forcing depends on 1) the prevailing temperature, and on 2) the prevailing growth competence of the buds (Fig. 2).

The effect of the prevailing temperature on the rate of forcing is modelled in the present study by calculating the potential rate of forcing, m_{frc}. Among the various temperature response curves presented for m_{frc} (Sarvas 1972, 1974, Landsberg 1974, Richardson et al. 1974), the following equation that has been developed for Finnish forest tree species was selected for use in the present study (*forcing unit model*, Fig. 1c, Sarvas 1972, Hänninen 1990b):

$$m_{frc}(t) = \begin{cases} 0 \text{ FU day}^{-1}, & T(t) \leq 0 \text{ °C} \\ \dfrac{28.361 \text{ FU day}^{-1}}{1 + e^{-0.185 \text{ °C}^{-1} \cdot (T(t) - 18.431 \text{ °C})}}, & T(t) > 0 \text{ °C} \end{cases} \qquad (8)$$

where $T(t)$ is prevailing air temperature, °C.

The effect of growth competence on the rate of forcing is modelled in the present study with the aid of a competence function, C. The determination of the value of the competence function C varies among the models considered in the study. In all models, the prevailing state of chilling and the chilling requirement affect the value of C. Furthermore, in one of the models the value of C also depends on the prevailing forcing temperature (Figs. 2, 3). The dimensionless value of the competence function varies from zero (no growth competence, i.e. no forcing effect) to unity (full growth competence, i.e. forcing effect at maximum rate determined by the forcing temperature) (see Hari et al. 1970, 1977). Thus, the rate of forcing M_{frc} is obtained by multiplying the value of the potential rate of forcing m_{frc} (the effect of prevailing temperature) by the value of competence function C (the effect of growth competence):

$$M_{frc}(t) = C(t) \cdot m_{frc}(t) \qquad (9)$$

The state of forcing S_{frc} is obtained by integrating the rate of forcing from the beginning of the rest period until the moment under consideration:

$$S_{frc}(t) = \int_0^t M_{frc}(\tau) \, d\tau \qquad (10)$$

Bud burst takes place, when the state of forcing attains a genotype-specific value FU_{crit}, i.e. the forcing requirement of the bud burst (Sarvas 1972, 1974):
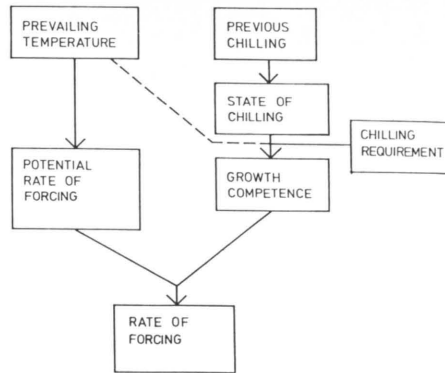
$$S_{frc}(t) \geq FU_{crit} \qquad (11)$$

Fig. 2. Factors influencing the rate of forcing in models of bud dormancy release of trees. Broken line indicates a relationship not involved in all of the models considered in the present study.

Genotype-specific developmental units

In the modelling approach adopted in the present study, each genotype has its own CU scale for the rest break and an own FU scale for ontogenetic development, since the values of the model parameters CU_{crit} (the chilling requirement of rest completion and FU_{crit} (the forcing requirement of the bud burst) are genotype-specific (Sarvas 1972, 1974). The momentary value of the state of chilling $S_{chl}(t)$, for instance, indicates the amount of chilling received by the bud up to the given moment. The ratio $S_{chl}(t)/CU_{crit}$ in turn indicates *the relative state of rest break*, i.e. how large a proportion of the rest breaking processes required for rest completion has taken place up to the given moment. Similarly, the ratio $S_{frc}(t)/FU_{crit}$ indicates *the relative state of ontogenetic development*, i.e. how large a proportion of the ontogenetic processes required for the bud burst has taken place up to the given moment. These ratios should be used when comparing dormancy release among different genotypes with different values of CU_{crit} and FU_{crit}.

23. Differences in the premises among the models

231. Model types

The original models of dormancy release were grouped in the present study into five model types, according to differences in the main premises among the models (Table 2). The model types I_A and I_B will be jointly referred to later as "model type I" in cases where they do not deviate from each other. The model types differ from each other with respect to 1) the effects of high temperatures ($T > 10.4$°C) on the rest break (Figs. 1a,b, Table 2) and 2) the growth competence during the rest period (Fig. 3, Table 2). Other differences in the premises among the original models were neglected in the present study. The neglected differences concern 1) temperature responses of the rate of chilling and the potential rate of forcing, 2) year-to-year variation in the developmental state of buds before the onset of the rest period (Landsberg 1974), and 3) effects of the night length on dormancy release (Vegis 1964, Campbell 1978).

232. Effects of high temperatures on rest break

In model type I_B high temperatures ($T > 10.4$°C) counteract during the rest period the rest breaking effect of previous chilling by diminishing the value of the state of chilling, S_{chl} (Eqn. (5), Fig. 1b, Table 2). No negative

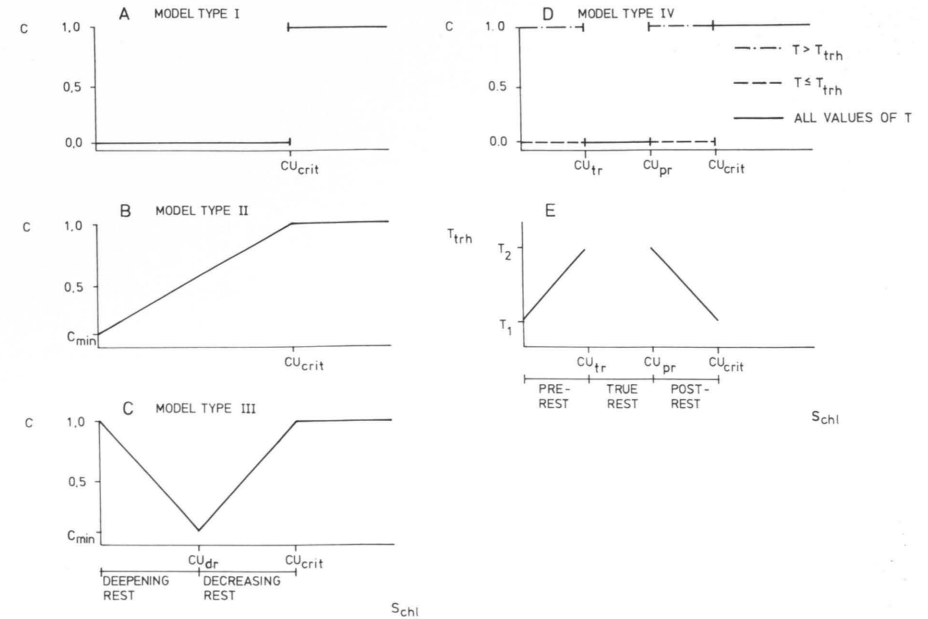

Fig. 3. Effects of state of chilling S_{chl} and prevailing forcing temperature T on the growth competence of buds in trees. (A-C) Dependence of value of competence function C on S_{chl} for model types I—III. (D) Dependence of value of competence function C on S_{chl} and on T for model type IV. (E) Dependence of a threshold temperature T_{trh} on S_{chl} for model type IV.

Table 2. Division of models of bud dormancy release into five model types.

Model type	Factors influencing growth competence	Growth competence during rest period	Changes in growth competence	Sub-periods of rest	Effects of high temperatures on rest break	References
I_A	Previous chilling	No	Abrupt	None	None	Sarvas (1972, 1974)
I_B	Previous chilling	No	Abrupt	None	Counteract of previous chilling	Richardson et al. (1974)
II	Previous chilling	Reduced	Gradual	None	None	Landsberg (1974) Campbell (1978) Cannell and Smith (1983)
III	Previous chilling	Reduced	Gradual	Deepening rest (decreasing growth competence) Decreasing rest (increasing growth competence)	None	Fuchigami et al. (1982) Kobayashi et al. (1982) Kobayashi and Fuchigami (1983 a, b)
IV	Previous chilling, prevailing forcing temperature	Full or no	Abrupt	Prerest (increasing threshold temperature for full growth competence) True rest (no growth competence) Postrest (decreasing threshold temperature for full growth competence)	None	Vegis (1964)

values of S_{chl}, however, are calculated even in the case of model type I_B. In the other model types high temperatures do not alter the rest-breaking effect of previous chilling, i.e. no change in the value of S_{chl} takes place, if the prevailing temperature is above 10.4 °C (Eqn. (4), Fig. 1a, Table 2).

233. Growth competence during rest period

Model type I

In model type I the rest period has a strict end point. The bud has no growth competence when the state of chilling S_{chl} has a value smaller than CU_{crit} (the chilling requirement of rest completion). When S_{chl} attains the value of CU_{crit}, then the bud abruptly attains full growth competence (Fig. 3a, Table 2):

$$C(t) = \begin{cases} 0, & S_{chl}(t) < CU_{crit} \\ 1, & S_{chl}(t) \geq CU_{crit} \end{cases} \qquad (12)$$

Model type II

In model type II, no strict end point of the rest period exists. Unchilled buds have a minimum growth competence indicated by the minimum value C_{min} of the competence function C. In this model, the growth competence of buds increases gradually with the increasing state of chilling, S_{chl}, until full growth competence is attained when S_{chl} attains the value of CU_{crit} (Fig. 3b, Table 2):

$$C(t) = \begin{cases} C_{min} + (\frac{1-C_{min}}{CU_{crit}}) \cdot S_{chl}(t), & S_{chl}(t) < CU_{crit} \\ 1, & S_{chl}(t) \geq CU_{crit} \end{cases} \qquad (13)$$

Model type III

Changes in growth competence in model type III are gradual, as in model type II. In model type III, however, the rest period is divided into two sub-periods, according to the changing effect of chilling on growth competence (Fig. 3c, Table 2). Unchilled buds have full growth competence. During the deepening rest period, growth competence decreases with the increasing state of chilling S_{chl}, until the minimum growth competence is attained with S_{chl} equal to the value of CU_{dr} (the chilling requirement for attaining a decreasing rest period). Thereafter, during the decreasing rest period the growth competence increases with the increasing S_{chl}, until full growth competence is attained with $S_{chl} = CU_{crit}$ (Fig. 3c, Table 2):

$$C(t) = \begin{cases} 1- (\frac{1-C_{min}}{CU_{dr}}) \cdot S_{chl}(t), & S_{chl}(t) < CU_{dr} \\ C_{min} + (\frac{1-C_{min}}{CU_{crit}-CU_{dr}}) \cdot (S_{chl}(t)-CU_{dr}), & CU_{dr} \leq S_{chl}(t) < CU_{crit} \\ 1, & S_{chl}(t) \geq CU_{crit} \end{cases} \qquad (14)$$

Model type IV

Among the various conceptual models presented by Vegis (1964), the specific model considered in the present study concerns plants growing under environmental conditions with a regularly occurring cold season. This conceptual model was converted into a mathematical form. In the resulting model type IV, changes in the growth competence of buds are abrupt, as in model type I (Fig. 3d). In model type IV, however, the growth competence is determined according to an interaction of the state of chilling S_{chl} and the prevailing forcing temperature T; and the rest period is divided into three sub-periods on the basis of this interaction (Figs. 2, 3d,e, Table 2).

During the prerest and postrest periods the bud has full growth competence if the forcing temperature is above a specific threshold value, and it has no growth competence if the forcing temperature is below that threshold value. During true rest the buds have no growth competence in any forcing temperature (Fig. 3d, Table 2):

$$C(t) = \begin{cases} 1, & S_{chl}(t) < CU_{tr}, T(t) > T_{trh}(t) \\ 0, & S_{chl}(t) < CU_{tr}, T(t) \leq T_{trh}(t) \\ 0, & CU_{tr} \leq S_{chl}(t) < CU_{pr} \\ 0, & CU_{pr} \leq S_{chl}(t) < CU_{crit}, T(t) \leq T_{trh}(t) \\ 1, & CU_{pr} \leq S_{chl}(t) < CU_{crit}, T(t) > T_{trh}(t) \\ 1, & S_{chl}(t) \geq CU_{crit} \end{cases} \qquad (15)$$

where CU_{tr} and CU_{pr} are the chilling requirements for attaining true rest and postrest periods respectively. $T_{trh}(t)$ is the temperature threshold for full growth competence during pre- and postrest (Fig. 3d). Chilling affects the growth competence via this threshold temperature (Fig. 3e). During the prerest period the value of the threshold temperature increases with the increasing state of chilling S_{chl}, i.e. the growth-promoting temperature range narrows, until true rest is attained with $S_{chl} = CU_{tr}$. During the postrest period the threshold temperature decreases with the increasing state of chilling S_{chl}, i.e. the growth-promoting temperature range widens, until full growth competence in any forcing temperature is attained at $S_{chl} = CU_{crit}$ (Figs. 3d,e, Table 2):

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$$T_{trh}(t) = \begin{cases} T_1 + \left(\dfrac{T_2-T_1}{CU_{tr}}\right) \cdot S_{chl}(t), & S_{chl}(t) < CU_{tr} \\[12pt] T_1 + \left(\dfrac{T_1-T_2}{CU_{crit}-CU_{pr}}\right) \cdot (S_{chl}(t)-CU_{crit}), & CU_{pr} \leq S_{chl}(t) < CU_{crit} \end{cases} \qquad (16)$$

where T_1 and T_2 are the lower and upper limits respectively for the temperature range, where growth competence varies according to the prevailing temperature during pre- and postrest periods (Fig. 3 e).

234. Rest period and basic annual cycle

The annual cycle was determined in the present study in a wide sense, including all developmental events of trees that are repeated similarly under natural conditions every year (Hänninen 1990 a). According to Sarvas (1972, 1974), however, two further requirements are set for the phenomena that belong to the annual cycle. First, only irreversible developmental events belong to the annual cycle (*irreversibility requirement*). Secondly, the developmental states that belong to the annual cycle must be attained sequentially, one by one, and no state can be skipped (*sequentiality requirement*). This restricted concept of annual cycle will be referred to later as *basic annual cycle*.

The ontogenetic developmental phenomena, e.g. vegetative bud burst and cessation of height growth, or meiosis in flower buds, belong to the basic annual cycle (Sarvas 1972, 1974, Luomajoki 1986). Several physiological phenomena of the annual cycle in the wide sense, however, do not belong to the basic annual cycle. The photosynthetic capacity (Pelkonen 1980,1981) or frost hardiness of trees (Proebsting 1963,1970, Cannell and Sheppard 1982, Repo et al. 1990), for instance, have a clear annual trend, and in

that way, belong to the annual cycle in the wide sense. These phenomena, however, are at least partially reversible (Proebsting 1963, 1970, Pelkonen 1980, Pelkonen and Hari 1980, Cannell and Sheppard 1982), and in this way, do not form part of the basic annual cycle.

The five model types of bud dormancy release that were considered in the present study deviate from each other with respect to the relationship of the rest period to the basic annual cycle. In the case of model type I_A each phase of rest, i.e. each value of the state of chilling S_{chl} from zero to CU_{crit}, has to be attained *sequentially*, one by one, before ontogenetic development and subsequent bud burst take place. Furthermore, the rest-breaking processes caused by chilling are *irreversible*, since the value of S_{chl} is never diminished (Fig. 1 a). Thus in model type I_A, the rest period can be regarded as belonging to the basic annual cycle, similarly to ontogenetic growth events.

In the case of model type I_B the value of the state of chilling S_{chl} is diminished in high temperatures (Fig. 1 b), i.e. the rest break is not *irreversible*. On the other hand, in model types II—IV it is not necessary to attain *sequentially* each value of S_{chl} from zero to CU_{crit} in order to cause ontogenetic development and subsequent bud burst. Ontogenetic development takes place even without chilling, i.e. with $S_{chl} = 0$ (Figs. 3b—d). Thus in the case of the model types I_B, II, III, and IV, the rest period cannot be regarded as belonging to the basic annual cycle.

3. Implications of the models for experimental testing

31. Calculation algorithm

A common calculation algorithm for the five model types was developed in the present study (Fig. 4). A time step of one day is used in the algorithm. Thus for a given day i, the mean rate of chilling $M_{chl}(i)$ and mean potential rate of forcing $m_{frc}(i)$ are calculated using the daily mean temperature $T(i)$ as an argument in the temperature response functions (Eqns. (4), (5), (8), Fig. 1). The daily value of the competence function $C(i)$ is calculated on the basis of the state of chilling during the preceding day $S_{chl}(i—1)$, and in the case of model type IV, also on the basis of the prevailing daily mean temperature $T(i)$ (Fig. 3).

The integrations for calculating the state of chilling $S_{chl}(i)$ and the state of forcing $S_{frc}(i)$ (Eqns. (6), (10)) are carried out by summing the previous values of the corresponding daily mean rate variables. The calculations are repeated in the algorithm for each day i = 1, 2, 3,..., until the state of forcing S_{frc} attains the forcing requirement of bud burst, FU_{crit}. The day of the attainment of FU_{crit} is determined as the day of bud burst, t_{BB} (Fig. 4).

32. Priorities for experimental testing of the models

321. Temperature data and calculations

Simulations with each of the five model types with field temperature data were carried out using the algorithm developed in the study (Fig. 4), in order to establish priorities for the experimental testing of the models. A small difference in the simulated timing of bud burst between any two models implied low priority for testing between the two models, and correspondingly a great difference implied a high priority for testing between the models.

Temperature data collected by the Finnish Meteorological Institute in Jyväskylä in Central Finland (62°14'N, 25°44'E, 86 m asl)
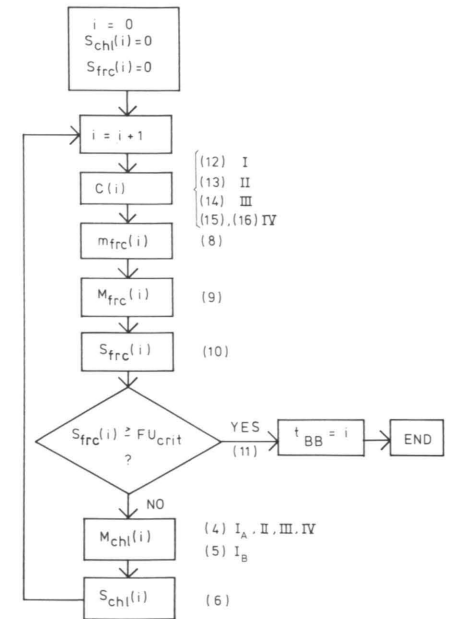
Fig. 4. Calculation algorithm for models of bud dormancy release of trees. The Arabic numerals in parentheses indicate the respective equation in the text. The Roman numerals indicate the model type when the same equation is not used with all of the five model types. Index i indicates running number of day. For other symbols, see text.

were used in the simulations. Temperature records were measured in standard meteorological screens 2 m above the ground. The daily mean temperature was calculated as the mean value of the records measured at 08 00 h, 14 00 h and 20 00 h. The temperature data covered the period 1902—1980. The years 1912—1916 were ignored due to missing observations. Dormancy release was simulated for a total of 73 years.

With each of the five model types, simulations with ten values of the chilling requirement of rest completion CU_{crit} (from 5 to 50, step 5 CU) and four values of the

forcing requirement of bud burst FU_{crit} (50, 100, 150, and 200 FU) were carried out. Thus, in all, $5 \cdot 10 \cdot 4 = 200$ simulations were carried out, each simulation being determined by the model type and the combination of the values of the model parameters CU_{crit} and FU_{crit}. The following values of the model-specific parameters were used in the simulations:

$C_{min} = 0.1$ (Figs. 3b,c),
$CU_{dr} = 0.5 \cdot CU_{crit}$ (Fig. 3c),
$CU_{tr} = 0.33 \cdot CU_{crit}$, $CU_{pr} = 0.66 \cdot CU_{crit}$
    (Fig. 3d),
$T_1 = 10\,°C$, $T_2 = 20\,°C$ (Fig. 3e).

In each simulation, the day for bud burst was calculated for each year, initiating the calculations each year on September 1 (deliberate starting point for rest period). The results of each simulation were summarized by determining the mean day of bud burst (t_{BB}) as the mean value of the annual days of bud burst over the 73 years.

322. Results

With model types I_A and I_B, the value of the state of forcing S_{trc} did not increase from zero during the autumn until rest completion was attained at $S_{chl} = CU_{crit}$ (Figs. 5a,b, see Fig. 3a). With the other models the value of S_{frc} already started to increase at the beginning of September (Figs. 5c—e, see Figs. 3b—d). The increase was especially pronounced with model type III (Fig. 5d). These differences in the time course of S_{frc} generated parallel differences in the timing of bud burst. Model types I_A and I_B implied the latest bud burst, followed by model types II, IV, and III (Fig. 6). In most cases, the mean day of bud burst implied by model types III and IV were clearly too early, compared with the timing of bud burst of trees under Central Finnish conditions (Hertz 1929, Huikari and Paarlahti 1967, Raulo and Leikola 1974).

For some years, rest completion was slightly delayed with model type I_B (Fig. 5b), as compared with model type I_A (Fig. 5a). This was due to the counteractive effect of temperatures above $10.4\,°C$ in model type I_B (Fig. 1b), an effect which was not involved in model type I_A (Fig. 1a). This difference, however, generated only minor differences

between these two models in the timing of bud burst (Fig. 6).

On the basis of the simulations, testing among the main model types I—IV was found to have a high priority (large differences in t_{BB}), while testing between the model type I_A and I_B was found to have a low priority (small differences in t_{BB}) (Fig. 6).

33. Model predictions for experimental testing

331. Calculations

Simulations with each of the four main model types with temperature data for a chilling experiment were carried out with the algorithm developed in the study (Fig. 4), in order to obtain predictions of the main model types for the outcome of the experiment. It was assumed in the simulations that each treatment group consists of seedlings belonging to nine sub-populations, and that the relative proportion of each of the sub-populations is the same from one treatment group to another. The value of CU_{crit} (the chilling requirement of rest completion) varied among the sub-populations, whereas the value of FU_{crit} (the forcing requirement of bud burst) was common to them (Table 3). In the case of the model specific parameters, the same values as in Chap. 32 were used in the simulations.

In the experimental design the seedlings were first exposed to *a rest breaking chilling temperature* of T = 3.5 °C. Seventeen durations of the chilling period, ranging from zero to sixteen weeks, were applied. After the chilling period, the seedlings were exposed to one of three *forcing temperatures* of 12 °C,

17 °C, or 22 °C. In this way, $17 \cdot 3 = 51$ treatment groups, i.e. combinations of duration of chilling and forcing temperature, were applied in the simulations. Subsequently, the values of two test variables were determined for each treatment group (Hänninen 1987).

Dormancy release ratio DRR indicates the proportion of the bud bursting seedlings out of the total number of seedlings in the treatment group. The value of DRR was obtained for each treatment group by summing the relative proportions of those sub-populations

Table 3. Division of the seedling population into nine sub-populations in a hypothetical chilling experiment. CU_{crit} = chilling requirement of rest completion, FU_{crit} = forcing requirement of bud burst.

Sub-population	CU_{crit}	FU_{crit}	Relative proportion
I	40	240	0.01
II	45	240	0.05
III	50	240	0.10
IV	55	240	0.15
V	60	240	0.38
VI	65	240	0.15
VII	70	240	0.10
VIII	75	240	0.05
IX	80	240	0.01

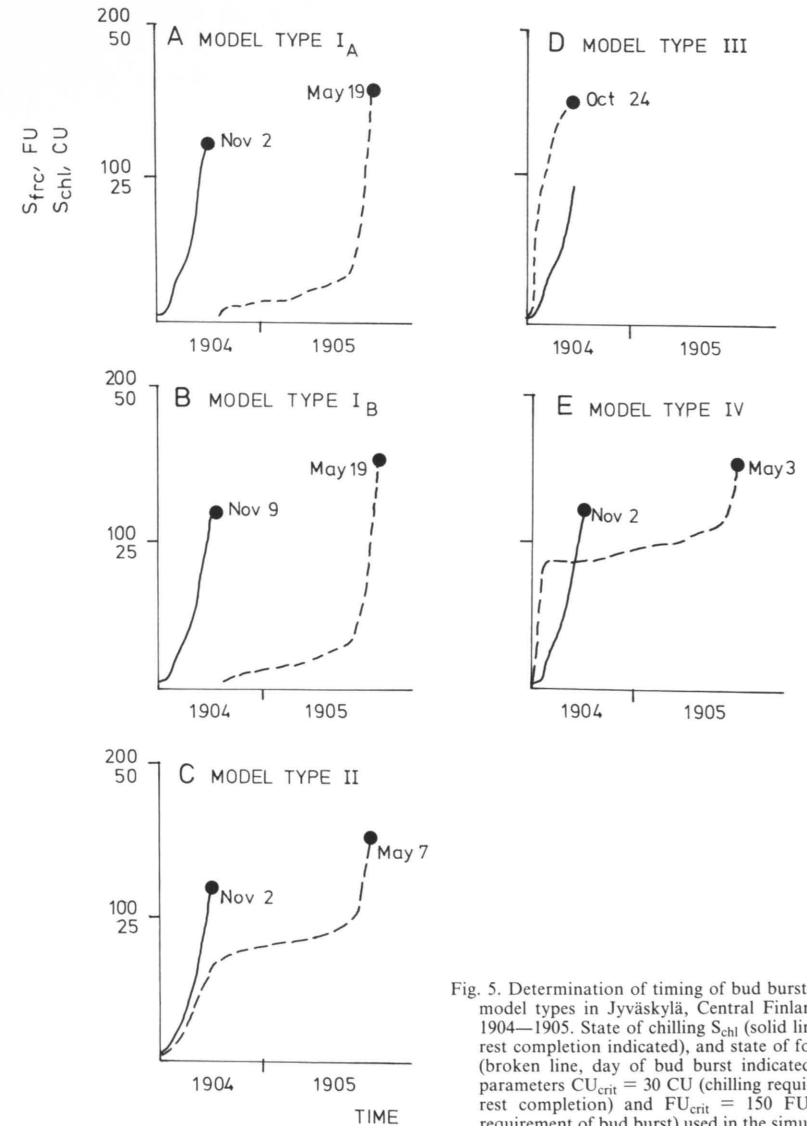Fig. 5. Determination of timing of bud burst with five model types in Jyväskylä, Central Finland during 1904—1905. State of chilling S_{chl} (solid line, day of rest completion indicated), and state of forcing S_{frc} (broken line, day of bud burst indicated). Model parameters $CU_{crit} = 30$ CU (chilling requirement of rest completion) and $FU_{crit} = 150$ FU (forcing requirement of bud burst) used in the simulations.

of the group which had a non-zero value for the competence function at the end of the chilling period (Fig. 3, Table 3). *Mean days to bud burst* DBB indicates for the treatment group the mean number of days between the beginning of the forcing period and the day of bud burst. The value of DBB was first calculated separately for each of those sub-populations of a given treatment group which had a non-zero value for the competence function at the end of the chilling period. The calculation took place by counting the number of days required in the forcing conditions to attain the forcing requirement of bud burst, FU_{crit}. The DBB value of the treatment group was then obtained by weighing the DBB values of the sub-populations by their relative proportions (Table 3). In the analysis of the results, the values of both DRR and DBB were presented as a function of the duration of the previous chilling period, and of the forcing temperature (Hänninen 1987).

332. Results

Dormancy release ratio

With model types I, II, and III, the forcing temperature did not affect the value of the dormancy release ratio DRR (Figs. 7a,c,e). This was because in these model types, the value of the competence function is independent of the forcing temperature (Figs. 3a—c). With model type I, the value of DRR increased sigmoidally from zero at five weeks of chilling to unity at 11 weeks of chilling (Fig. 7a). This was due to the corresponding increase in the proportion of the sub-populations with a non-zero value for the competence function at the end of the chilling period, with increasing duration of chilling. On the other hand with model types II and III the value of DRR was unity for all durations of chilling (Figs. 7c, e), because the competence function always has a non-zero value with these model types (Figs. 3b, c).

With model type IV, the DRR values generally increased with an increasing forcing temperature (Fig. 7g), since during pre- and postrest periods the value of the competence function also depends on the forcing temperature (Figs. 3d, e). With each of the three forcing temperatures, the values of DRR first decreased and then increased with an increasing duration of chilling (Fig. 7g). This was because the proportion of seedlings in the true rest state first increased and then decreased with an increasing duration of chilling (see Fig. 3d); and because the temperature threshold T_{trh} for full growth competence first increased and then decreased with an increasing duration of chilling (Fig. 3e). At ten weeks of chilling DRR reached the value of unity with all forcing temperatures, since 1) no seedlings were in the true rest state any longer, and 2) all of the three forcing temperatures were above the threshold value T_{trh} for those seedlings that were still in a postrest state (see Figs. 3d, e).

Mean days to bud burst

With all of the model types, the values of DBB decreased with an increasing forcing temperature (Figs. 7b,d,f,h). This was because the rate of forcing increased with an increasing forcing temperature (Fig. 1c).

With model type II the value of DBB declined exponentially with an increasing duration of chilling (Fig. 7d), since the values of the competence functions of the sub-populations first increased and then levelled off with an increasing duration of chilling (Fig. 3b). With model type III, a bell-shaped DBB curve was obtained (Fig. 7f), since the values of the competence functions of the sub-populations first decreased, then increased, and finally levelled off, with increasing duration of chilling (Fig. 3c).

Compared with the DBB-curves obtained with model types II and III, (Figs. 7d, f), the values of DBB obtained with model types I and IV were relatively independent from the duration of chilling (Figs. 7b, h). This was because the non-zero values of the competence functions of the sub-populations were always unity with model types I and IV, i.e. they were not influenced by the duration of chilling (Figs. 3a, d).

In the model types I and IV, the value for the state of forcing S_{frc} increased slowly in the chilling conditions of T = 3.5°C after attainment of CU_{crit} (the chilling requirement of rest completion) (Fig. 1c). Thus, with the increasing duration of chilling an increasing value of S_{frc} was already obtained in the chilling conditions, and a decreasing number of days was required in the forcing conditions for attainment of the forcing requirement of bud burst, FU_{crit}. This explains why the DBB-curves declined slightly with model types I and IV with increasing duration of chilling (Figs. 7b, h).

The implications of the models concerning the outcome of a chilling experiment differ from each other drastically (Fig. 7). This makes it possible to test the models experimentally.

Fig. 6. Simulated mean day of bud burst t_{BB} in Jyväskylä, Central Finland during the past 73 years, as a function of the chilling requirement of rest completion CU_{crit} and the forcing requirement of bud burst FU_{crit}. The positive values on the horizontal axes indicate the Julian date, and the negative values number of day counted backwards from December 31. Roman numerals indicate the model type used in the simulation. Separate asterisks indicate the results of model type I_B when different from results of model type I_A.
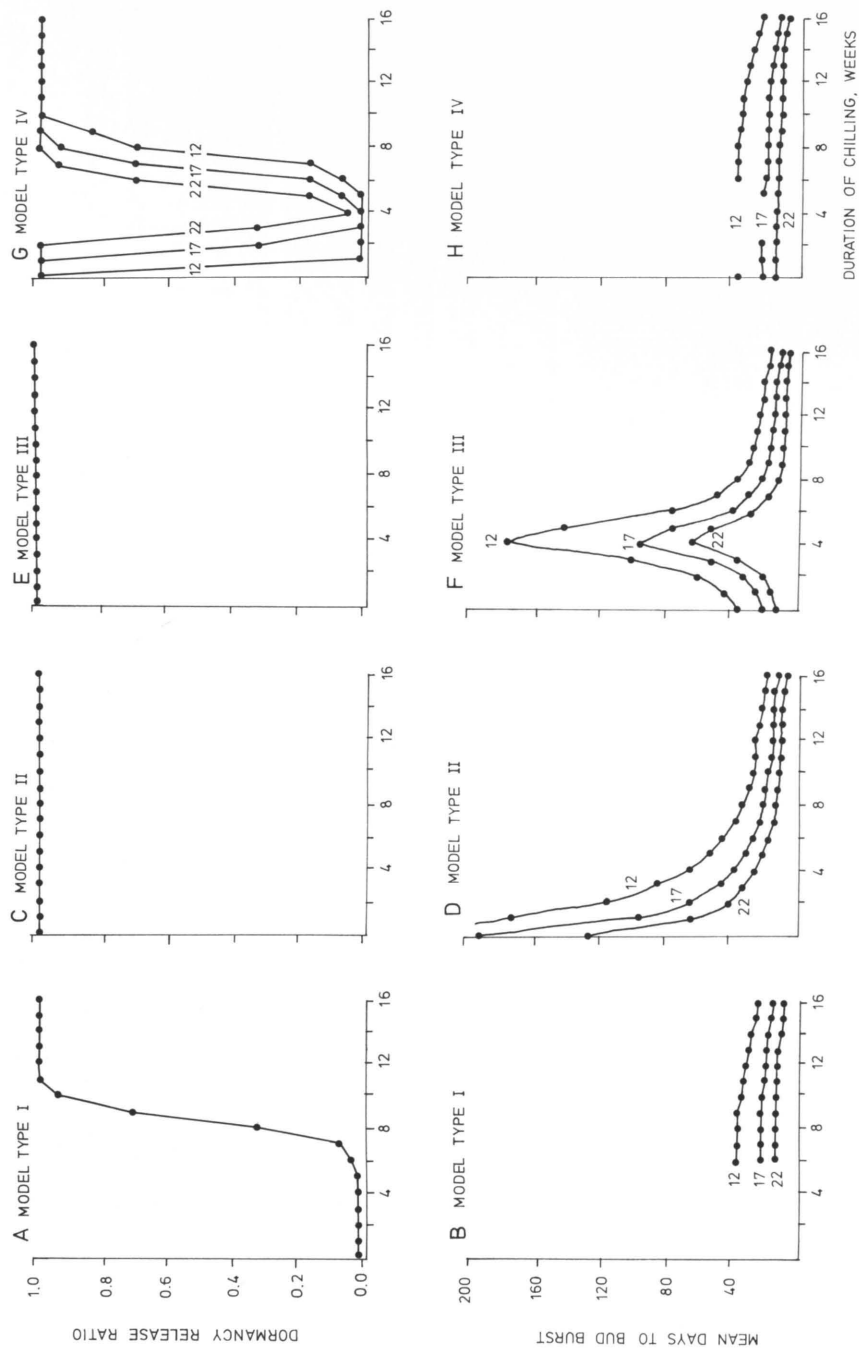
Fig. 7. Predictions of the four main model types (A,C,E,G) of the dormancy release ratio DRR, and (B,D,F,H) of the mean days to bud burst DBB; as a function of the duration of the previous chilling period and the forcing temperature. The arabic numerals indicate the forcing temperature, a single line indicates results common for all three forcing temperatures.

4. Experimental testing of the models

41. Materials and methods

411. Experimental design and analysis of the results

The models of the effects of air temperature on bud dormancy release in trees were tested during 1986—1988 in four chilling experiments with two-year-old seedlings of Scots pine and Norway spruce (Table 4), with an experimental design similar to that presented in Chap. 33.

Model types

The four main model types were tested by examining the values for the dormancy release ratio DRR and the mean days to bud burst DBB, as a function of the duration of chilling and the forcing temperature (Fig. 7). When calculating the value of DRR, seedlings that died before the end of the experiment without having bursted bud (on average, 1.9 seedlings per group) were excluded from the analysis. When examining the results, the time required for the melting of the seedlings (Chap. 413) was added to the original duration of chilling.

Chilling requirement of rest completion

According to the prediction of the chilling unit model (Fig. 1a, Eqn. (4)), the average accumulation of chilling units required for the rest completion of a given tree provenance is constant, irrespective of temperature conditions prevailing during chilling, or of other environmental conditions prevailing before or during chilling.

In order to test the chilling unit model, the durations of chilling of the treatment groups which were forced in 17 °C were converted into accumulated chilling units. The daily accumulation rate of chilling units was calculated using the daily mean temperature as an argument in Eqn. (4). The daily mean temperature was determined according to hourly temperature records. In experiment II, temperature was measured at three points for part of the chilling period, and in the other experiments two to three chilling chambers were used for the whole chilling period (Chap. 413). In these cases, two or three mean temperatures represented the chilling conditions on a given day. For these data, the daily accumulation rate of the chilling units was first calculated separately for each of the two or three daily mean temperatures, and the final value of the daily accumulation rate of the chilling units was determined as the mean value of the two to three original values. The time required for the melting of the seedlings (Chap. 413) was taken into account when calculating the accumulation of chilling units.

Means and 95 per cent confidence intervals for the accumulation of chilling units required for attaining rest completion for half of the seedlings (DRR = 0.5) of a given provenance in a given experiment (Table 4) were calculated using the Probit-procedure (Finney 1971, SAS 1985, p. 639—645). Subsequently, the chilling unit model was tested by comparing the results obtained for a given provenance in different experiments. Variation in the chilling requirement among the species and provenances was examined in a similar way.

Forcing requirement of bud burst

According to the prediction of the forcing unit model (Fig. 1c, Eqn. (8)), bud burst of fully chilled seedlings of a given provenance takes place on the average at a constant accumulation of forcing units, regardless of temperature conditions during forcing or of other environmental conditions prevailing before or during forcing.

In order to test the forcing unit model, the durations of forcing required for bud burst of the individual seedlings obtained after 12—16 weeks of chilling were converted to corresponding accumulated forcing units. The daily accumulation rate of the forcing

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Table 4. Chilling experiments of the study.

Experiment, years	Seedling material	Chilling Type, intended temp., °C	Chilling Temp. x̄ ± S.D., °C	Chilling Duration, weeks	Chilling Light conditions	Forcing Type, intended temp. °C	Forcing Temp. x̄ ± S.D., °C	Forcing Photo-period, h	Forcing Photon flux density, $\mu Em^{-2}s^{-1}$
I 1986—87	Central Finnish Scots pine	Growth chamber 4	3.9 ± 1.3	0—20	Dark	Growth chamber 12	12.8 ± 1.2	12	5—35
						Greenhouse, growth chamber 17	17.7 ± 1.8	12[1]	5—80
						Growth chamber 22	21.6 ± 2.0	12	5—35
II 1986—87	Central Finnish Scots pine Northern Finnish Scots pine	Natural	−0.8 ± 5.2	0—24	Natural	Growth chamber 12	12.8 ± 1.2	12	5—35
						Greenhouse, growth chamber 17	17.7 ± 1.8	12[1]	5—80
						Growth chamber 22	21.6 ± 2.0	12	5—35
III 1987—88	Central Finnish Scots pine Central Finnish Norway spruce	Growth chamber, initial freezing 4	4.3 ± 1.6	0—16	Dark	Growth chamber 12	12.1 ± 0.7	12	5—35
						Greenhouse, growth chamber 17	17.3 ± 1.1	12	5—80
IV 1987—88	Central Finnish Scots pine Central Finnish Norway spruce	Growth chamber 4	4.4 ± 1.4	0—16	Dark	Greenhouse, growth chamber 17	17.3 ± 1.1	12	5—80

1) Slightly higher during first two weeks of experiment

units was calculated using the daily mean temperature as argument in Eqn. (8). The daily mean temperature was determined according to hourly temperature records. During the last weeks of the experiments, the 17°C forcing took place in two to three growth chambers (Chap. 413). In these cases, two or three mean temperatures represented the forcing conditions of a given day. For these data, the daily accumulation rate of forcing units was first calculated separately for each of the two or three daily mean temperatures, and the final daily accumulation rate of forcing units was obtained as the mean value of the original two or three values.

The forcing unit model was tested by comparing the means and standard deviations of the accumulation of forcing units required for the bud burst of a given provenance in the different forcing temperatures in different experiments (Table 4). Variation in the forcing requirement of bud burst among the species and provenances was examined in a similar way.

412. Raising of seedlings

Experiments I and II

Seedlings from a Central Finnish provenance of Scots pine were raised in Central Finland at the Suonenjoki commercial nursery (62°40′N, 27°00′E, 130 m asl) using seeds of local origin (Table 4). The seeds were sown on June 11, 1985 in a greenhouse in paper pots in a mixture of peat and sand. The seedlings were transferred out of doors on August 11, 1985. After their second growing season at the end of August in 1986, the seedlings were transplanted into larger containers (500 cm³) in a mixture of peat and sand. On September 1, 1986, the seedlings were transferred to the Botanical Garden of University of Joensuu (62°36′N, 29°43′E, 81 m asl).

The seedlings from a Northern Finnish provenance of Scots pine were raised in Northern Finland at the Imari commercial nursery (66°29′N, 25°33′E, 100 m asl) using seeds gathered from the area covering about 67°N—68°N, 29°E, 150 m asl (Table 4). The seeds were sown on May 27, 1985 in a greenhouse in paper pots. The seedlings were transferred out of doors on July 26, 1985.

After their second growing season at the end of August 1986, the seedlings were transplanted into larger containers (500 cm³) in a mixture of peat and sand. The seedlings were transferred to the Botanical Garden of University of Joensuu on September 4, 1986.

The experimental treatments of experiments I and II were initiated at the Botanical Garden of University of Joensuu on September 10, 1986, and stopped on May 31, 1987.

Experiments III and IV

Seedlings of both Scots pine and Norway spruce were raised at the Suonenjoki commercial nursery using seeds of local origin (Table 4). Seeds of Scots pine were sown in a greenhouse in paper pots on May 12, 1986, and the seedlings were transferred out of doors on August 1, 1986. Seeds of Norway spruce were sown in a greenhouse in paper pots on April 25, 1986, and the seedlings were transferred out of doors on September 1, 1986. At the end of their second growing season on August 17, 1987, the seedlings of both species were transferred into a greenhouse in order to avoid exposure to frost temperatures. A slight frost, however, occurred during the night before the transfer. The temperature in the greenhouse fluctuated between 10°C and 25°C. The seedlings were transplanted in the greenhouse into larger containers (500 cm³) at the end of September 1987.

The experimental treatment of the seedlings in experiment III was initiated at the Suonenjoki nursery on October 6, 1987 (freezing treatment, Chap. 413), while the seedlings of experiment IV remained in the greenhouse (T = 10°C — 25°C). All of the seedlings were transferred to the Botanical Garden of University of Joensuu on October 13, 1987, where the experimental treatments of experiment III were continued and the experimental treatments of experiment IV were initiated during the day of the transfer. The treatments of both experiments were stopped on May 26, 1988.

413. Growing conditions

Thermographs model 'Lambrecht 252' were used in most cases in each growing place for monitoring of temperature. After the first

five weeks in experiment II, however, a soil thermograph model 'Lambrecht 257' was used for measuring air temperature under snow cover in the outdoor chilling place. In this case, three measurement points were applied; otherwise temperature was monitored in one point in each growing place. An air circulator was used in all indoor growing places in order to minimize temperature gradients.

Chilling conditions

In experiments I, III, and IV, chilling took place in dark growth chambers (Table 4). In each of these experiments, two to three growth chambers were used. During the first week of chilling in experiment III, the seedlings were exposed at the Suonenjoki nursery to an initial *freezing treatment* in darkness: two days in +5 °C, then two days in −2.5 °C, and finally three days in +5 °C. Otherwise the intended chilling temperature was 4 °C in all chilling treatments. Due to technical shortcomings, however, the real temperatures deviated from the intended one (Table 4). In experiment II chilling took place under natural temperature and light conditions at the Botanical Garden of the University of Joensuu (Table 4). The mean weekly temperatures during the first and last chilling week were 8.6 °C and −3.3 °C, respectively. The minimum of the mean weekly temperatures during the chilling period was −9.4 °C. The seedlings were irrigated regularly in the indoor chilling places in experiments I, III, and IV.

Forcing conditions

The intended forcing temperatures were 12 °C, 17 °C, and 22 °C, but due to technical shortcomings, the real forcing temperatures deviated from the intended values (Table 4). Generally, the 12 °C and 22 °C forcing took place in growth chambers, and the 17 °C forcing in a greenhouse. After the first 26 weeks in experiments I and II, and after the first 22 weeks in experiments III and IV, however, the 17 °C forcing took place in two to three growth chambers. In these cases, the seedlings of each of the treatment groups were divided equally in the growth chambers. The length of photoperiod was 12 h, with the exception of the first two weeks in the forcing temperature of 17 °C in experiments I and II, when the natural day length slightly exceeded 12 h. Fluorescent tubes (model 'Airam L65/80W — 1XC, Daylight deluxe') were used in both the growth chambers and the greenhouse. The photon flux density at plant height was generally 5—35 $\mu Em^{-2}s^{-1}$. In the greenhouse (17 °C forcing), however, the photon flux density was 40—80 $\mu Em^{-2}s^{-1}$ during sunny weather. The seedlings were irrigated regularly in the forcing places.

Sampling and transfer of the seedlings

In experiments I, III, and IV, a total of 15 seedlings for a given treatment group were sampled on the scheduled day of transfer to the forcing conditions (Chap. 411). An equal number of seedlings was sampled at random in each of the two to three indoor chilling places. A similar procedure was also followed in the case of the early transfer groups with outdoor chilling in experiment II. In the case of the late transfer groups, however, in experiment II it was necessary to sample the treatment groups before snow cover appeared, i.e. several weeks before the transfer to the forcing conditions took place.

The seedlings in a given treatment group were transferred on the scheduled transfer day from the chilling places to the forcing place at 12 °C, regardless of the forcing temperature of the group. Subsequently, the 17 °C and 22 °C seedlings were transferred to their final forcing temperatures in a gradual way: the following day at 17 °C, and to 22 °C on the day thereafter (22 °C seedlings). In this way, the seedlings were gradually acclimatized to increasing temperatures. In experiment II, the seedlings in the late transfer groups were frozen on the scheduled transfer day. In these cases, the seedlings were transferred first to a dark growth chamber to melt in a temperature of +3 °C. After the seedlings and the soil in the containers had been completely melted, the seedlings were transferred to the forcing places in a gradual way, like the other seedlings. Melting took two to seven days.

414. Determination of bud burst

The bud burst of Scots pine seedlings was determined with the aid of growth measurements of the terminal bud. A small needle was pushed about 5 mm below the terminal bud and the distance between the needle and the tip of the bud was measured two to three times a week. The values for days without a measurement were determined using linear interpolation. The seedling was considered to have burst bud if the total growth of the bud exceeded 5 mm. The day of bud burst was determined as the day when the growth exceeded 2 mm.

The bud burst of Norway spruce seedlings was determined with the aid of visual inspection of the terminal bud. The growth status of the bud was determined two or three times a week using the following classification: 0 = dormant, + = swelling, no new needles visible, 1 = new needles visible. The day of bud burst for the seedling was determined as the median day between the last day with a "+"-sign and the first day with a "1"-sign. If the new needles did not appear, the seedling was considered not to have burst bud.

42. Results and discussion

421. Model types

With the exception of two cases with forcing at 12 °C (Figs. 11a, 12a), the DRR-values showed a similar pattern in each experiment with each species, provenance, and forcing temperature (Figs. 8a—14a). The DRR-values obtained with no or short chilling were zero. After two to four weeks of chilling the DRR-values started to increase with increasing duration of chilling, reaching in most cases the value of unity at 10—16 weeks of chilling. This increasing pattern of the DRR-values is in agreement with model type I, and disagrees with the other model types (Fig. 7).

The DRR-values obtained with Scots pine in experiment III with chilling durations longer than six weeks were smaller at a forcing temperature of 12 °C than at a forcing temperature of 17 °C (Fig. 11a). Similarly with Norway spruce in experiment III, the values of DRR obtained after 10—16 weeks of chilling were smaller at 12 °C than at 17 °C (Fig. 12a). These findings are in agreement with model type IV, in the case of the post-rest period (Fig. 7g).

The DBB-values obtained with forcing at 12 °C declined exponentially with the increasing duration of chilling, whereas the DBB-values obtained with forcing at 17 °C or 22 °C were relatively insensitive to the duration of chilling (Figs. 8b—14b). These findings indicate an interaction of duration of chilling and forcing temperature in the determination of growth competence: with short durations of chilling the growth competence increases with an increasing forcing temperature. This kind of interaction was not involved in any of the model types (Figs. 3, 7). In model type IV, however, another kind of interaction of duration of chilling and forcing temperature in determining the growth competence of the buds was involved (Figs. 3d, e, 7g).

Regarding the model types of bud dormancy release, Hänninen and Pelkonen (1988a,b) found results in a preliminary study similar to those in the present study. They worked with similar seedling material and similar growing conditions to those used in the present study. In contrast, other previous findings with Scots pine (Hoffmann and Lyr 1967) and with Norway spruce (Nienstaedt 1967, Worrall and Mergen 1967) deviate drastically from the findings of the present study (Chap. 51). The reason for this inconsistency is unclear. It is possible that differences in the age or raising of the experimental material or differences in the experimental conditions generated the different results. The most probable reason, however, is the difference between the present and the previous studies as to their provenances. Obviously all of the provenances in the previous studies were more southern than the provenances of the present study, or in the study of Hänninen and Pelkonen (1988a,b).

422. Chilling requirement of rest completion

Chilling unit model

In experiment III with its initial frost treatment, virtually the same chilling requirements were found as in the corresponding experiment IV without frost treatment (Figs. 15a,b). Thus, in this case, the chilling unit model was able to describe the rest completion of the seedlings.

In the experiments during 1986—1987 with Central Finnish Scots pine, a drastically greater number of chilling units was required for rest completion with chilling in the
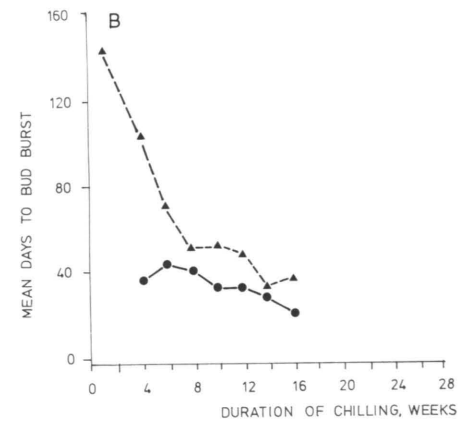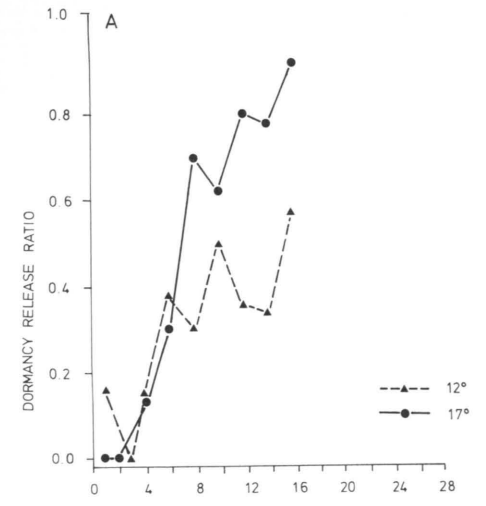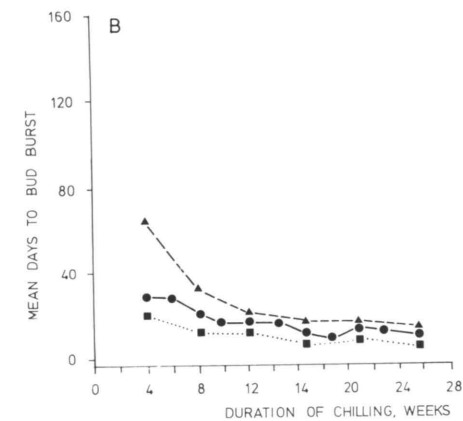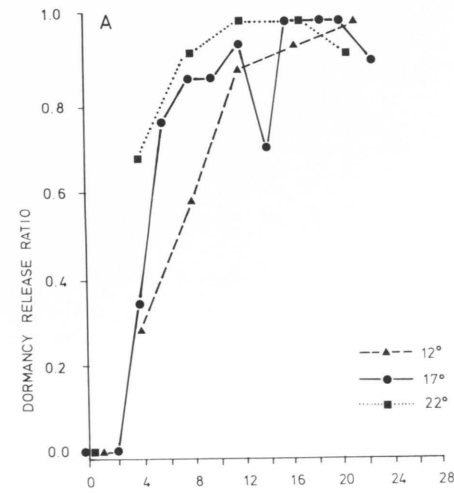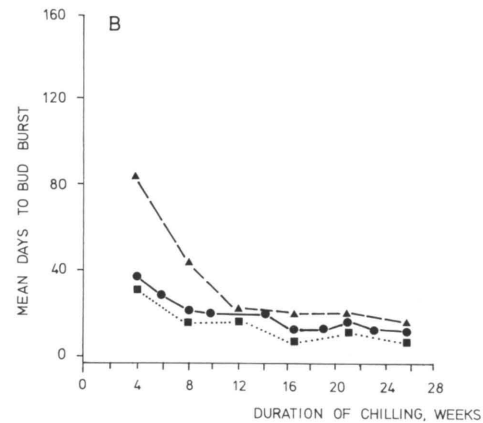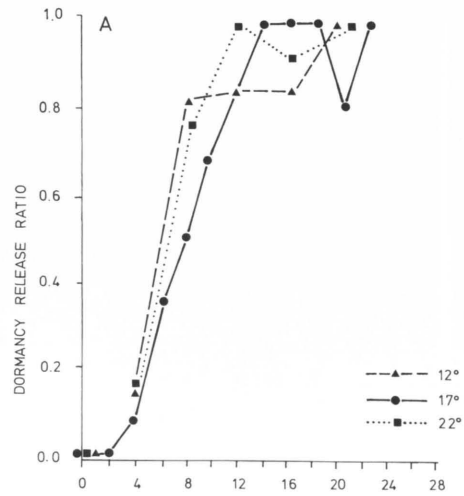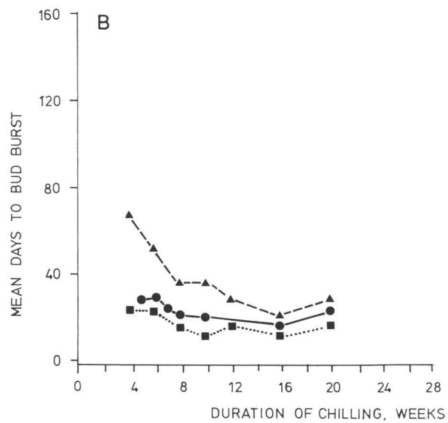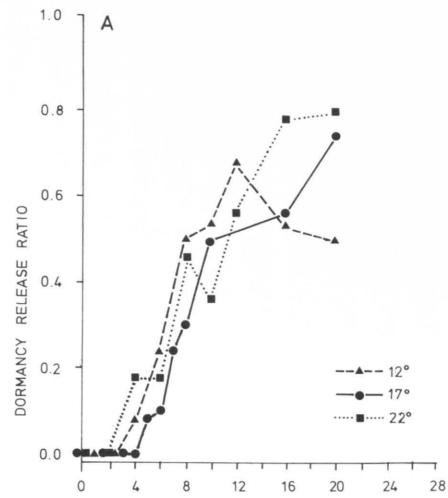
Fig. 8. (A) Dormancy release ratio, and (B) mean days to bud burst, as a function of the duration of the previous chilling and of the forcing temperature. Symbols for the forcing temperatures indicated in (A). Central Finnish provenance of two-year-old seedlings of Scots pine, experiment I (chilling in growth chamber, see Table 4).

Fig. 9. As Fig. 8, but Central Finnish provenance of two-year-old seedlings of Scots pine, experiment II (chilling under natural conditions, see Table 4).

Fig. 10. As Fig. 8, but Northern Finnish provenance of two-year-old seedlings of Scots pine, experiment II (chilling under natural conditions, see Table 4).

Fig. 11. As Fig. 8, but Central Finnish provenance of two-year-old seedlings of Scots pine, experiment III (chilling in growth chamber with initial freezing treatment, see Table 4).

growth chamber in experiment I than with chilling in natural conditions in experiment II (Fig. 15 a). During 1987—1988, however, the amount of chilling units required in growth chambers in experiments III and IV was only slightly higher than with chilling in

natural conditions in experiment II during 1986—1987 (Fig. 15 a). These inconsistencies suggest that the chilling unit model (Fig. 1a) requires further development.

The seedlings in experiments I and II belonged to the same population, had the same pre-experiment history, and were forced under the same conditions. Thus, the reason for the inconsistent results (Fig. 15 a) has to be

found in differences in the chilling conditions. Chilling in relative constant temperatures in a growth chamber in experiment I may have been less efficient than chilling in naturally fluctuating temperatures in experiment II. This hypothesis is in agreement with the findings of Erez et al. (1979 a), Couvillon and Erez (1985), and Erez and Couvillon (1987) for *Prunus persica* (L.) Batsch.

The hypothesis of the superior efficiency of fluctuating temperatures over constant temperatures in a rest break does not explain the difference between the results of experiments I and IV (Fig. 15 a). The seedlings in both experiments were chilled under similar conditions in a growth chamber, and forced under similar conditions in either a greenhouse or a growth chamber. Thus, in this
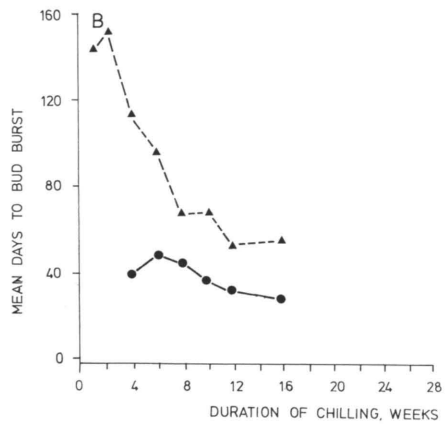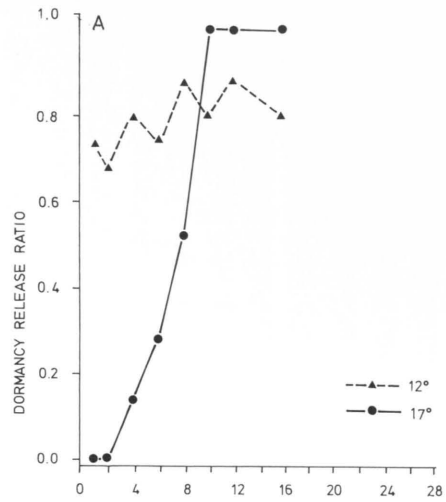
Fig. 12. As Fig. 8, but Central Finnish provenance of two-year-old seedlings of Norway spruce, experiment III (chilling in growth chamber with initial freezing treatment, see Table 4).

Fig. 13. As Fig. 8, but Central Finnish provenance of two-year-old seedlings of Scots pine, experiment IV (chilling in growth chamber, see Table 4).

Fig. 14. As Fig. 8, but Central Finnish provenance of two-year-old seedlings of Norway spruce, experiment IV (chilling in growth chamber, see Table 4).

case, an explanation for the differences must be found in differences in the pre-experiment conditions of the seedlings. It is possible that the extended period of warm short days prior to chilling in experiment IV reduced the chilling requirement, in comparison with experiment I. This hypothesis is in accordance with previous findings with *Picea glauca* (Moench) Voss (Nienstaedt 1966), with *Tsuga*
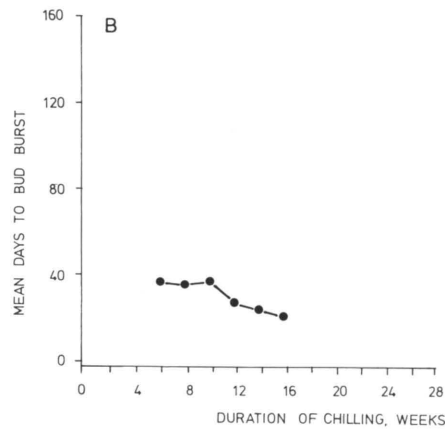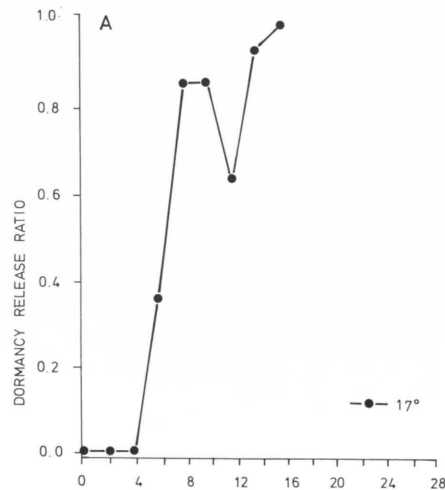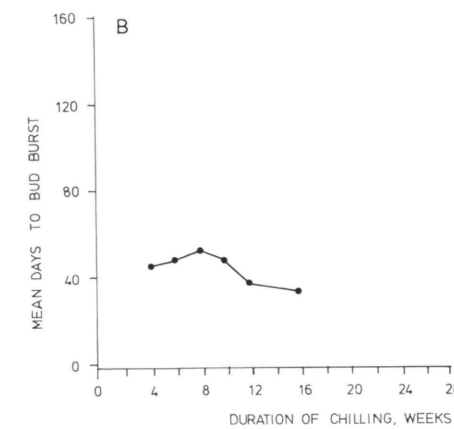
heterophylla (Rafin.) Sarg. (Nelson and Lavender 1979), and with *Pseudotsuga menziesii* (Mirb.) Franco (Lavender and Stafford 1985).

The DRR values obtained with Norway spruce in experiment III with forcing at 12 °C were about 0.8, irrespective of the duration of the chilling (Fig. 12a). In the case of seedlings of Scots pine forced at 12 °C, after one week of chilling in experiment III the value

of DRR was higher than zero (Fig. 11a). These findings suggest that, contrary to the assumption of the present study (Fig. 1a), the low forcing temperatures near 12 °C have a slight rest-breaking effect. The following evidence supports this suggestion:

1) The phenomenon occurred in experiment III (Figs. 11a, 12a), but not in experiments I or

II (Figs. 8a—10a). This was obviously because the real forcing temperature in experiments I and II (12.8 ±1.2 °C, Table 4) exceeded the upper limit for the rest-breaking temperature range for all of the seedlings, while this was not the case in experiment III with the slightly lower forcing temperature (12.1 ±0.7 °C, Table 4).

2) The maximum values of DBB were higher in experiment III (140 days, Fig. 11b) than in experiment I and II (about 80 days, Figs. 8b—10b). This was obviously because in experiment III a lot of time was required for rest completion in the forcing conditions of 12 °C, whereas in experiments I and II the smaller maximum values of DBB with 12 °C forcing were generated solely due to the interaction of the duration of chilling and the low forcing temperature in determining the growth competence, as suggested above.

3) Similar results for the rest-breaking effects of temperatures near 10 °C have been previously reported for Scots pine and Norway spruce by Hänninen and Pelkonen (1988 a, b, and for *Pseudotsuga menziesii* by Campbell and Sugano (1975, 1979).

The values of DRR obtained at 12 °C in experiment III after a short duration of chilling were much higher for Norway spruce (Fig. 12a) than for Scots pine (Fig. 11a). This finding suggests that the applied forcing temperature near 12 °C acted as a rest-breaking temperature for a larger proportion of the Norway spruce seedlings than for the Scots pine seedlings. Accordingly, the upper limit for the rest-breaking temperature range appears to be at a higher temperature for Norway spruce than for Scots pine.

Variation in the chilling requirement of rest completion

High within-provenance variation in the chilling requirement of rest completion, as indicated by the DRR-curves, was found in the present study. The difference between the minimum and maximum chilling requirement was generally 6—12 weeks (Figs. 8a—14a).

In experiment II a slightly greater accumulation of chilling units was required for rest completion with Central Finnish Scots pine (Fig. 15a) than with Northern Finnish Scots pine (Fig. 15c). In experiments III and IV, the chilling requirements were slightly higher for Central Finnish Scots pine (Fig. 15a) than for Central Finnish Norway spruce

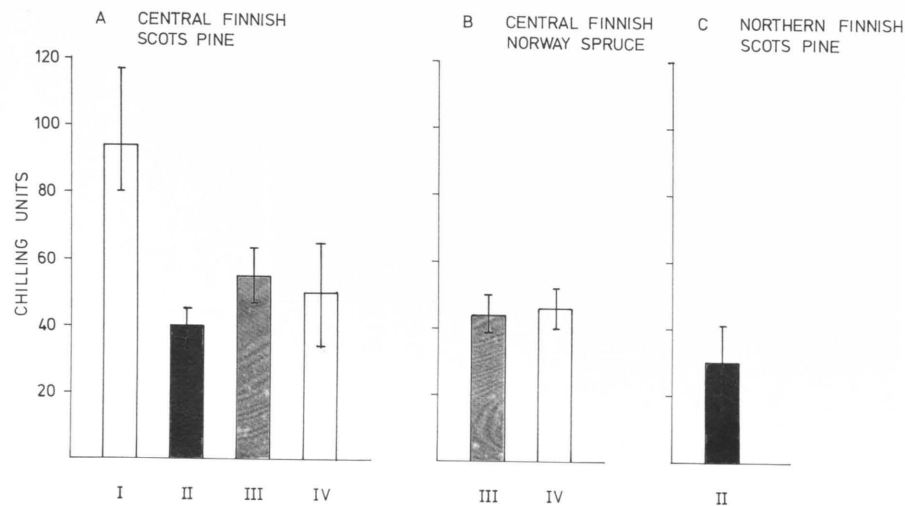Fig. 15. The accumulation of chilling units required for the rest completion of half of two-year-old Scots pine and Norway spruce seedlings in four chilling experiments. The Roman numerals indicate the experiment (see Table 4). The vertical bars indicate the 95 per cent confidence intervals of the estimated values. Light histograms: chilling under controlled conditions without freezing; slightly shaded histograms: chilling under controlled conditions with initial freezing; dark histograms: chilling under natural conditions.

tion of forcing units required for bud burst of a given provenance increased slightly with increasing forcing temperature (Fig. 16). Despite the great variation within each forcing temperature, this consistent finding suggests that the slope of the temperature response curve of potential rate of forcing is actually smaller than was assumed in the present study (Fig. 1c).

In the case of Scots pine the forcing requirements were smaller during 1986—1987 in experiments I and II than during 1987—88 in experiments III and IV (Fig. 16a). The forcing requirements in 1986—1987 were slightly smaller after natural chilling in experiment II than after controlled chilling in experiment I (Fig. 16a). Furthermore, the values of forcing units required for bud burst were unnaturally high compared with the accumulation of forcing units at the time of bud burst under Central Finnish natural conditions (Hänninen 1990a). All these findings suggest that the forcing unit model requires further development. As in the case of the chilling unit model, one possible hypothesis

for the further development is the superiority of naturally fluctuating temperatures over constant temperatures in causing ontogenetic development.

Variation in the forcing requirement of bud burst

Great within-provenance variation in the forcing requirement of bud burst was found in the present study. The standard deviation of the required accumulation of forcing units was in most cases about 20—40 per cent of the mean (Fig. 16).

In experiment II, the Central Finnish Scots pine (Fig. 16a) required in all three forcing temperatures a greater accumulation of forcing units for bud burst than the Northern Finnish Scots pine (Fig. 16c). In experiments III and IV, Norway spruce seedlings (Fig. 16b) required a greater accumulation of forcing units for bud burst than the Scots pine seedlings (Fig. 16a). These findings, however, were greatly masked by

(Fig. 15b). Considering the large confidence limits (Fig. 15), however, no conclusions concerning the differences in the chilling requirement among species and provenances can be drawn on the basis of these data.

Contrary to the findings of the present study with the two Finnish provenances of Scots pine, Perry and Wang (1960) found a clinal pattern in the chilling requirement of rest completion in *Acer rubrum* L. Provenances from the north-eastern United States had a definite chilling requirement of rest completion, whereas bud burst in provenances from Florida was even delayed by previous chilling. Similarly, Kriebel and Wang (1962) found that the chilling requirement of *Acer saccharum* Marsh. increases with the increasing latitude of the geographical origin of the provenance.

Differences in the DRR- and DBB-curves between the present and previous studies with Scots pine and Norway spruce (Chap. 51) make any comparison between the chilling requirements of rest completion found in these studies cumbersome. This difficulty is further emphasized due to the fact that the DRR-curves have not been

explicitly indicated in previous studies (Hoffmann and Lyr 1967, Nienstaedt 1967, Worrall and Mergen 1967). On the basis of the limited information concerning DRR in the previous studies it can be concluded, however, that the absolute chilling requirement of growth competence, i.e. the amount of chilling required to produce subsequent bud burst regardless of the value of DBB, is greater in the present study (about 4—16 weeks, Figs. 8a—14a) than in the previous studies (less than 4 weeks). On the contrary, if also levelling off of the DBB curve is required for rest completion, then there appear no striking differences in the chilling requirement between the present study and the previous studies with Scots pine and Norway spruce (Hoffmann and Lyr 1967, Nienstaedt 1967, Worrall and Mergen 1967).

423. Forcing requirement of bud burst

Forcing unit model

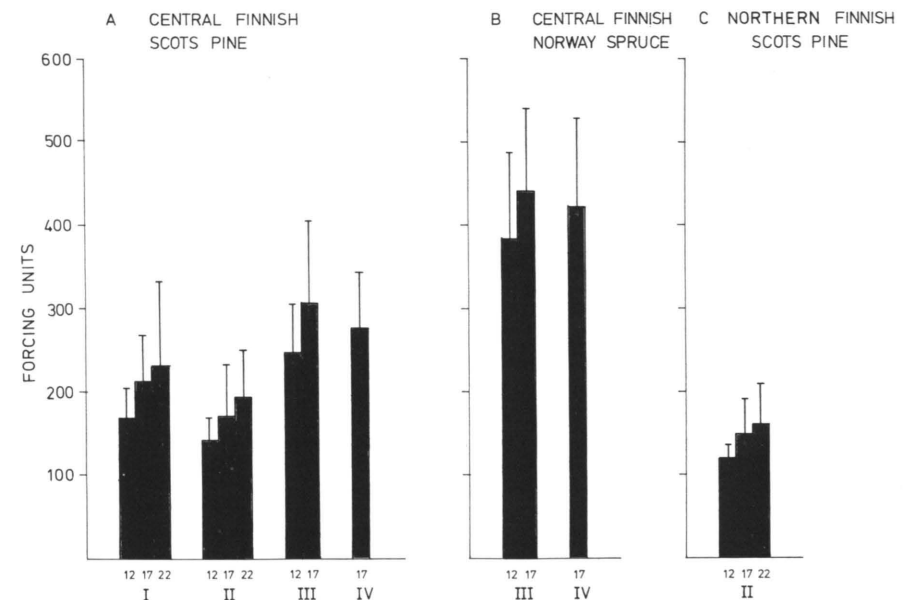In all experiments with more than one forcing temperature, the average accumula-

Fig. 16. Accumulation of forcing units ($\overline{x} \pm$ S.D.) required for the bud burst of two-year-old seedlings of Scots pine and Norway spruce, chilled previously for 12—16 weeks in four experiments. The Roman numerals indicate the experiment, and the arabic numerals the forcing temperature (see Table 4).

large within-provenance variation. Furthermore, strict comparisons with the Northern Finnish Scots pine are unwarranted owing to the differing raising environment of this provenance. Despite these shortcomings, the observed differences are in agreement with previous observations: a greater accumula-

tion of forcing units is required for bud burst in Norway spruce than in Scots pine (Raulo and Leikola 1974), and also in southern provenances as opposed to northern provenances of a given tree species (Kriebel and Wang 1962, Worrall and Mergen 1967, Dormling et al. 1968, Dormling 1982).

5. Synthesis model

51. Experimental results of previous studies

The results of most previous studies with Scots pine (Hoffmann and Lyr 1967) and Norway spruce (Nienstaedt 1967, Worrall and Mergen 1967) can be summarized as follows. 1) The DRR-curves were not explicitly reported. On the basis of the information given by the authors, however, it can be concluded that the value of DRR increased in most cases with increasing chilling, as in the present study (Figs. 8 a—14 a). However, obviously less chilling was required to reach the value of unity for DRR, i.e. the absolute chilling requirement of growth competence was smaller than in the present study. 2) An exponentially declining DBB curve was found also at high forcing temperatures (T > 15 °C), contrary to the findings of the present study (Figs. 8 b—14 b). This pattern of DRR- and DBB-curves has also been found in abundant earlier studies with several other tree species (Lamb 1948, Kriebel and Wang 1962, Nienstaedt 1966, 1967, Farmer 1968, Landsberg 1974, Campbell and Sugano 1975, 1979, van den Driessche 1975, Nelson and Lavender 1979, Gilreath and Buchanan 1981, Hinesley 1982, Cannell and Smith 1983, Garber 1983, Sorensen 1983, Ritchie 1984, Cannell et al. 1985 a, Carlson 1985, Burr et al. 1989, Murray et al. 1989). These results are not in agreement with any of the model types, but are intermediate to the predictions of model types I and II (Fig. 7).

A bell-shaped DBB-curve has been found in some studies with fruit trees (Fuchigami et al. 1977, Kobayashi et al. 1982, Kobayashi and Fuchigami 1983 a), and recently also in the case of *Pinus taeda* L. (Boyer and South 1989). These results support model type III (Fig. 7 f).

In the literature review of the present study, no experimental results that support model type IV were found. Here, however, commentary notes concerning the interpretation of Vegis' (1964) original conceptual model are necessary.

When formulating model type IV, the original conceptual model of Vegis (1964) was interpreted in the present study in a strict sense. Accordingly, Vegis' (1964) concept of the "widening and narrowing of growth promoting temperature range" was interpreted to refer to changes between no and full growth competence of the buds (Figs. 3 d,e). Campbell (1978) and Cannell (1989, 1990) interpreted Vegis' (1964) concept in a different way, referring to model type II. In the case of model type II, the DBB-curves level off with a shorter duration of chilling at a high (22 °C) than at a low (12 °C) forcing temperature (Fig. 7 d). For instance, at two weeks of chilling the difference in the DBB-values between these two forcing temperatures is about 80 days, whereas at eight weeks of chilling, the difference is only about 20 days (Fig. 7 d). In this sense chilling also widens the growth promoting temperature range in the case of model type II. The limited amount of previous experimental data about bud dormancy release with forcing at more than one temperature is in accordance with this prediction (Campbell and Sugano 1975, 1979, van den Driessche 1975). This kind of promotion was further emphasized in the experimental results of the present study (Figs. 8 b—12 b). Nygren (1987) found similar results for dormancy release in seeds of Scots pine. Thus, according to the interpretation referring to model type II (Campbell 1978, Cannell 1989, 1990) all these results are in accordance with the concept of

postrest (Vegis 1964): with increasing chilling, the rate of ontogenetic development becomes less dependent on the forcing temperature.

To conclude the literature review of the present study, 1) relatively few experimental results strictly support any of the model types I—IV, and 2) most of the experimental results are intermediate to the predictions of model type I and II.

52. Premises and implications of the synthesis model

A synthesis model of effects of air temperature on bud dormancy release in trees was developed in the present study. The model is based on previous models and on the experimental results of the present and previous studies. The following postulates constitute the synthesis model:

1) An absolute chilling requirement of growth competence, CU_{abs}, exists. Before this requirement is met the buds have no growth competence, i.e. the value of competence function C is zero when the state of chilling $S_{chl} < CU_{abs}$ (Fig. 17 a, compare model type I, Fig. 3 a).

2) Further chilling after attaining CU_{abs} gradually increases the growth competence of buds until full growth competence is attained at rest completion, i.e. in the range $CU_{abs} < S_{chl} < CU_{crit}$ the value of the competence function gradually increases with increasing S_{chl} (Fig. 17 a, compare model type II, Fig. 3 b).

3) Before rest completion, the growth competence of buds increases with an increase in the forcing temperature, i.e. in the range $CU_{abs} < S_{chl} < CU_{crit}$ the value of the competence function increases with an increase in the forcing temperature (the interaction of the duration of chilling and the forcing temperature in determining the growth competence of the buds) (Fig. 17 a).

The postulates (1) — (3) are fulfilled by calculating the value of competence function C as follows (Fig. 17 a):

$$C(t) = \begin{cases} 0, & S_{chl}(t) < CU_{abs} \\ \left(\dfrac{1 - C_{min} - \Delta C(t)}{CU_{crit} - \Delta CU(t) - CU_{abs}} \right) \cdot (S_{chl}(t) - CU_{abs}) + C_{min} + \Delta C(t), & CU_{abs} \leq S_{chl}(t) < (CU_{crit} - \Delta CU(t)) \quad (17) \\ 1, & S_{chl}(t) \geq (CU_{crit} - \Delta CU(t)) \end{cases}$$

where C_{min} is minimum growth competence, $\Delta C(t)$ is the increase in the minimum growth competence caused by the forcing temperature, and $\Delta CU(t)$ is the decrease in the chilling requirement for attaining full growth competence, caused by the forcing temperature, and CU_{abs} is the absolute chilling requirement of the growth competence. $\Delta C(t)$ is calculated as follows (Fig. 17 b):

$$\Delta C(t) = \begin{cases} 0, & T(t) < T_3 \\ \left(\dfrac{\Delta C_{max}}{T_4 - T_3} \right) \cdot (T(t) - T_3), & T_3 \leq T(t) < T_4 \quad (18) \\ \Delta C_{max}, & T(t) \geq T_4 \end{cases}$$

where ΔC_{max} is the maximal increase in the minimum growth competence caused by the forcing temperature $T(t)$, and T_3 and T_4 are the lower and upper limits for the temperature (°C) range where the growth competence

increases with increasing temperature. $\Delta CU(t)$ is calculated as follows (Fig. 17 c):

$$\Delta CU(t) = \begin{cases} 0, & T(t) < T_3 \\ \left(\dfrac{\Delta CU_{max}}{T_4 - T_3} \right) \cdot (T(t) - T_3), & T_3 \leq T(t) < T_4 \quad (19) \\ \Delta CU_{max}, & T(t) \geq T_4 \end{cases}$$

where ΔCU_{max} is the maximal decrease in the chilling requirement for attaining the full growth competence, caused by the forcing temperature.

The synthesis model was applied for the same hypothetical chilling experiment as the five original model types (Chap. 33) with two sets of parameter values. With the first set, results similar to those obtained in the experiments of the present study (Figs. 8— 14) were also obtained with the synthesis model: 1) a sigmoidally increasing DRR-curve (Fig. 18 a), 2) a DBB-curve that first declines and then levels off at forcing tem-
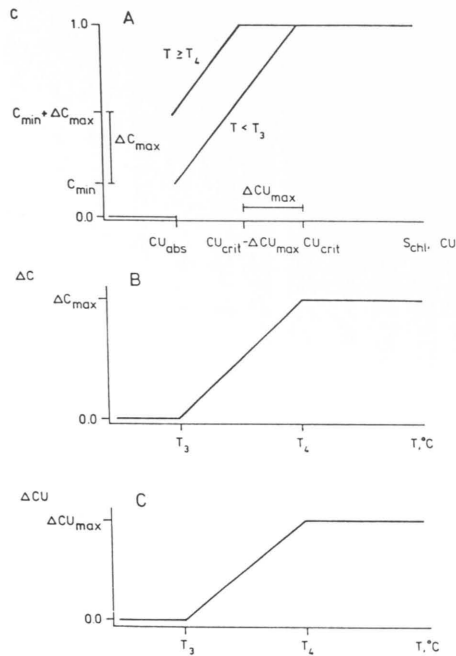
Fig. 17. Synthesis model for the effects of air temperature on bud dormancy release in trees. (A) Dependence of value of competence function C on the state of chilling S_{chl} and on the prevailing forcing temperature T. Temperature dependence of (B) increase in minimum growth competence (ΔC), and (C) decrease in chilling requirement for attaining full growth competence (ΔCU). In (A), two extreme cases with respect to forcing temperature T are shown: $T \geq T_4$ (maximum increase in growth competence caused by forcing temperature, $\Delta C = \Delta C_{max}$, $\Delta CU = \Delta CU_{max}$), and $T < T_3$ (no increase in growth competence, $\Delta C = 0$, $\Delta CU = 0$ CU).

perature of 12 °C (Fig. 18 b), and 3) a DBB-curve relatively insensitive to the duration of chilling at forcing temperatures of 17 °C and 22 °C (Fig. 18 b). With the second set of parameter values results similar to those obtained in most previous studies were obtained with the synthesis model (Lamb 1948, Kriebel and Wang 1962, Nienstaedt 1966, 1967, Hoffmann and Lyr 1967, Worrall and Mergen 1967, Farmer 1968, Landsberg 1974, Campbell and Sugano 1975, 1979, van den Driessche 1975, Nelson and Lavender 1979, Gilreath and Buchanan 1981, Hinesley 1982, Cannell and Smith 1983, Garber 1983, Sorensen 1983, Ritchie 1984, Cannell et al.
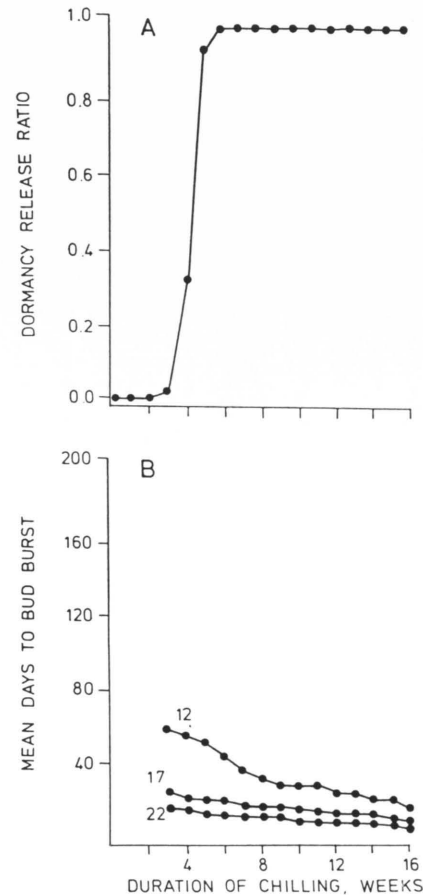

Fig. 18. Predictions of a synthesis model of bud dormancy release in trees of (A) the dormancy release ratio DRR, and (B) the mean days to bud burst DBB; as a function of the duration of previous chilling period and the forcing temperature. The arabic numerals indicate the forcing temperature, a single line in (A) indicates results common for all three forcing temperatures. Parameter values used in the simulations: $T_3 = 10$ °C, $T_4 = 15$ °C, $C_{min} = 0.4$, $\Delta C_{max} = 0.5$, $\Delta CU_{max} = 0.2 \cdot CU_{crit}$, and $CU_{abs} = 0.5 \cdot CU_{crit}$ (see Chap. 33 for details of the experiment).

1985 a, Carlson 1985, Burr et al. 1989, Murray et al. 1989): 1) a DRR-curve increasing steeply to unity with short durations of chilling (Fig. 19 a), and 2) a DBB-curve declining steeply exponentially, regardless of the forcing temperature (Fig. 19 b).
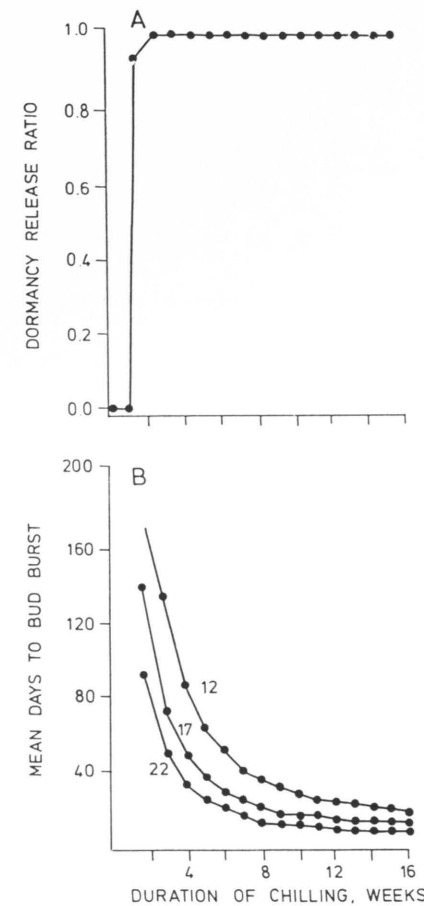

Fig. 19. As Fig. 18, but with parameter values $T_3 = 10$ °C, $T_4 = 20$ °C, $C_{min} = 0.1$, $\Delta C_{max} = 0$, $\Delta CU_{max} = 0$ CU, and $CU_{abs} = 0.2 \cdot CU_{crit}$.

53. Synthesis model as a framework for experimental studies

The wide variety of models proposed in the literature for the temperature regulation of bud dormancy release in trees presumably reflects genetic variation in trees. In the case of the synthesis model developed in the present study, this variation is taken into account by adjusting the parameter values of

the model. In this way, two of the original model types emerge as special cases of the synthesis model. The synthesis model reduces to model type II, if 1) the absolute chilling requirement is removed by setting $CU_{abs} = 0$ CU; and 2) the effect of the forcing temperature on growth competence is removed by setting $\Delta C_{max} = 0$ and $\Delta CU_{max} = 0$ CU (Figs. 3 b, 17 a). On the other hand, the synthesis model reduces to model type I if the gradual effect of chilling on growth competence is removed by setting $CU_{abs} = CU_{crit}$. By this means, the effect of the forcing temperature on growth competence is implicitly removed (Figs. 3 a, 17 a).

Within the framework of the synthesis model the model types I and II can be interpreted as extremes on a continuum of concepts of strict vs. gradual end point of rest period (Figs. 3 a, b, 17 a). In addition to covering this continuum, the synthesis model further introduces the interaction of the previous chilling and the prevailing forcing temperature, to determine the growth competence of the buds. The extent of this interaction forms another continuum in the synthesis model: the interaction may be absent (Fig. 19) or present to varying degrees (e.g. Fig. 18).

The parameters of the synthesis model represent aspects of bud dormancy release that should be addressed in experimental work separately with each tree species and provenance: 1) Does an absolute chilling requirement of growth competence exist ($CU_{abs} > 0$ CU)? 2) If so, then is the chilling requirement of the rest completion identical to the absolute chilling requirement of the growth competence ($CU_{crit} = CU_{abs}$), or does further chilling after attaining CU_{abs} gradually increase the growth competence of buds ($CU_{crit} > CU_{abs}$)? 3) Does the forcing temperature affect the growth competence of buds ($\Delta C_{max} > 0$, $\Delta CU_{max} > 0$ CU)? 4) If it does, then in what temperature range does the growth competence increase with an increasing forcing temperature (T_3, T_4)? In this way, the synthesis model provides a framework for experimental studies of the temperature regulation of bud dormancy release in trees from cool and temperate regions.

6. General discussion and outlines for further model development

61. Conceptual and methodological remarks

Arbitrary developmental units

In the models considered in the present study, bud dormancy release is simulated by accumulating two kinds of developmental units, i.e. chilling units for rest break and forcing units for ontogenetic development. The developmental units are arbitrary, since it is not practically possible to measure the processes of rest break and ontogenetic development in direct quantitative terms. As an example, the temperature response curve of the potential rate of forcing was partially based on observations of the rate of meiosis in forest trees (Sarvas 1972). The time required to progress from one meiotic phase to the next decreased with increasing temperature, hence yielding the rising curve for the rate of development (Fig. 1c). The resulting curve is necessarily in arbitrary units, since it is not practically possible to express the various developmental states during meiosis in a quantitative way, e.g. to express the amount of development at metaphase I in a microspore mother cell (Sarvas 1972, 1974). Despite the use of arbitrary developmental units, the models of dormancy release can be tested, since they imply predictions that are amenable for testing in terms of time (e.g. Chap. 33).

Levels of biological organization

When the modelling approach to bud dormancy release is applied at the whole-tree level, as in the present study, the exact essence of the phenomena that are described with the accumulation of the chilling and forcing units remains unknown. The models can be tested only in the case of the *outcome* of dormancy release, i.e. bud burst (Fig. 7). The modelling of dormancy release would be facilitated considerably if physiological and morphological observations at lower biological levels, i.e. at the levels of organs, cells, cellular organs and molecules, could be used

(Landsberg 1974, 1977). In this case, the models could be tested for the whole *process* of dormancy release. This approach, however, seems problematic in the case of rest break, because the rest-breaking role of the abundant biochemical changes observed during the rest period remains unknown (Smith and Kefford 1964, Perry 1971, Wareing and Phillips 1978, p. 269—275, Hanover 1980, Dennis 1987, Powell 1987). In the case of ontogenetic development, microscopic observations of buds prior to bud burst would be readily utilized in modelling work as indicators of the state of development (Sarvas 1972, 1974).

Observations at the whole-tree level can be used in planning experiments at lower biological levels. For example, Hänninen and Pelkonen (1989) found that intermittent periods of high temperature at a late phase of a rest-breaking chilling period nullified most of the effects of previous chilling in seedlings of Scots pine and Norway spruce, whereas early intermittent periods had no such effect. Useful cues for clarification of the biochemical regulation of rest break could be attained by repeating the experiment with biochemical observations. The biochemical changes that take place during the late interruptions, but not during the early interruptions, are obviously related to the rest break in some way.

Efficiency of models of annual rhythm

Häkkinen and Hari (1988) introduced the concept of efficiency for analysing the models of the annual rhythm of trees. If a tree functions according to an efficient model, then it maximizes utilization of the growing season, given that no heavy frost damages occur (see Lockhart 1983). Häkkinen and Hari (1988) compared the efficiencies of various models of the timing of bud burst, with the aid of computer simulations using long term climatic data as input. Hänninen et al. (1990) applied a similar approach in examining timing models of growth cessation. This kind of theoretical

approach is useful, since it aids in establishing priorities for the experimental testing of the regulation models: it may be assumed that the probability of any given regulation model to be realized in tree populations increases with the increasing efficiency of the model.

Limitation of the experimental approach

The controlled experimental conditions that were applied in the present study differ drastically from the natural growing environment of the trees. This may have generated artefacts in the experimental results. Thus in the further testing of the models, the present approach has to be accompanied by another approach with observations under natural conditions (Sarvas 1972, 1974). Model predictions are also readily generated for the natural conditions by means of computer simulations (Fig. 5).

62. Study problems

621. Onset of rest period

It was assumed in the simulations of the present study that the rest period has a strict starting point, where the full rest breaking effect of chilling is attained abruptly. Furthermore, the starting point was deliberately set each year at September 1 (Chap. 32). The concept of a strict starting point has also been applied in many previous simulation studies of bud dormancy release. Arbitrary starting points that have been used include the day of the first autumn frost (Landsberg 1974), the day with the greatest negative accumulation of chilling units (Richardson et al. 1974), and November 1 (Cannell and Smith 1983).

A more physiological criteria for the strict starting point of the rest period has been used in two cases. Walser et al. (1981), when simulating the rest break in buds of *Prunus persica* initiated the accumulation of chilling units on the day of one/half defoliation of trees. This method improved the accuracy of the model in predicting the timing of rest completion, as compared with using the day of greatest negative value of accumulated chilling units (Richardson et al. 1974) as the starting point. In the °GS model (Fuchigami

et al. 1982, Kobayashi et al. 1982) the accumulation of chilling units is initiated at a developmental state called "vegetative maturity". Trees have attained vegetative maturity if leaf removal no longer stimulates dormant buds to resume growth. This method facilitated the prediction of the timing of bud burst in *Cornus sericea* L. (Kobayashi and Fuchigami 1983b).

It may be hypothesized that, contrary to the prevailing concept of a strict starting point of the rest period, the rest-breaking effect of chilling is attained gradually. Experimental results where the chilling requirement has varied according to the environmental conditions prevailing before chilling (Nienstaedt 1966, Nelson and Lavender 1979, Lavender and Stafford 1985) support this alternative concept of the gradual start of the rest period. The gradual onset of the rest period could be simulated by calculating the gradually increasing value of a "chilling competence function", according to environmental conditions prevailing during the rest period.

622. Further effects of air temperature

Temperature responses of the rate of development

In the present study, information on Finnish forest tree species was utilized when formulating the temperature responses of the rate of chilling for the rest break and the potential rate of forcing for the ontogenetic development. The original data consisted of the rate of rest break in seedlings and seeds of *Betula pubescens* Ehrh. (Fig. 1a, Sarvas 1974), and of the rate of meiosis and the rate of opening of male catkins in several forest tree species (Fig. 1c, Sarvas 1972).

The temperature response curves for the rate of development vary among different species, and possibly among provenances of a given species. In the case of *Prunus persica*, the maximum rate of rest break has been obtained at +8 °C (Gilreath and Buchanan 1981, Erez and Couvillon 1987), i.e. at a temperature 4.5 °C higher than what was found by Sarvas (1974) for Finnish *Betula pubescens* (Fig. 1a). The results of the present study suggest that 1) the upper limit for the rest-breaking temperature range is for Finnish species near 12 °C rather than near 10 °C,

as suggested by Sarvas (1974) (Fig. 1a); and that this temperature limit is slightly higher for Norway spruce (Fig. 12) than for Scots pine (Fig. 11). Evidently, more information is needed to facilitate modelling even with Finnish species, in the case of possible genetic variation in the temperature response of the rate of the rest break.

In calculations with models of bud dormancy release, the continuous effect of temperature on the rate of development is approximated numerically by using the mean temperature for a given time step as argument in the response functions (Fig. 1). In the present study a time step of one day was used. Using this method erroneous results are obtained, since with non-linear response functions the response obtained using the mean value of temperature is not equal to the response obtained using momentary values of temperature (see Smolander 1984). As an unnatural but striking example, if the hourly mean temperatures during a given day were −5 °C for twelve hours, and +11 °C for the other twelve hours, then no chilling units would be accumulated for that day on an hourly basis. On the basis of the daily mean temperature (+3 °C), however, an almost maximum accumulation of chilling units would take place (Fig. 1a). This error in numerical approximation can be reduced by using temperature records for so short a time step that the variation in temperature during the time step is negligible.

In addition to its importance in generating error in numerical approximation, a fluctuation of air temperature may be important for its effects *per se* on the processes of dormancy release.

Fluctuating temperatures have been found to be more efficient in the rest break than constant temperatures (Erez et al. 1979a, Couvillon and Erez 1985, Erez and Couvillon 1987). Some of the results of the present study supported this concept (Fig. 15a). On the basis of these data it is obvious that several biochemical reactions with different temperature optima are involved in the rest break. In this case, any temperature response curve of the rate of the rest break obtained at constant temperatures (e.g. Fig. 1a) may give erroneous results when applied at fluctuating temperatures. In Fishman et al.'s (1987a) model, the effects of fluctuating temperatures on the rest break are taken into account. Using this model, Fishman et al. (1987b)

were able to simulate complicated patterns of rest break in *Prunus persica* under various regimes of fluctuating temperatures, observed previously by Erez et al. (1979a,b), Couvillon and Erez (1985), and Erez and Couvillon (1987).

Campbell and Sugano (1975) and van den Driessche (1975) found that a greater accumulation of forcing units is required for bud burst in one-year-old seedlings of *Pseudotsuga menziesii* at constant rather than at fluctuating temperatures. Accordingly, it was found in the present study that the accumulation of forcing units required for bud burst in the greenhouse at relative constant temperatures is much higher than the accumulation of forcing units required under natural conditions (Chap. 423). Obviously, the effect of fluctuating temperatures also has to be taken into account in further development of the forcing unit model.

It was assumed in the present study that the temperature responses of the rate of chilling (rest break, Figs. 1a,b) and the potential rate of forcing (ontogenetic development, Fig. 1c) are static, i.e. they remain constant during the development. In the °GS model, the temperature responses of the rate of development are assumed to be dynamic, i.e. they change continuously during development (Fuchigami et al. 1982, Kobayashi et al. 1982, Kobayashi and Fuchigami 1983a,b; see Winter 1973, Pelkonen and Hari 1980, Cannell et al. 1985b, Repo et al. 1990). According to Hänninen and Pelkonen (1988a), the temperature response of the rate of the rest break in Scots pine and Norway spruce seedlings changes at least slightly during the rest period. Further experiments are needed to reveal the extent of these changes.

Cumulative effects of air temperature

It was generally assumed in the present study that the effects of air temperature on the rest break and on ontogenetic development are strictly cumulative. As an exception, a negation of the rest-breaking effect of chilling by high temperatures was assumed in model type I_B (Fig. 1b). However, model type I_B was not tested separately, since its implications for the timing of bud burst under natural conditions did not deviate noticeably from the implications of model type I_A (Fig. 6). This was because daily mean tempera-

tures above 10 °C are quite rare under Central Finnish conditions after the beginning of September.

High temperatures have been shown under experimental conditions to negate the rest-breaking effects of previous chilling in *Prunus persica* (Overcash and Campbell 1955, Erez and Lavee 1971, Erez et al. 1979a,b, Couvillon and Erez 1985). Furthermore, in southern areas with warm winters prolonged dormancy during spring has constituted a serious problem for the cultivation of fruit trees and cultivars with a high chilling requirement (Chandler et al. 1937). This phenomenon has been attributed partly to chilling negation by high temperatures, although another explanation has been a lack of chilling under such conditions (Weinberger 1954). Hänninen and Pelkonen (1989) found a chilling negation effect caused by high temperatures in seedlings of Scots pine and Norway spruce. However, one to three intermittent warm periods of one week with exposure to an unnaturally high temperature of 17 °C were applied in the study in question. Thus, on the basis of the findings of Hänninen and Pelkonen (1989), no conclusions regarding the existence of chilling negation under natural Finnish conditions can be drawn.

In all of the models considered in the present study, forcing units are also accumulated during autumn and winter. Hence, the temperature conditions of a relatively long interval affect the timing of bud burst (Fig. 5). It is, however, possible that the climatological accumulation of forcing units in autumn or winter is not physiologically effective, or is less effective than the accumulation of forcing units later, in the spring. Low wintertime temperatures, for instance, can counteract the effect of previous high temperatures. This would not be the case if all of the developmental events that are simulated by the accumulation of forcing units were irreversible morphological changes. However, presumably reversible biochemical reactions are also involved, hence making the counteractive effect of low temperatures possible. This suggestion finds support in studies where it has been possible to predict the timing of bud burst (Valentine 1983, Häkkinen 1990) or flowering (Boyer 1973) under natural conditions by initiating the accumulation of forcing units on a fixed day during spring, without considering the timing of rest completion.

Effects of chilling on growth vigour

In the present study, relatively low criteria for the occurrence of bud burst were applied (Chap. 414). This was due to the low irradiance levels that were applied in the forcing conditions. In many cases even seedlings chilled for several months in natural conditions grew only a few millimeters in the forcing conditions. However, a chilling treatment that is just effective enough to cause bud burst in the sense of the present study may still be too inefficient to cause vigorous growth (Hoffmann and Lyr 1967, Garber 1983, Boyer and South 1989). Thus, it is important also to examine the effect of chilling on the amount of subsequent growth. For this case, forcing conditions similar to the natural growing conditions of the seedlings should be used in the experiments.

623. Effects of other environmental factors

Night length

Night length is, for most tree species from the cool and temperate regions, a key factor affecting the induction of bud dormancy, the abscission of leaves, and the cessation of cambial activity, i.e. developmental phenomena that are related to completion of the active growth period and the beginning of the dormant period (Wareing 1956, cf. Nitsch 1957, Koski and Selkäinaho 1982, Koski and Sievänen 1985). In dormancy release night length generally appears to play a more minor role. Short nights have been shown, however, to substitute at least partially for a lack of chilling in the rest break in Scots pine (Jensen and Gatherum 1965, Hoffmann and Lyr 1967), in Norway spruce (Nienstaedt 1967, Worrall and Mergen 1967), and in several other tree species (Nienstaedt 1966, Farmer 1968, Hinesley 1982, Garber 1983).

Other effects of night length on the rest break, besides the substitution of a lack of chilling, have been reported in a few cases. Wareing (1953) found that seedlings of *Fagus sylvatica L.* possess an absolute short night requirement for rest break. Campbell and Sugano (1975) found that a decrease in the night length increased the rate of ontogenetic development in the case of one-year-old seedlings of *Pseudotsuga menziesii* also after long periods of chilling. Nizinski and Saugier

(1988) found that the accumulation of forcing units required for bud burst in naturally growing mature *Quercus petraea* (Matt.) Liebl. in France declined with a decrease in night length (see Koski and Selkäinaho 1982, Koski and Sievänen 1985). In this case it is unclear whether the effect of night length was a substitution for insufficient chilling, or whether night length had some other promoting effect on ontogenetic development.

On the basis of the information available it is evident that the effect of night length has to be taken into account in further model development of bud dormancy release in trees.

Soil temperature

The effect of soil temperature on the bud dormancy release of trees has attracted relatively little attention. In field experiments in Central Finnish and Northern Finnish conditions, Huikari and Paarlahti (1967) found no difference in the timing of bud burst in mature Scots pine between sample plots with artificially cooled soil and control plots with warmer soil.

Lavender et al. (1973) and Sorensen and Campbell (1978) found that under experimental conditions with seedlings of *Pseudotsuga menziesii*, the initiation of ontogenetic development towards bud burst was regulated by soil temperature. Despite this, Sorensen and Campbell (1978) concluded that under natural conditions in the north-western United States soil temperature plays a minor role in determining the timing of bud burst, because 1) the rate of ontogenetic development rather than the time of its initiation was revealed to be decisive; and 2) soil temperature had a minor effect on the rate of development. In Emmingham's (1977) study, however, soil temperature was found to affect the timing of bud burst in thirteen-year old saplings of *Pseudotsuga menziesii* in the north-western United States.

Harding et al. (1976) found that to include the soil temperature for March in a multiple regression model improved the accuracy of the model when predicting the timing of flowering of *Malus pumila* Mill. in England. They concluded, however, that the high accuracy obtained did not establish any cause-and-effect relationship. Hammond and Seeley (1978) found that frozen soil causes a delay

in the anthesis of *Malus domestica* Borkh., *Prunus persica*, and *Prunus avium* (L.) L. Otherwise soil temperature did not affect the timing of anthesis.

On the basis of the limited information available, the effect of soil temperature on the bud dormancy release of trees cannot be ruled out in further model development.

624. Differences related to age of tree and position of bud

Models of bud dormancy release in trees were tested in the present study in the case of terminal buds of two-year-old seedlings of Scots pine and Norway spruce. For two reasons the results should be interpreted with care. First, the environmental responses of dormancy release change as trees get older. Ununger et al. (1988), for instance, found that the timing of bud burst in Norway spruce was delayed with the increasing age of the seedlings. Secondly, there exists some variation in the timing of bud burst among different parts of the crown. It has been found, for instance, that lateral buds burst earlier than terminal buds in *Pseudotsuga menziesii* (van den Driessche 1975) and in *Tsuga heterophylla* (Nelson and Lavender 1979). Ideally, models of dormancy release should be tested separately for each part of the crown at different ages of the trees.

625. Application of models of bud dormancy release

Accurate models of bud dormancy release could be applied in many fields of practical forestry and horticulture (Cannell 1985). These fields involve e.g. the planning of provenance transfers (Campbell 1974, Cannell and Smith 1984), and the assessment of effects of predicted climatic warming on the survival and growth of trees (Cannell and Smith 1986, Kellomäki et al. 1988, Murray et al. 1989, Hänninen 1990 b). In applying the models, calculations similar to those in Chap. 32 are carried out. Long-term climatic data representing the growing site are required as input for the model. The model and its parameter values represent the tree genotype. As a result of the simulations, the predicted day of bud burst is obtained for each year. The adaptness of the genotype

to the growing conditions is studied by examining distributions of the annual values of 1) post-dormant minimum temperature (risk of frost damage), and 2) post-dormant accumulation of forcing units (utilization of the growing season) (see Häkkinen and Hari 1988, Hänninen et al. 1990).

When applying models of dormancy release it is implicitly assumed that the trees are frost hardy before bud burst, and susceptible to frost after bud burst. It is, however, well-known that the frost hardiness of trees also varies within the period of dormancy and to a lesser extent within the period of active growth (Cannell and Sheppard 1982, Repo and Pelkonen 1986, Rikala and Repo 1987). Thus, for practical applications it is ultimately important to model the time course of the frost hardiness of trees and not only the bud dormancy release. Nevertheless, the temperature dependence of frost hardiness has been shown to vary according to the phase of the dormancy of the buds (Proebsting 1963, 1970, Mac Irving and Lanphear 1967, Litzow and Pellett 1980, Kobayashi et al. 1983, Valkonen 1988), and at the time of bud burst a large part of the tree's potential to frosthardening is lost (Weiser 1970, Fuchigami et al. 1982). Thus, for the modelling of frost hardiness of trees it is also necessary to have sub-models for bud dormancy release (Winter 1973, Fuchigami et al. 1982, Kobayashi et al. 1982, 1983, Kobayashi and Fuchigami 1983a,b).

63. Concluding remarks

In the present study a modelling approach was applied to the bud dormancy release of trees from the cool and temperate regions. This approach is characterized by 1) emphasis on conceptual work, 2) formal hypotheses, and 3) the alternation of experimental and simulation studies.

Conceptual work is especially required in modelling dormancy release, since models of dormancy release involve several concepts

that are not generally established in the natural sciences. For instance, the concepts of chilling unit, forcing unit, and competence function have to be strictly defined (Chap. 22), and their relationship to experimental studies has to be demonstrated (Chap. 33). Only in this way is the use of these concepts and models warranted.

Formal hypotheses are essential in any effort to obtain a quantitative understanding of bud dormancy release in trees. With the aid of exact mathematical equations it is possible, for instance, to study how the rate of the rest break depends on the prevailing temperature. In this way one can aim at developing accurate models for the prediction of the timing of bud burst. This is not possible if the rest break is approached only with informal conceptual hypotheses.

The alternation of experimental and simulation studies facilitates the research in several ways. Simulations produce model predictions for various experimental designs (Chap. 33). The models are developed further by comparing the predictions of the models with experimental results (Chaps. 4—6). Simulations also facilitate experimental work by revealing the priorities for testing any alternative hypotheses. In the present study priorities for testing the models of bud dormancy release were elucidated with the aid of simulations (Chap. 32). In conclusion, simulations facilitate the planning of informative experiments.

Research into bud dormancy in trees is currently challenged by several problems in practical forestry and horticulture. Among these challenges, the effects of the predicted climatic warming on the survival and growth of trees now appears the most important. At present few strict answers can be given to the practical problems, since much research on the environmental and genetic regulation of the bud dormancy release of trees remains to be done. Nevertheless, the quantitative modelling approach to bud dormancy release provides a promising tool for answering the challenges of the future.

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