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A Framework for Modelling the Annual Cycle of Trees in Boreal and Temperate Regions

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Models of the annual development cycle of trees in boreal and temperate regions were reviewed and classified on the basis of their ecophysiological assumptions. In our classification we discern two main categories of tree development: 1) fixed sequence development, which refers to irreversible ontogenetic development leading to visible phenological events such as bud burst or flowering, and 2) fluctuating development, which refers to reversible physiological phenomena such as the dynamics of frost hardiness during winter. As many of the physiological phenomena are partially reversible, we also describe integrated models, which include aspects of both fixed-sequence and fluctuating development. In our classification we further discern simple E-models, where the environmental response stays constant, and more comprehensive ES-models, where the environmental response changes according to the state of development. On the basis of this model classification, we have developed an operational modelling framework, in which we define an explicit state variable and a corresponding rate variable for each attribute of the annual cycle considered. We introduce a unifying notation, which we also use when presenting a selection of previously published models. To illustrate the various developmental phenomena and their modelling, we have carried out model simulations. Finally, we discuss the ecophysiological interpretation of the model variables, methodological aspects of the empirical development and testing of the models, the introduction of new aspects to the modelling, other closely related models, and applications of the models.

Keywords bud burst, climatic adaptation, climatic change, dormancy, frost hardiness, phenology, photosynthetic capacity
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1 Introduction

The climate of boreal and temperate regions is characterised by large seasonal changes in air temperature. In order to adapt to these conditions, trees must both survive during the cold season (survival adaptation) and use the growth resources of the site during the warm season (capacity adaptation) (Levitt 1969, Heide 1985, Leinonen and Hänninen 2002). The survival and capacity adaptation of trees in boreal and temperate regions is manifested in their annual cycle of development (Weiser 1970, Perry 1971, Sarvas 1972,1974, Fuchigami et al. 1982). The cyclic alternation between the frost-tolerant dormant phase and the susceptible active growth phase of trees is synchronised with the annual course of air temperature at their natural growing sites. It is a prerequisite for the survival and growth of the trees that this synchronisation is realised each year, including the years with the most exceptional temperature conditions (Koski and Sievänen 1985).

The annual cycle of trees is of crucial importance in practical forestry and horticulture, where man controls both the genetic properties of trees (breeding and use of exotic species and provenances; Campbell 1974, Cannel et al. 1985, Koski and Sievänen 1985) and the environmental conditions (nursery and greenhouse practices; Grossnickle et al. 1991, Luoranen 2000). The practical importance of the annual cycle is being further emphasised by the predicted climate change, as climatic changes may have important implications to both the survival and the capacity adaptation of trees (Cannell 1985, Kramer 1995a,b, Kramer et al. 1996, Hänninen et al. 2001, Saxe et al. 2001, Hänninen 2006).

The genetic and environmental regulation of the annual development of trees is still only partially understood. The annual cycle has been approached with different methods, and various theories describing tree development have been formulated. The theories have also given rise to various mathematical models of the annual cycle (for reviews, see Cannell 1989,1990, Hänninen 1990a, Hunter and Lechowicz 1992, Repo 1993, Kramer 1996, Leinonen 1997, Häkkinen 1999a, Chuine 2000, Linkosalo 2000a). Although the modelling approach dates back to the early work of Réaumur (1735), the models were not widely used until computers became available. During the last two decades, the models have been used increasingly for assessing the ecological implications of the climate change (see Hänninen et al. 2001 and Saxe et al. 2001 for reviews). Recently, the modelling approach has also been applied to dwarf shrubs in the arctic tundra (Pop et al. 2000, Van Wijk et al. 2003).

In this study, the models for the annual cycle of trees in boreal and temperate regions are classified according to their ecophysiological assumptions, i.e. models addressing similar type of phenomena in the annual cycle are assigned to the same class. The classification is based on a literature review, but no attempt will be made to provide a complete reference list of all published models. On the basis of the classification, an operational framework for the modelling studies is developed and put to use in a presentation of a selection of previously published models. The various developmental phenomena and their modelling are illustrated by model simulations. We approach the annual cycle at the whole-tree level, but the introduction of more mechanistic aspects into the models will also be discussed. Due to the large number of species and phenomena addressed, we do not aim at an extensive testing of the models presented. Thus, rather than providing a selection of validated models to be used in studies addressing the effects of climatic change, for instance, our ultimate goal is to facilitate the development of such models for any tree species growing in the boreal and temperate zones.

2 Conceptual Classification of the Models of the Annual Cycle

2.1 Basic Concepts

In the present study, the concept of the annual cycle of trees is defined as all those developmental events normally recurring in trees once a year. The concept ‘developmental’ is used in a broad sense here, i.e. in addition to the ontogenesis addressed in the classical definition of plant developmental biology (Taiz and Zeiger 1998), seasonal physiological changes are also included. Thus the annual cycle involves not only the occurrence of the distinct morphological events of the annual ontogenesis such as bud burst (Cannell and Smith 1983), flowering (Sarvas 1972,1974, Luomajoki 1986), height growth cessation and bud set (Koski and Sievänen 1985), but also the annual courses of physiological characteristics such as the photosynthetic capacity of the needles of conifers (Pisek and Winkler 1958, Pelkonen 1980, 1981a,b, Linder and Lohammar 1981, Korpilahti 1988, Mäkelä et al. 2004) and the frost hardiness of various tree tissues (Repo 1992, Leinonen 1996a, Greer et al. 2001).

In the modelling approach, the momentary value of the variable state of development, $S(t)$, quantitatively represents a specified attribute of the annual cycle, e.g. the phase of dormancy or the level of frost hardiness, prevailing at instant t. The corresponding variable rate of development, $R(t)$, is the first time derivative of the state of development, describing the rate of change in the state of development (Hari et al. 1970, Hari 1972). By definition, the state of development is obtained by integrating the rate of development over time, starting from a specified zero point (Sarvas 1972, Luomajoki 1993), i.e. from instant t_0, where the state of development is defined as equal to zero ($S(t_0)=0$):

$$S(t)=\int_{t_0}^{t} R(t)dt \tag{1}$$

In many models, the environmental response of the rate of development is assumed to stay constant over time. These models can generally be formulated as

$$R(t)=f(E(t)) \tag{2}$$

where f denotes a function describing the dependence of the rate of development on one or more environmental factors, $E(t)$. These models will be referred to as E-models. The well-known temperature sum (day degree) model (Arnold 1959, Wang 1960) belongs to this category. In this case, the time series of environmental factors, $E(t)$, is represented by the time series of air temperature, $T(t)$, and the rate of development at instant t, $R(t)$, is zero at temperatures below the given threshold temperature and increases linearly with temperatures above the threshold.

In more comprehensive models the change in the environmental response of the rate of development is addressed, i.e. the rate of development depends on both environmental factors and the prevailing state of development. Such models will be referred to as ES-models in the following. The variable state of development, $S(t)$, may itself involve several attributes and can be described thus:

$$S(t)=S_i(t), i=1,2,3... \tag{3}$$

In the simplest of the ES-models, attribute i of the state of development affects its own rate of development (feedback):

$$R_i(t)=f_i(E(t),S_i(t)) \tag{4}$$

It is also possible, however, that the rate of development of the given attribute i of the annual cycle is affected by another attribute j:

$$R_i(t)=f_i(E(t),S_j(t)) \tag{5}$$

The response function f (Eqs. 2, 4, and 5) and the values of the model parameters involved in it represent the genetic features of the tree. The prevailing climatic conditions at the growing site are represented by the time-series of the environmental factor(s), $E(t)$. Consequently, f and $E(t)$ together determine the rate of development at all instants t (i.e. the time course of $R_i(t)$) and thereby, as a mathematical necessity (Eq. 1), also the time course of the state of development, $S_i(t)$.

According to the approach outlined in Eqs. 4 and 5, the environmental regulation of tree development can be divided into 1) direct short-term regulation by prevailing environmental conditions, and 2) indirect long-term regulation by previous environmental conditions, taking place via the regulation of the prevailing state of development (Hari et al. 1970, Hari 1972). The concept of potential rate of development (Hänninen 1990a, 1995) is introduced to describe the direct short-term regulation and the concept of response competence to describe the indirect long-term regulation (Landsberg 1977, Hänninen 1990a). Using these concepts, a multiplicative model can be presented for the rate of development (Hari et al. 1970, Hari 1972, Hänninen 1990a):

$$R_i(t) = C_i(t) \cdot R_{i,\text{pot}}(t) \tag{6}$$

where $R_i(t)$ is the momentary rate of development of aspect i of the annual cycle, $R_{i,\text{pot}}(t)$ is the corresponding potential rate, and $C_i(t)$ is the response competence of attribute i. The value of $C_i(t)$ ranges from zero (no response competence, with the rate of development at zero in any environmental conditions) to unity (maximum response competence, with the rate of development equal to the potential rate). Considering that the potential rate is determined by the prevailing environmental conditions, $E(t)$, and the response competence by the prevailing state of development of aspect j of the annual cycle, $S_j(t)$, Eq. 6 is transformed into

$$R_i(t) = C_i(S_j(t)) \cdot R_{i,\text{pot}}(E(t)) \tag{7}$$

Attribute i of the annual cycle can be identical to attribute j, i.e. $i=j$ as in Eq. 4. In that case, the attribute is assumed to affect its own rate of development (feedback). In other cases, however, it is assumed that the rate of development of one attribute is regulated by the state of development of some other attribute, i.e. $i \neq j$ as in Eq. 5.

The essential aims in studies of the annual cycle of trees are 1) to define the physiological and morphological attributes $i = 1, 2, 3\ldots$ whose annual courses are described by the variable state of development, $S_i(t)$, and 2) to determine, for each attribute i of the genotype under consideration, the corresponding functions f_i (Eqs. 4 and 5) describing the environmental response of the rate of development of each attribute.

2.2 Fixed-Sequence Development

The developmental phenomena belonging to the annual ontogenesis follow a pattern of a genetically fixed sequence of developmental events. For instance, the annual cycle of the flower buds of trees is marked by a sequence of meiotic phases leading to flowering (Sarvas 1972,1974, Luomajoki 1986). In such cases, the following aspects of the developmental phenomena are essential for modelling the development (see also the contrasting case of fluctuating development below):

(i) The driving force of development is environmental conditions per se, not their fluctuations. Thus, even though fluctuations in environmental factors cause variation in the rate of development, no environmental fluctuation is required for the tree to proceed from one developmental event to the next. A sufficient condition for reaching the next developmental event is simply that the environmental factors remain at their development-facilitating range. In the case of bud burst, for instance, the air temperature is required to be high enough, but no fluctuation in it is required.

(ii) The essential role of genetic factors in determining the developmental pattern leaves environmental factors only the relatively limited role of determining the rate at which the tree proceeds from one developmental event to the next.

(iii) The development is irreversible, and a given state of development can occur only once during the annual cycle. This implies that the state of development $S_i(t)$ can only remain constant or increase but not decrease, so that the rate of development $R_i(t)$ must always be zero or positive.

Aspects (i)–(iii) imply that the seasonality of tree development does not necessarily require seasonality in the environmental factors. The tree will pass through the whole annual cycle even in constant environmental conditions as long as the rate of development stays above zero (Sarvas 1972, 1974).

In most cases of fixed-sequence development, no specific short-term environmental signals are required. Thus the rate of development changes continuously according to the changing environmental factors (Eqs. 2, 4, and 5), and the state of development prevailing at any given moment is determined by those previous environmental factors which have prevailed a relatively long time (Eq. 1). In some cases, however, a short-term environmental trigger is required for the development to proceed to the next event (triggered development; see Koski and Selkäinaho 1982). The effect of night length on the cessation of tree growth is a well-known example of such signal regulation: the attainment of a genotype-specific critical night length is the signal that triggers the tree's development towards growth cessation (Wareing 1956, Vaartaja 1959, Ekberg et al.

1979). Triggered phenomena can be described in models of fixed-sequence development by assuming a rate of development equal to zero, irrespective of the prevailing environmental factors, until the triggering signal occurs. After the occurrence of the signal, the environmental factors regulate the rate of development as a continuous process again (Eqs. 4 and 5; see Fuchigami et al. 1982).

2.3 Fluctuating Development

Contrary to the developmental phenomena belonging to the annual ontogenesis, the annual course of many physiological characteristics involves fluctuation in the state of development according to the fluctuations of environmental factors. To some extent, this is the case with the annual course of photosynthetic capacity (Pelkonen 1980, Pelkonen and Hari 1980, Korpilahti 1988, Suni et al. 2003, Hari and Mäkelä 2003) and the frost hardiness of various tree tissues (Repo and Pelkonen 1986, Repo et al. 1990, Repo 1992, Leinonen 1996a, Beuker et al. 1998). In such cases, the following aspects of the developmental phenomena are essential for modelling the development (see also the contrasting case of fixed-sequence development above):

(i) The driving force of development is change in the environmental conditions, not the environmental conditions per se. Thus, in any constant environmental conditions the development of the tree will stop sooner or later, i.e. its state of development will become constant.

(ii) For this reason, the role of environmental factors is relatively more pronounced than in the case of fixed-sequence development. A specific condition of the environment is matched by a specific target state of development, i.e. the stationary state of development (Repo et al. 1990, Repo 1993, Leinonen et al. 1995, Leinonen 1996a). The state of development changes continuously towards the stationary state determined by the prevailing environmental conditions. If the environmental conditions remain constant for a sufficiently long period, then the tree will attain the stationary state and will remain at this state as long as the environment stays constant. However, due to the comparatively slow rates of physiological reactions, changes in the state of development are usually slower than changes in the environmental factors whose fluctuations drive the development. Consequently, the models of fluctuating development involve one or more time constants, which determine the inertia of the response of the state of development to the changes in the environmental conditions.

(iii) The development is reversible because the state of development fluctuates according to fluctuations in the environmental factors instead of following a genetically fixed pattern. This implies that the state of development, $S_i(t)$, can also decrease, so that the rate of development, $R_i(t)$, can also be negative. For instance, a tree that has already dehardened due to a rise in air temperature may reharden when the air temperature drops again (Repo 1991, Leinonen et al. 1997).

Aspects (i)–(iii) imply that the seasonality of tree development requires seasonality in the environmental factors. This means, for instance, that if a tree is kept in a greenhouse under environmental conditions similar to the warm season, then according to the prediction of a fluctuating-development model it will stay in the active growth state as long as the environmental conditions of the warm season prevail.

3 An Operational Modelling Framework

3.1 Models of Fixed-Sequence Development

3.1.1 A Conceptual Model of Bud Burst

Modelling the timing of the vegetative bud burst (or the flowering of generative buds) is a typical case of modelling fixed-sequence development. In the present study, a generalized conceptual model for the timing of bud burst was developed (Fig. 1a) on the basis of models by Sarvas (1972,1974), Richardson et al. (1974), Landsberg (1974), Fuchigami et al. (1982), Cannell and Smith (1983), Hänninen (1987,1990a,1995), and Kramer (1994a,b). The annual ontogenetic cycle is divided into two phases, i.e. active growth and dormancy, on the basis of whether there is visible growth of the apical meristem taking place or not

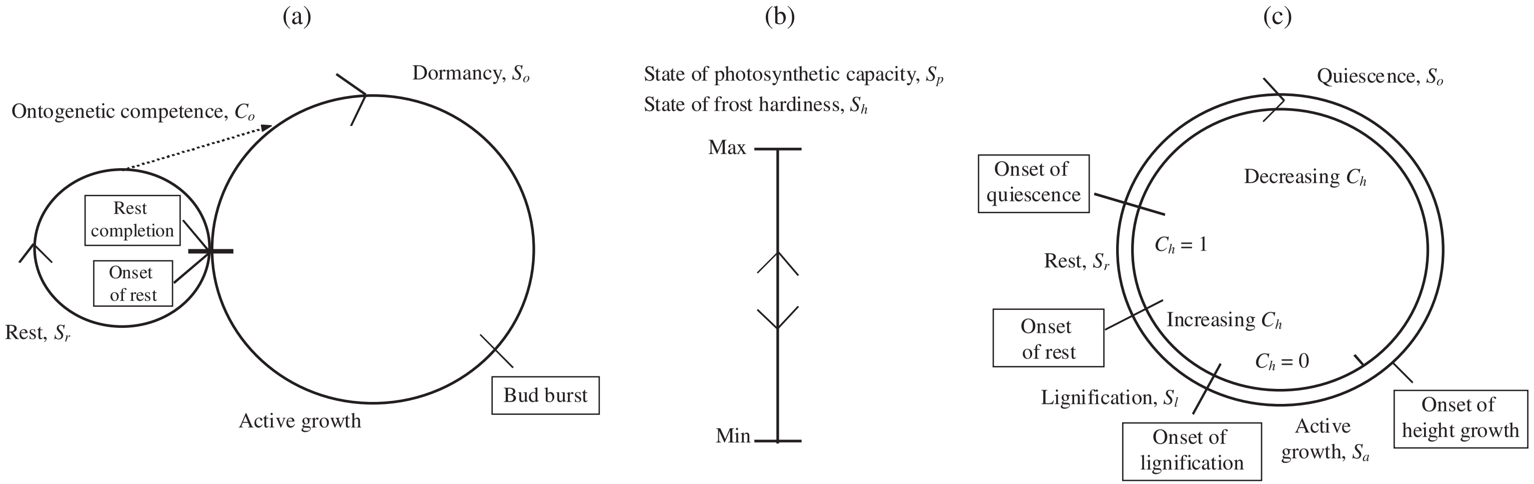

Fig. 1. Conceptual models for the annual cycle of development of trees in boreal and temperate regions. (a) A generalised model of bud burst (fixed-sequence development). The momentary developmental status of the tree is described simultaneously with two state variables: the state of ontogenetic development (S_o, larger circle), and the state of rest (S_r, smaller circle). The effect of rest on the ontogenetic cycle is mediated by ontogenetic competence, C_o. In both cases, the development is irreversible; hence the cyclic diagrams. (b) A generalised model of reversible physiological phenomena (fluctuating development). The momentary developmental status of the tree is expressed with one state variable, i.e. the state of photosynthetic capacity, S_p, or the state of frost hardiness, S_h. The development is completely reversible, i.e. the state variable in question fluctuates between its minimum and maximum values according to environmental factors; hence the linear non-cyclic diagram. For natural conditions, however, a cyclic development is predicted (see Fig. 3c). (c) A model of frost hardiness addressing aspects of both fixed-sequence and fluctuating development (integrated model; Kellomäki et al., 1992, 1995, Leinonen 1996a). The outer circle describes the annual ontogenetic cycle and the inner circle the annual cycle of hardening competence, C_h (S_a= state of active growth, S_l = state of lignification, the other symbols as in (a)). For references and further explanations, see text.

(Romberger 1963, Hänninen 1990a). (Thus, the concept of "dormancy" is used in a general sense here; for the more specific concepts "rest" and "quiescence", see below). When only the timing of bud burst is modelled, only the dormancy phase is considered, i.e. the modelling stops where bud burst (i.e. the onset of the active growth period) is predicted to occur. The conceptual model of bud burst addresses two developmental processes which take place during the dormancy phase.

The first process to be addressed is the progress of ontogenetic development during dormancy, i.e. the sequence of microscopic structural changes (cell division and growth in vegetative buds, meiotic phases in generative buds) taking place in the bud and leading to visible bud burst (or flowering); this process is portrayed by the larger circle in Fig. 1a. The process is described in terms of the variable state of ontogenetic development, S_o, whose value increases from zero at the beginning of dormancy to a critical value at bud burst. Ontogenetic development is promoted by high air temperatures, so that in practice the value of S_o is calculated by means of a temperature sum of some kind.

The second process to be addressed is the physiological process of rest break. It has been known for a long time that after the cessation of growth in the autumn, ontogenetic development is arrested due to physiological factors inside the bud (Coville 1920, Perry and Wang 1960, Perry 1971, Myking and Heide 1995). This physiological condition is referred to by the concept of rest, and the physiological process whereby the growth-arresting conditions are removed is referred to by the concept of rest break (Romberger 1963, Weiser 1970, Hänninen 1990a, 1995, Kramer 1994a,b). The exact physiological mechanism of rest break is not known, but from regrowth tests it appears to be a cumulative process, thus resembling the process of ontogenetic development (Sarvas 1974). At the time of rest completion, the growth-arresting conditions are fully removed, i.e. the bud attains the phase of quiescence (Fuchigami et al. 1982; this phase is not explicitly portrayed in Fig. 1a).

The progress of rest break is portrayed by the smaller circle in Fig. 1a. This process is described in terms of the model variable state of rest, S_r, whose value increases from zero at the onset of rest to a critical value at rest completion. Rest break is promoted by chilling temperatures, so that in practice the value of S_r is calculated by means of a chilling-unit sum of some kind (Sarvas 1974, Richardson et al. 1974, Landsberg 1974). The state of rest, S_r, affects the rate of ontogenetic development, R_o (i.e. the rate of change of the state of ontogenetic development, S_o), via ontogenetic competence, C_o (Fig. 1a). In this way, the conceptual model presented in Fig. 1a is an example of the approach outlined in Eq. 7: aspect i = ontogenetic development, and aspect j = rest break. Hence, the developmental status of the bud is described by a two-valued variable, i.e. the state of rest, S_r, and the state of ontogenetic development, S_o.

There is experimental evidence for the notion that in some cases high air temperatures may negate the effects of previous chilling (Erez and Lavee 1971, Erez et al. 1979a,b, Hänninen and Pelkonen 1989). To account for this, rest break can be modelled as a reversible process, i.e. the rate of rest break, $R_r(t)$, may attain negative values (Richardson et al. 1974; Appendix, Eq. B1c). In this case, only ontogenetic development is modelled as fixed-sequence development.

3.1.2 E-Models of Bud Burst

Modelling the timing of various developmental events, including bud burst, in terms of simple E-models has a long history, dating back to the eighteenth century (Réaumur 1735). In E-models, several types of temperature responses for the rate of ontogenetic development, R_o, (function f in Eq. 2) can be used. The response can be either linear with a threshold (Arnold 1959), exponential (Hari et al. 1970), or sigmoidal (Sarvas 1972) (Appendix, Eqs. A1a–A1c). The state of ontogenetic development, S_o, is obtained by integrating the rate of ontogenetic development, R_o, from a fixed calendar day, t_0, in winter or early spring (zero point; Sarvas 1972, Luomajoki 1993) until the moment under consideration (see also Eq. 1):

$$S_o(t) = \int_{t_0}^{t} R_o(t)\,dt \qquad (8)$$

The integral of the original equations for $R_o(t)$ is alternatively referred to as day degree sum (Bergh et al. 1998), temperature sum (Sarvas 1967), heat sum (Koski and Sievänen 1985), thermal time (Cannell and Smith 1983), state of forcing (Hänninen 1990a, Kramer 1994a,b, Chuine 2000), or forcing unit sum (Hänninen 1990b), i.e. it indicates in all cases the accumulated sum of the meteorological developmental units. Bud burst is predicted to occur when the accumulated sum of the units attains a genotype-specific critical value, H_{crit}, (high-temperature requirement of bud burst, Hänninen 1995). In this case, each genotype has its own scale for the development. In order to facilitate the comparison of different genotypes and to emphasise the ecophysiological interpretation of the meteorological units, a relative approach is applied in the present study, i.e. the original accumulation rate of the meteorological units is multiplied by $100/H_{\mathrm{crit}}$ (Hänninen 1995, Hänninen and Hari 1996) (Appendix, Eqs. A1a–A1c). In this way the genetic differences in the rate of development are explicitly addressed in the calculation of the rate of ontogenetic development, and with all genotypes bud burst is predicted to occur when the state of ontogenetic development, $S_o(t)$, attains the critical value of 100. $S_o(t)$ values < 100 indicate the percentage of cumulative ontogenetic development towards bud burst that has taken place up to time instant t.

In simplified E-models, the phenomenon of rest is not explicitly addressed, i.e. the model variable state of rest, S_r, (Fig. 1a) is not used. Instead, it is assumed that the buds have no ontogenetic competence before the zero point, t_0, and have full ontogenetic competence after that.

3.1.3 ES-Models of Bud Burst

From the 1970s on, a variety of ES-models explicitly addressing the rest phenomenon have been presented for fruit and forest trees (for reviews see Cannell 1989,1990, Hänninen 1990a, Kramer 1996, Chuine 2000, Chuine et al. 2003, Häkkinen 1999a). These models contain varying assumptions of 1) the effect of chilling on the rate of rest break, 2) the effect of temperature on the potential rate of ontogenetic development, i.e. on the assumed rate with no limitations caused by rest ($R_{i,\mathrm{pot}}(t)$ in Eqs. 6 and 7), and 3) the effect of rest on ontogenetic competence, C_o, and hence on the rate of ontogenetic development (Fig. 1a). Hänninen (1990a, 1995) and Kramer (1994a,b) presented the following framework, where different models of the phenology of bud burst or flowering can be presented as a synthesis of three sub-models, each addressing the corresponding ecophysiological phenomenon.

The effect of chilling on the rate of rest break. It has been found in indirect regrowth tests that the rate of rest break is at its highest in temperatures near +5 °C, as demonstrated for *Betula pubescens* Ehrhart by Sarvas (1974) and for *Prunus persica* (L.) Batch by Erez and Couvillon (1987). Thus, several dome-shaped temperature responses for the rate of rest break, $R_r(t)$, have been presented (Appendix, Eqs. B1a–B1c). The state of rest break at a given moment, $S_r(t)$, is obtained by integrating the rate of rest break, $R_r(t)$, from the time of the onset of rest, t_{rest}, up to moment t (see also Eq. 1):

$$S_r(t) = \int_{t_{\mathrm{rest}}}^{t} R_r(t)\,dt \tag{9}$$

By definition, the state of rest break equals zero at the moment of the onset of rest ($S_r(t_{\mathrm{rest}}) = 0$). The integral of the original equations for $R_r(t)$ has been referred to as accumulation of chill units (Richardson et al. 1974), chill days (Cannell and Smith 1983), the state of chilling (Hänninen 1990a, Kramer 1994a,b, Chuine 2000), or chilling unit sum (Hänninen 1990b), i.e. it indicates in all cases the accumulated sum of the meteorological developmental units. Rest completion is predicted to occur when the accumulated sum of the units attains a genotype-specific critical value, C_{crit} (chilling requirement of rest completion; Hänninen 1995). However, as in the case of ontogenetic development above, a relative approach is applied in the present study, i.e. the original accumulation rate of the meteorological units is multiplied by $100/C_{\mathrm{crit}}$ (Hänninen and Hari 1996) (Appendix, Eqs. B1a–B1c). In this way the genetic differences in the rate of development are explicitly addressed in the calculation of the rate of rest break, too, and with all genotypes, rest completion is predicted to occur when the state of rest break, $S_r(t)$, attains the critical value of 100. Values of $S_r(t) < 100$ indicate the percentage of cumulative development of rest break that has taken place up to time instant *t*.

The effect of temperature on the potential rate of ontogenetic development. The temperature responses of the potential rate of ontogenetic development, $R_{o,\mathrm{pot}}(t)$, are identical to the temperature responses used in the E-models, i.e. either linear with a threshold (Arnold 1959), exponential (Hari et al. 1970), or sigmoidal (Sarvas 1972) (Appendix, Eqs. A1a–A1c). Similarly to the E-models, a relative [0,100] scale is used for the state of ontogenetic development for all genotypes with different values of the high-temperature requirement of bud burst, H_{crit}.

The effect of rest on ontogenetic competence. The variable ontogenetic competence, $C_o(t)$, is introduced to mediate the effects of rest on the rate of ontogenetic development (Figs. 1a, 2; Hänninen 1990a, 1995, Kramer 1994a,b). Variable $C_o(t)$ is dimensionless, ranging from 0 (no ontogenetic competence, therefore no ontogenetic development towards bud burst in any prevailing temperature) to 1 (full ontogenetic competence, with ontogenetic development towards bud burst at the rate determined by the prevailing temperature). With the values $0 < C_o(t) < 1$ the bud has reduced ontogenetic competence, and thus it develops towards bud burst at a lower rate than would be expected on the basis of the prevailing temperature alone.

Sarvas (1972, 1974) and Richardson et al. (1974) assumed that the bud has no ontogenetic competence during rest and that full ontogenetic competence is attained abruptly at the time of rest completion (Fig. 2) (Appendix, Eq. B4a). Thus ontogenetic development towards bud burst takes place only after the tree has completed its rest phase. This model has therefore been referred to as the sequential model (Hänninen 1987, Kramer 1994a,b, Chuine et al. 1998,1989). In the sequential model, the rest phase can be described as a part of the major ontogenetic cycle, i.e. the period of dormancy is subdivided into sequential periods of rest and quiescence (Fig. 1c), which makes it a special case of the more general model developed in the present study (Fig. 1a).

Landsberg (1974) and Campbell (1978) made the contrary assumption that ontogenetic competence increases gradually as the process of rest break progresses (Fig. 2) (Appendix, Eq. B4b). In this case, ontogenetic development during dormancy is possible without rest completion. The tree passes through both cycles in a parallel manner, and the corresponding model has therefore been referred to as the parallel model (Hänninen 1987, Kramer 1994a,b, Chuine et al. 1998, 1999). Thus, the period of dormancy cannot be subdivided into periods of rest and quiescence, as was the case in the sequential model. Rather, a minor cycle of rest is attached to the major cycle, and the state of rest affects the rate of ontogenetic development on a quantitative basis (Fig. 1a).

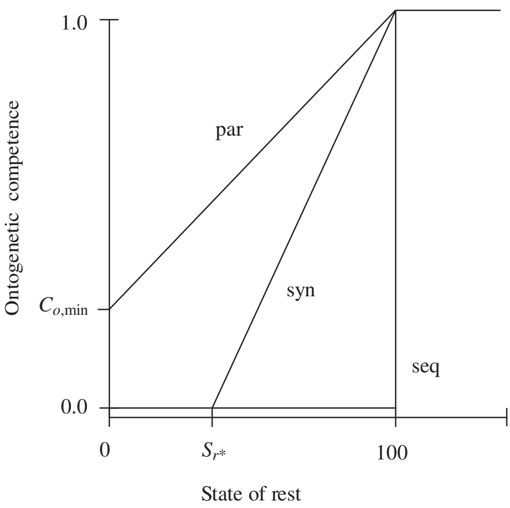

Fig. 2. Dependence of ontogenetic competence, C_o, on the state of rest, S_r, in the sequential (seq), the parallel (par), and the synthesis (syn) models of bud burst (Appendix, Eqs. B4a, B4b, B4c). $C_{o,\min}$ = minimum ontogenetic competence, prevailing at the onset of rest according to the parallel model, S_{r^*} = the state of rest required for an increase of C_o from zero according to the synthesis model (Hänninen, 1990a, 1995, Kramer 1994a,b).

Hänninen (1990a) concluded that most data from chilling experiments support an intermediate model between the two extremes; so he developed a synthesis model involving two chilling requirements (Fig. 2) (Appendix, Eq. B4c). The bud has no ontogenetic competence until the attainment of the smaller chilling requirement corresponding to the state of rest $S_r(t) = S_r^*$ (Fig. 2). From then onwards, ontogenetic competence increases with increasing state of rest until the attainment of the greater chilling requirement, C_{crit}, when $S_r = 100$ and full ontogenetic competence is attained (Fig. 2).

An overall model. Once each of the three submodels has been formulated, then the rate of ontogenetic development towards bud burst can be calculated as follows (see also Eq. 6):

$$R_o(t) = C_o(t) \cdot R_{o,\mathrm{pot}}(t) \tag{10}$$

Taking into account the notion that ontogenetic competence, $C_o(t)$, is determined by the state of rest break, $S_r(t)$, and that the potential rate, $R_{o,\mathrm{pot}}(t)$, is determined by air temperature, $T(t)$, Eq. 10 can be transformed into (see also Eq. 7):

$$R_o(t) = C_o(S_r(t)) \cdot R_{o,\mathrm{pot}}(T(t)) \tag{11}$$

Air temperature thus affects the rate of ontogenetic development towards bud burst in two ways: directly via the potential rate and indirectly via the state of rest and ontogenetic competence. In this case, then, the rate of development of one aspect of the annual cycle is affected by the state of another aspect, i.e. $i \neq j$ as in Eq. 7.

The state of ontogenetic development, $S_o(t)$, is obtained by integrating the rate of ontogenetic development, $R_o(t)$, from the time of the onset of rest, t_{rest}, up to moment t (see also Eq. 1):

$$S_o(t) = \int_{t_{\mathrm{rest}}}^{t} R_o(t)dt \tag{12}$$

As in the case of the E-models, bud burst is predicted to occur when the state of ontogenetic development, $S_o(t)$, attains the value of 100.

3.1.4 *Predictions of the Models of Bud Burst*

The predictions of the E-model, the sequential ES-model, and the parallel ES-model were examined in simulations of the timing of bud burst in the conditions of central Finland. For the temperature responses of the potential rate of ontogenetic development (i.e. the rate of ontogenetic development in the E-model) and the rate of rest break, sigmoidal and triangular curves, respectively, were used with the parameter values suggested by Leinonen (1996a) for Scots pine (*Pinus sylvestris* L.) in central Finland (Appendix, Eqs. E10, E7). With the parallel ES-model, the value of $C_{o,\mathrm{min}} = 0.1$ was used (Fig. 2). The simulations were initiated on 1 September 1971 (t_{rest} in Eqs. 9 and 12) for the two ES-models and on 1 January 1972 (t_0 in Eq. 8) for the E-model.

According to the simple E-model, the state of ontogenetic development, S_o, starts to increase after the fixed zero point $t_0 = 1$ January (Figs. 3a & b), when air temperature begins to rise. According to this model, only the temperature conditions of late winter and early spring affect the predicted timing of bud burst. In contrast, according to the more complicated ES-models, S_o can start increasing in autumn and early winter already, so that the timing of bud burst is affected by temperature conditions over a longer period (Figs. 3a, b). This is the case especially with the parallel model, which does not assume a full arresting of ontogenetic development during rest (Fig. 2). According to the sequential model, no ontogenetic development is possible before the chilling requirement for rest completion has been met (Fig. 2), so that the prediction of this type of ES-model is intermediate between the other two models (Fig. 3b; Häkkinen et al. 1998). The irreversibility of fixed-sequence development was demonstrated in all the simulation results, i.e. the values of the state variables did not decrease in any case (Fig. 3b).

The difference between the sequential and the parallel model facilitate their testing with chilling experiments (Hänninen, 1987, 1990a). According to the sequential model, no ontogenetic development takes place and no bud burst is observed if a seedling is experimentally transferred from chilling conditions to high temperature conditions before rest completion (partially chilled seedling). According to the parallel model, in contrast, bud burst will take place in partially chilled seedlings, too, but it takes longer than in fully chilled seedlings.

3.1.5 *Models of Growth Cessation*

In trees with a predetermined growth habit, the cessation of height growth follows the fixed-sequence principle. Thus, the timing of their height growth cessation can be predicted by

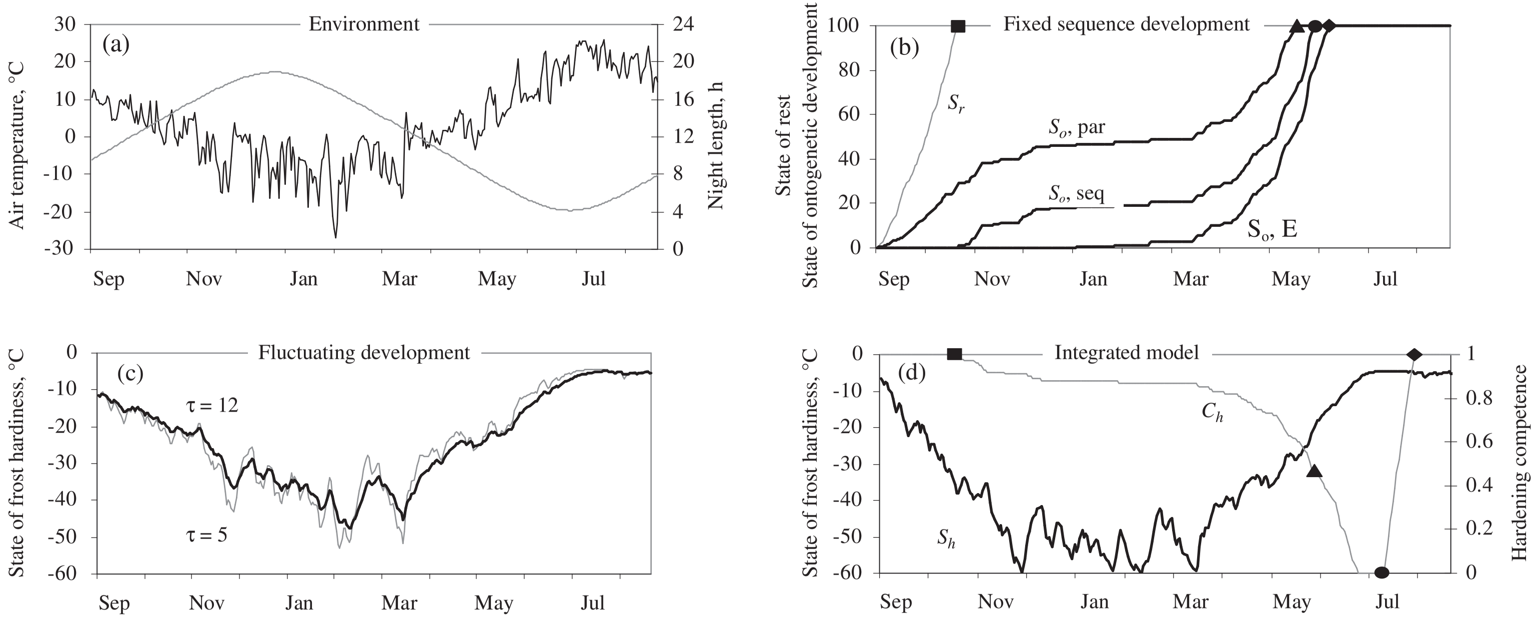

Fig. 3. Predictions of the models of the annual cycle of trees for Jyväskylä (62°14´N, 25°44´E, 86 m asl), Central Finland, for the period of September 1, 1971, to August 15, 1972. (a) Environmental driving variables: daily mean temperature (black line) and night length (grey line, used only in simulations with the integrated model). The daily minimum temperature was also used as a driving variable in the simulations of fluctuating development and partially also with the integrated model, but for clarity's sake it is not presented here. (b) Predictions of three models of bud burst (fixed-sequence development). S_r = the state of rest (grey line; ■ = rest completion on October 21, 1971). S_o = the state of ontogenetic development (black lines) for a parallel ES-model ('par'; ▲= bud burst on May 14, 1972), for a sequential ES-model ('seq'; ● = bud burst on May 25, 1972), and for an E-model ('E'; ◆ = bud burst on June 2, 1972). The state of rest, S_r, is part of the two ES-models. (c) Predictions of the first-order model of frost hardiness (fluctuating development). The state of frost hardiness, S_h, with time constant τ = 5 days (grey line) and τ = 12 days (black line). (d) Predictions of the integrated model of frost hardiness. Hardening competence, C_h, (grey line) and the state of frost hardiness, S_h, (black line, describing, in this case, the frost hardiness of previous year's needles). Hardening competence is determined by the annual ontogenetic cycle, which contains four distinct developmental events (Fig. 1c). The timing of the developmental events is as follows: ■ = rest completion (onset of quiescence) on October 16, 1971; ▲ = onset of height growth on May 23, 1972; ● = height growth cessation (onset of lignification) on July 4, 1972; and ◆ = onset of rest on July 24, 1972. For references and further explanations, see text; for the equations, see the Appendix.

means of simple temperature-sum models, in a way basically similar to that of predicting bud burst by means of the E-models (Koski and Sievänen 1985) (Appendix, Eqs. E1–E3). In tree species with a indeterminate growth habit, night length has a major influence on growth cessation. According to the main line of thought prevailing in the literature, night length is the most important environmental factor regulating growth cessation (Wareing 1956, Vaartaja 1959, Ekberg et al. 1979). Accordingly, the attainment of a critical night length induces the cessation of growth (triggered development, see Section 2.2). In this case, the modelling of growth cessation is done simply by examining whether the prevailing night length exceeds the critical night length or not. There is, however, increasing evidence to suggest that growth cessation in several tree species is regulated jointly by night length and air temperature (Koski and Selkäinaho 1982, Koski and Sievänen 1985, Partanen and Beuker 1999, Partanen 2004a,b). Accordingly, Koski and Sievänen (1985) presented a model of growth cessation where the critical night length triggering growth cessation decreases with increasing temperature sum (see also Viherä-Aarnio et al. 2005).

3.2 Models of Fluctuating Development

3.2.1 A Conceptual Model of Reversible Physiological Phenomena

According to a strict interpretation, the phenomena belonging to the category of fluctuating development are fully reversible. Though apparently a simplifying assumption, the concept of fluctuating development has served well in the formulation of models of the annual development of photosynthetic capacity (Pelkonen and Hari 1980, Mäkelä et al. 2004) and frost hardiness (Repo et al. 1990). A generalized conceptual model of fluctuating development is presented in Fig. 1b. Contrary to the corresponding model of fixed-sequence development (Fig. 1a), no cyclic development is assumed a priori. Rather, the state of photosynthetic capacity, S_p, (or the state of frost hardiness, S_h) fluctuates between its minimum and maximum values. Whether or not this results in a prediction of cyclic tree development depends on the prevailing environmental factors (Figs. 3c,4).

3.2.2 First-order Models of Photosynthetic Capacity and Frost Hardiness

The concept of fluctuating development was first applied to the modelling of the annual scycle of forest trees by Pelkonen and Hari (1980), who modelled the spring-time recovery of the photosynthetic capacity of shoots of Scots pine. Their model is an example of the first-order models, i.e. there is one time constant involved in it. The model belongs to the ES-category, i.e. it assumes that the rate of development is affected both by environmental factors and by the state of development. Furthermore, it assumes that photosynthetic capacity affects its own rate of development, i.e. the term state of photosynthetic capacity, $S_p(t)$, appears in the formulation for the rate of change of photosynthetic capacity, $R_p(t)$ (feedback). The observations agreed with the predictions of the model, with the exception that the model overestimated the state of photosynthetic capacity after night frosts (Pelkonen and Hari 1980). This was because the model was designed to describe only relatively slow changes in photosynthetic capacity caused by the fluctuation of air temperature, not abrupt damaging effects of frost. The latter were addressed in the model of Bergh et al. (1998) later on (for a more comprehensive comparison of the models of Pelkonen and Hari (1980) and Bergh et al. (1998), see Hänninen and Hari (2002)). Korpilahti (1988, p. 34–36) found that the cessation of Scots pine photosynthesis in central Finland autumn conditions was affected by sudden cold nights. To describe this short-term effect, she added a sub-model to the long-term model of Pelkonen and Hari (1980). This combined model was able to predict the carbon exchange of Scots pine in clear autumn days following cold nights.

Repo et al. (1990) presented a first-order model of the frost hardiness of stems of Scots pine seedlings. The ecophysiological assumptions of their model are almost identical to those of the photosynthetic capacity model of Pelkonen and Hari (1980). Due its different formulation, however, the model of Repo et al. (1990) is more general than that of Pelkonen and Hari (1980), hence also facilitating the introduction of new ecophysiological assumptions (see below). The model of Repo et al. (1990) is formulated as follows:

$$S_h^s(t) = a \cdot T(t) + b \tag{13}$$

$$R_h(t) = \frac{1}{\tau}(S_h^s(t) - S_h(t)) \tag{14}$$

where $S_h{}^s(t)$ is stationary frost hardiness (see Section 2.3), $T(t)$ is air temperature, a and b are genotype-specific parameters determining the linear dependence of stationary frost hardiness on air temperature, $R_h(t)$ is the rate of change of frost hardiness, $S_h(t)$ is the state of frost hardiness, and τ is a genotype-specific time constant. As seen in Eqs. 13 and 14, the model of Repo et al. (1990) also belongs to the category of ES-models, with the state of frost hardiness, S_h, affecting its own rate, R_h (see Eq. 4). The simple model defined by Eqs. 13 and 14 predicted the annual development of the frost hardiness of stems of Scots pine seedlings surprisingly well (Repo et al. 1990).

3.2.3 A Second-order Model of Frost Hardiness

The experimental evidence presented by Leinonen et al. (1995) concerning *Pseudotsuga menziesii* seedlings suggested that the response of frost hardiness to a change in the environmental conditions is not immediate, as was assumed in the first-order model of Repo et al. (1990) (Eqs. 13 and 14). For this case, a second-order model with two time constants was developed by assuming inertia not only in the change of frost hardiness but also in the change of asymptotic frost hardiness as a response to a change in the environmental conditions (Leinonen et al. 1995):

$$R_h(t) = \frac{1}{\tau_1}(S_h^a(t) - S_h(t)) \tag{15}$$

$$R_h^a(t) = \frac{1}{\tau_2}(S_h^s(t) - S_h^a(t)) \tag{16}$$

In Eq. 15, $R_h(t)$ is the rate of change of frost hardiness, $S_h(t)$ is the state of frost hardiness, $S_h{}^a(t)$ is asymptotic frost hardiness, and τ_1 is a time constant determining how quickly the state of frost hardiness adjusts to the asymptotic state when the environment changes. In Eq. 16, $R_h{}^a(t)$ is the rate of change of asymptotic frost hardiness, $S_h{}^s(t)$ is stationary frost hardiness, $S_h{}^a(t)$ is asymptotic frost hardiness, and τ_2 is the time constant determining how quickly asymptotic frost hardiness adjusts to stationary frost hardiness when the environment changes.

Similarly to the first-order model, stationary frost hardiness, $S_h{}^s(t)$, is modelled as a function of the prevailing environmental factors (see Eq. 13). The concept of asymptotic frost hardiness introduces the difference between the first-order (Eq. 14) and the second-order (Eqs. 15 and 16) models. The second-order model reduces to the first-order model if τ_2 equals unity. In this case, asymptotic frost hardiness is always equal to stationary frost hardiness, which changes into its new value as soon as the environment changes, and thus no second inertia in the regulation of frost hardiness is assumed.

In addition to the second-order approach, Leinonen et al. (1995) introduced other new ecophysiological assumptions in their model. This was done in connection with formulating the environmental response of stationary frost hardiness.

3.2.4 Predictions of the Models of Frost Hardiness

Simulations of frost hardiness were carried out, both for a hypothetical experiment in controlled conditions and for the natural conditions of central Finland, with modified versions of the first-order model of Repo et al. (1990) and the second-order model of Leinonen et al. (1995). In the model of Repo et al. (1990), the linear temperature response of the stationary state of frost hardiness (Eq. 13) was replaced by a piecewise linear model, i.e., for temperatures higher than 11.3 °C, a maximum value of –4.5 °C was assumed for the stationary state of frost hardiness (Appendix, Eq. C1). (Due to the inverted temperature scale used in the determination of frost hardiness, this maximum value of stationary frost hardiness indicates the minimum level of frost hardiness of the trees). The same temperature response was also used for stationary frost hardiness with the model of Leinonen et al. (1995) (Appendix, Eq. D1) instead of the original more complex environmental response. At the beginning of the simulations, frost hardiness was assumed to equal the stationary frost hardiness determined by the air temperature prevailing at the time. The simulations for natural conditions were initiated on September 1, 1971.

The predictions of the first-order and the second-order frost hardiness models for the hypothetical experiment are demonstrated in Fig. 4. After a stepwise change in air temperature (Fig. 4a), the first-order model predicted that the state of frost hardiness would respond immediately and would exponentially approach the new stationary state determined by the new air temperature (Fig. 4b; Repo and Pelkonen 1986). The rate of change of frost hardiness increases with increasing magnitude of the change in air temperature (compare the responses to changes in temperature at 80 days and at 100 days, Figs. 4a,b). Furthermore, as expected, the rate of change of frost hardiness decreases with increasing values of the time constant (Fig. 4b). Thus, frost hardiness fluctuates according to the fluctuations of air temperature, but due to the inertia described by the time constant, the changes in frost hardiness are slower than the changes in air temperature (Figs. 4a,b; Repo and Pelkonen 1986).

According to the second-order model, the changes in the state of frost hardiness after a stepwise change in air temperature (Fig. 4a) are sigmoidal, i.e. the rate of change is not at its maximum immediately after the change in air temperature (Fig. 4c; Leinonen et al. 1995) as it is according to the exponential response of the first-order model (Fig. 4b). Furthermore, according to the second-order model, in the case of rapid fluctuations of air temperature the direction of change in frost hardiness (hardening or dehardening) does not change immediately after the change in air temperature (Leinonen et al. 1995). This is seen during the days between 80 and 93, i.e. despite the rapid fluctuations of air temperature (Fig. 4a), with the time-constant value of $\tau_2 = 20$ days, the second-order model predicts continuous dehardening (Fig. 4c). For the same period, the first-order model predicts a sequence of periods of dehardening and hardening (Fig. 4b) as immedi-

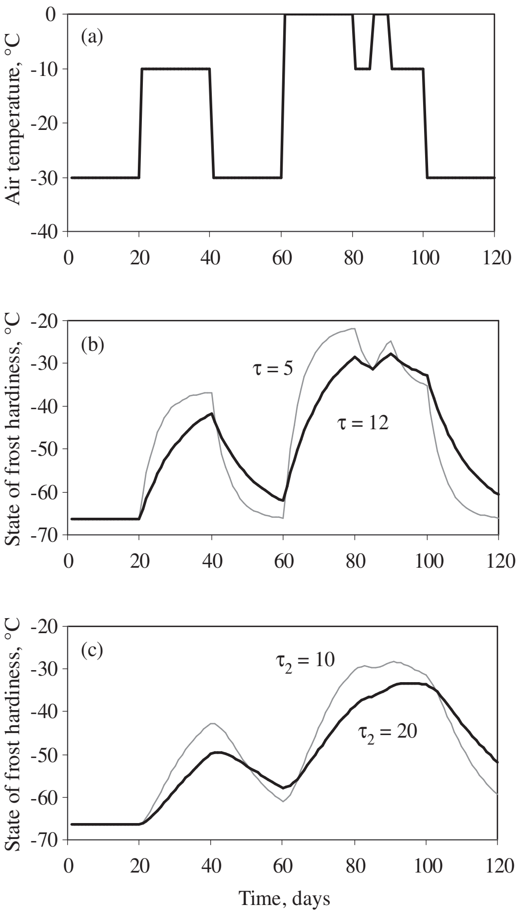

Fig. 4. Predictions of two models of frost hardiness for a hypothetical experiment in controlled conditions (fluctuating development). (a) The hypothetical temperature treatment used in the calculations. (b) Predictions of the first-order model of frost hardiness. The state of frost hardiness, S_h, with time constant $\tau = 5$ days (grey line) and $\tau = 12$ days (black line). (c) Predictions of the second-order model of frost hardiness. The state of frost hardiness, S_h, with second time constant $\tau_2 = 10$ days (grey line) and $\tau_2 = 20$ days (black line). The value of the first time constant τ_1 was 5 days in both cases. For references and further explanations, see text; for the equations, see the Appendix.

ate responses to the changes in air temperature. However, the first-order model, too, predicts that the direction of change in frost hardiness will not change if the change in air temperature is too small to alter the relative superiority of the values of state of frost hardiness and stationary frost hardiness. This is the case, for instance, when the state of stationary frost hardiness is above the state of frost hardiness before the change in air temperature, and due to the smallness of the drop in air temperature continues to do so even after the drop. Due to the second time-constant, however, behaviour of this kind is more pronounced with the second-order than the first-order model.

For natural conditions, the first-order model predicts a cyclic seasonal pattern of the state of frost hardiness following the cyclic seasonal pattern of temperature (Figs. 3a,c). However, superimposed on this long-term development, short-term fluctuations of the state of frost hardiness caused by short-term fluctuations of air temperature are visible. With increasing values of the time constant, the effect of this short-term fluctuation of temperature on the state of frost hardiness is increasingly dampened. Furthermore, with a low value of the time constant ($\tau = 5$ days) both the hardening and the dehardening are predicted to take place earlier than with a high value ($\tau = 12$ days) (Fig. 3c). As with the air temperature data for the hypothetical experiment (Fig. 4), the responses are slower with the second-order model than with the first-order model in natural conditions, too (results not shown).

The reversibility of fluctuating development is demonstrated in all of these simulation results. A period of hardening is interrupted by a period of dehardening whenever air temperature rises enough. Similarly, a period of dehardening is interrupted by a period of hardening whenever air temperature drops enough (Figs. 3a,c,4).

3.3 Integrated Models

3.3.1 A Conceptual Model of Frost Hardiness

Despite its surprisingly high accuracy, the simple model of Repo et al. (1990) fails to address several essential aspects of the environmental regulation of frost hardiness (Repo 1993). One of the neglected essential aspects is the fact that the environmental response of the rate of change of frost hardiness changes during the annual ontogenetic cycle. For instance, during the active growth phase the trees have only limited (if any) potential for hardening, so that the annual cycle of frost hardiness is only partially reversible (Fuchigami et al. 1982). For this reason, integrated models of frost hardiness, i.e. models combining the fixed-sequence and the fluctuating aspects of the annual cycle, are called for.

To our knowledge, the first integrated model was presented by Winter (1973). The best-known integrated model is probably the The Degree Growth Stage (°GS) model presented by Fuchigami et al. (1982). The °GS model has provided a conceptual framework for a large number of empirical studies addressing different phases and phenomena of the annual cycle. Kellomäki et al. (1992, 1995) constructed an integrated model by combining previous fixed-sequence development models of the annual ontogenetic cycle of Sarvas (1972,1974) and Koski and Sievänen (1985) with the fluctuating-development frost hardiness model of Repo et al. (1990). The annual ontogenetic cycle was divided into four phases (Fig. 1c), and the determination of stationary frost hardiness in the frost hardiness model varied from one phase to the next.

3.3.2 An Integrated Model of Frost Hardiness

Leinonen (1996a) introduced several new aspects into the integrated model of Kellomäki et al. (1992, 1995). In respect to the general principles of modelling, the most profound of these was the introduction of the concept of hardening competence, C_h, for describing the effects of the annual ontogenetic cycle on the dynamics of frost hardiness. Hardening competence is a [0–1]-multiplier which describes how large a part is realized of the potential increase in stationary frost hardiness determined by prevailing air temperature and night length. Hardening competence is at its maximum ($C_h = 1$) during rest, decreases during quiescence and the initial part of active growth, reaches zero slightly after the onset of growth, stays at zero until the beginning of lignification, and increases during lignification to reach its maximum again at the beginning of rest (Fig. 1c). In this way, the approach outlined in Eqs. 6 and 7 is applied here, i.e. the state of development of one aspect of the cycle (ontogenetic development) affects the rate of development of another aspect (frost hardiness).

In addition to the annual ontogenetic cycle and the annual course of frost hardiness, the model of Leinonen (1996a) also addresses the needle loss caused by frost damage (Appendix, Eqs. E21, E22). This property of the model, though not considered in detail in the present study, is essential for linking the model into forest stand and ecosystem models as their sub-model (see Section 4.5). All equations of the model of Leinonen (1996a) are given in the Appendix (Eqs. E1–E22), together with the parameter values Leinonen (1996a) used for Scots pine in central Finland.

3.3.3 Predictions of the Integrated Model of Frost Hardiness

Simulations of the annual ontogenetic cycle and the annual course of frost hardiness were carried out for the conditions of central Finland with the model of Leinonen (1996a) using the original parameter values determined for the frost hardiness of Scots pine needles in central Finland (Appendix, Eqs. E1–E20). The simulations were started on June 1, 1971, assuming that the active growth phase began on that day and that the state of frost hardiness had attained its maximum value (i.e. minimum frost hardiness). The summer of 1971 was then used for initializing the simulations and, as with the other models, the results are reported as of September 1 (Fig. 3).

In the prediction of the integrated model of Leinonen (1996a), two basic phenomena of the environmental regulation of the annual cycle of frost hardiness are visible: long-term regulation taking place via the annual ontogenetic cycle and short-term regulation taking place via the direct effects of air temperature and night length (Figs. 3a,d; Leinonen et al. 1997, Greer et al. 2001; see also Section 2.1). As hardening competence describes the effect of the irreversible annual ontogenetic cycle, no short-term fluctuations are observed in it (Fig. 3d). Such fluctuations are, however, visible in the state of frost hardiness, reflecting the direct effects of fluctuations in air temperature (Figs. 3a,d).

At the beginning of September, hardening competence is at its maximum. Due to the relatively short night lengths and high air temperatures, however, the rate of hardening is quite low at that time (Figs. 3a,d). After about one week the rate of hardening increases as a result of increasing night lengths and dropping air temperatures. The rate of hardening does not slow down after rest completion on October 16, even though hardening competence decreases slightly at that time due to some days with relatively high temperatures. The continued hardening with rather a constant rate is due to environmental factors (Fig. 3a), whose direct effect favours hardening at that time. In late November the state of frost hardiness attains its wintertime minimum (i.e. maximal frost hardiness). During mid-winter, frost hardiness fluctuates according to fluctuations in air temperature. Hardening competence decreases slightly during mild days in winter. In mid-March, air temperatures start to rise again, causing dehardening both directly and via the decrease in hardening competence. The dehardening of the previous year's needles also continues after the onset of growth on May 23 (Fig. 3d; Leinonen et al. 1997). At the beginning of July, frost hardiness again attains the minimum value prevailing during the active growth period (Fig. 3d).

4 Discussion

4.1 Ecophysiological Interpretation of the Model Variables

The ecophysiological interpretation of the model variable state of development is straightforward in the case of the physiological phenomena belonging to the category of fluctuating development (i.e. photosynthetic capacity and frost hardiness). This is because the corresponding actual values for these variables can be empirically determined during any phase of the annual cycle. This facilitates the testing of the different concepts and models, e.g. examining whether the development follows a first-order or a second-order model (Repo and Pelkonen 1986, Korpilahti 1988, Repo et al. 1990, Leinonen et al. 1995).

In the case of the ontogenetic phenomena belonging to the category of fixed-sequence development, in contrast, the ecophysiological interpretation of the model variable state of development is less clear. The state of rest, for instance, describes the cumulative physiological changes in the bud that remove the growth-arresting conditions. However, the exact nature of these changes remains unclear, so that one cannot directly measure the corresponding real value of the state of rest. This is why models for the rest break have to be developed and tested with indirect evidence from regrowth tests (Sarvas 1974, Erez and Couvillon 1987). It has been found that the duration of chilling required for a given growth response in subsequent forcing conditions depends on the prevailing temperature during the chilling conditions. With successively higher test temperatures, the duration required first decreases, attains a minimum somewhere near +5 °C, and then starts to increase. The rate of rest break is obtained as a reciprocal of the duration required, so that various dome-shaped temperature responses with the maximum value somewhere near +5 °C have been obtained for the rate of rest break (Sarvas 1974, Erez and Couvillon 1987). The state of ontogenetic development in turn describes the microscopic ontogenetic development inside the bud leading to bud burst (or flowering). For this reason the corresponding real state of development can principally be determined by microscopic observations on any day between bud set and bud burst. The time required for the tree to pass from one developmental event to the next decreases with successively higher test temperatures, so that the rate of development increases correspondingly (Sarvas 1972, 1974). In most cases, however, only the timing of bud burst is used in the testing of these models (Hari and Häkkinen 1991, Kramer 1994a,b, 1995b, Chuine et al. 1998, 1999, Chuine 2000, Häkkinen et al. 1998, Häkkinen 1999b, Linkosalo 2000b, Linkosalo et al. 2000; Fig. 3b).

In the case of the models of fixed-sequence development, the ecophysiological interpretation of the model variable state of development is further complicated by the fact that it is often referred to with meteorological concepts such as day degree sum (Bergh et al. 1998), temperature sum (Sarvas 1967), thermal time (Cannell and Smith 1983), chilling unit sum (Hänninen 1990b), or state of chilling (Kramer 1994a,b, Chuine 2000). In order to emphasise the ecophysiological interpretation, ecophysiological concepts (e.g. state of rest and state of ontogenetic development) are systematically used in the present study.

The idea of response competence was originally introduced by Hari et al. (1970) when modelling the rate of the height growth of trees. In that study the competence variable described the growth rhythm of the trees, i.e. the phases of increasing, maximum, and decreasing growth rate were separated by means of the competence variable. Thus, this theoretical concept straightforwardly addresses the long-known phenomenon that the ability of a plant to respond to environmental factors changes during its development (Landsberg 1977). Changes in the value of response competence summarise, at the whole-tree level, the complicated changes that take place at the tissue, cellular and sub-cellular levels. In the present study the concept of response competence was used for modelling the ontogenetic development taking place during dormancy (ontogenetic competence, $C_o(t)$, Figs. 1a,2), and for modelling frost hardiness (hardening competence, $C_h(t)$, Fig. 1c). Response competence is an especially useful concept for linking phenomena of fluctuating development to phenomena of fixed-sequence development ($i \neq j$, Eq. 6).

4.2 Empirical Development and Testing of the Models

It goes without saying that any model of the annual cycle of trees in boreal and temperate regions can be applied only after the model has been rigorously tested (Hänninen 1995b). Some information on the empirical tests of the models considered was provided above when introducing the models. However, a thorough review of the empirical support of the models considered is out of the scope of the present study. Empirical support for each of the models is described in the original publications, and several reviews on the topic are also available for different aspects of the annual cycle, i.e. for photosynthetic capacity (Pelkonen 1981a, Hänninen and Hari 2002), for frost hardiness (Repo 1993, Leinonen 1997), and for bud burst and flowering phenology (Cannell 1989, 1990, Hänninen 1990a, Kramer 1994a,b, 1996, Chuine 2000, Häkkinen 1999a, Linkosalo 2000a, Chuine et al. 2003). Here we limit ourselves to only some general methodological remarks about the empirical work.

Models are developed and tested by means of studies carried out both in controlled and in natural conditions. Experiments in controlled conditions are usually designed to explicitly address some specified details of the modelled phenomena, such as the temperature response of the rate of rest break (Sarvas 1974, Erez and Couvillon 1987) or the effects of the state of rest break on ontogenetic competence (Fig. 2; Hänninen 1990a). In studies using data from natural conditions, however, this is usually not possible, so that one has to resort to statistical model-fitting without observations on all the processes included in the models. This has caused problems for modelling bud burst in particular, as in this case models which describe a developmental process lasting several months and consisting of several part-processes described by sub-models are tested only by means of timing the end result of the process, i.e. bud burst (Fig. 3b) (Hänninen 1995, Hänninen et al. 2007). Kramer (1994b) found that the traditional numerical methods of estimating the parameter values for models of bud burst failed in several cases to yield realistic parameter estimates. Chuine et al. (1998,1999) introduced a method of simulated annealing, which does not have this drawback. By means of this method, an optimal set of parameter values can be found so that the model selected and parameterised is ecophysiologically as realistic as possible (see also Schaber and Badeck 2003).

4.3 Introducing New Aspects to the Modelling

When modelling the annual cycle of a new tree species, it may be enough to reconsider the parameter values of an earlier model developed for another species. This is because the main features of the environmental regulation of the annual cycle appear to be relatively universal among trees in boreal and temperate regions. With some species, however, it may be necessary to also revise the basic assumptions and the structure of the model. For instance, there is evidence that in *Fagus sylvatica*, both an accumulation of chilling and short night lengths are required to remove the growth-arresting physiological conditions during rest (Heide 1993). Thus, when modelling the rest break and ontogenetic competence of *F. sylvatica*, both chilling and night length probably need to be considered. Furthermore, there is increasing evidence for the notion that with other tree species, too, short night lengths may play a greater role in rest break than previously assumed (Nizinski and Saugier 1988, Partanen et al. 1998, Häkkinen et al. 1998, Hannerz 1999, Linkosalo 2000b, Linkosalo et al. 2000, Schaber and Badeck 2003, Partanen 2004b). However, the effect of night length on rest break can also be readily addressed in terms of the concept of ontogenetic competence (Hänninen 1995).

According to the recent findings of Zhang et al. (2003), a revision may also be necessary in modelling the annual frost hardiness cycle of Scots pine. Their data did not support the concept of additive effects of night length and air temperature (Chen and Li 1978, Greer 1983), which is essential in the model of Leinonen (1996a) (Appendix, Eq. E18). However, whatever new principles may replace the principle of additive effects in the new models, the concept of hardening competence will still be a useful tool for bringing the effect of the annual ontogenetic cycle in to the modelling.

The models considered in the present study address the effects of night length and the long-term cumulative effects of air temperature. However, in addition to these two major environmental factors, several other factors such as short-term freezing (Rinne et al. 1997, Bergh et al. 1998), soil temperature (Sorensen and Campbell 1978, Bergh and Linder 1999), drought (Chen and Li 1998), and nutrients (Rikala and Repo 1997) have been found to affect different aspects of the annual cycle of trees in boreal and temperate regions. In the present study no attempt was made to address these additional factors despite their potential importance. This was partly because these factors were not considered in the original models, but first and foremost because rather than providing an overall model addressing all cases, our aim was to present a framework. With the framework presented, the effects of the other environmental factors can also be readily modelled. When introducing new environmental factors to the modelling, however, one should remember that the biological realism of the models of the annual cycle is often, but not always, improved by increasing the complexity of the models. Increasing complexity also increases the number of technical difficulties. For instance, when adding new aspects to the model one usually increases the number of parameters, too, hence also increasing the amount of empirical work required. Thus, as in any other ecophysiological modelling, one often has to compromise between model complexity and model realism. The use of simplified models is often justified, especially when only a limited part of the annual cycle is considered (Greer et al. 2001).

4.4 Comparisons with Other Modelling Approaches

4.4.1 ES-Models of Bud Burst

Cannell and Smith (1983) found that the number of day degrees required for the bud burst of *Picea sitchensis* decreases exponentially as a function of accumulated chilling (hence the concept 'alternating model' was used by Kramer (1994a) in reference to their model). In this way, it is possible to predict the timing of bud burst by means of combining these two meteorological variables. The model of Cannell and Smith (1983) is ecophysiologically analogical to the parallel model of the present study. In their different ways, these two models describe the same ecophysiological phenomenon, i.e. the gradual effect of accumulated chilling on rest break (Fig. 2), due to which high temperatures cause ontogenetic development more effectively after a long than a short duration of chilling. The main advantage of the 'alternating approach' (Cannell and Smith 1983) is its simplicity: this model is relatively easy to parameterise and to communicate to other researchers. If the only purpose of the modelling is the prediction of the timing of bud burst, then the alternating model is a useful tool, as demonstrated by its applications in studies addressing the effects of climatic change (Cannell and Smith 1986, Murray et al. 1989, 1994).

The alternating model does not, however, explicitly address the ontogenetic development of the bud towards bud burst, i.e. in that model a given number of accumulated day degrees does not indicate a specific state of ontogenetic development. Thus, in respect to the process being modelled, the alternating model is an implication rather than a definition of the ecophysiological assumptions involved (i.e. the gradual effect of chilling) (see also Fig. 7d in Hänninen 1990a). For these reasons, the alternating model would be of little use in any study where a model prediction of the state of ontogenetic development before bud burst was needed. This is the case especially in integrated models, where, hardening competence is calculated on the basis of the state of ontogenetic development (Leinonen 1996a) (Appendix, Eqs. E13–E15). For these cases, an explicit variable for the state of ontogenetic development is needed. This is in accordance with the approach of the present study, where an explicit state variable is defined for each ecophysiological process addressed (Figs. 3b–d).

Chuine (2000) introduced a unified ES-model for the bud burst of trees. Her unified model has much in common with the approach developed by Hänninen (1990a, 1995) and Kramer (1994a,b) and refined in the present study, i.e. in both approaches the basic idea is that the prevailing models can be regarded as special cases of a more general model. In this way, the model is in both cases actually a modelling framework rather than a specified model. The unified model of Chuine (2000), however, differs in three respects from the corresponding model of bud burst presented in the present study.

Firstly, in the model of Chuine (2000) no a priori assumptions are made about the temperature responses of the rate of rest break and the rate of ontogenetic development. The triangular and sigmoidal functions applied in the present study (Appendix, Eqs. B1a, A1c) are replaced by a flexible equation, which produces all necessary response types as special cases. Naturally, this approach is especially suitable for cases where no a priori information on the responses is available. In the present study the general forms of the responses were fixed, assuming that there was sufficient a priori information to validate this. Secondly, rather than explicitly addressing the state of ontogenetic development as in the present study, the model of Chuine (2000) applies the alternating model (Cannell and Smith 1983) in the final phase of the calculations. Thus, like the original alternating model, the model of Chuine (2000) is well suited for predicting the timing of bud burst, whereas it is of little use in cases where the dynamics of the state of ontogenetic development before bud burst is to be considered. Thirdly, in Chuine's (2000) approach special emphasis is devoted to estimating the parameter values of the sub-models in cases where the estimation is carried out on the basis of data on the timing of bud burst and air temperature only, i.e. where no specific experimental data for the sub-models is available.

In conclusion, despite their seemingly high similarity of scopes, the present model of bud burst and that of Chuine (2000) have been designed for partially different purposes. The present ES-model of bud burst emphasises the explication and clarification of the ecophysiological theory, a priori information possibly obtained from experimental studies, and the linking of the model of ontogenetic development and bud burst into other models of seasonality. The model of Chuine (2000), in contrast, has been designed most of all for fitting predictive models of bud burst to long-term historical phenological data.

4.4.2 Mechanistic Models of Rest Break

Even though the exact mechanisms of rest break are not known, two attempts have been made to model the process of rest break mechanistically. Fishman et al. (1987a,b) developed a theoretical mechanistic model with an emphasis on the effects of fluctuating temperatures on the progress of rest break and the chilling negation taking place in high temperatures (for a closer description and discussion of the model, see Cannell (1989,1990) and Pitacco (1990)). The model of Fishman et al. (1987a,b) was able to simulate several complicated patterns of rest break in *Prunus persica*. More recently, Schaber and Badeck (2003) presented generalised physiology-based models for predicting the timing of the bud burst of trees in temperate regions. In their models they addressed the dynamics of theoretical growth promoters and inhibitors. In general, the models of Schaber and Badeck (2003) predicted the bud burst of several tree species more accurately than the classical models of bud burst did.

Recent advances in understanding the basic mechanisms of rest break (Viémont and Crabbé 2000, Horvath et al. 2003, Rinne and van der Schoot 2003) call for the development of further mechanistic models for that phenomenon. Models of that kind can be readily introduced into the framework of the present study, even though much of the framework was developed with reference to whole-tree level black-box models. The only prerequisite for such introducing is that the time course of the outcome of the complex equations addressing the mechanisms of rest break can be described by the time course of one variable, i.e. the state of rest break, $S_r(t)$. After that the framework can be implemented in the same way (Fig. 1a) as with the black box models in the present study.

4.4.3 Integrated Models of Frost Hardiness

The Degree Growth Stage (°GS) model (Fuchigami et al. 1982) was operationalised for simulating the annual growth cycle and frost hardiness of *Cornus sericea* by Kobayashi et al. (1982, 1983), and Kobayashi and Fuchigami (1983a,b). Though sharing much with the integrated model of Leinonen (1996a), the °GS model differs from the model of Leinonen (1996a) in three major aspects.

Firstly, in the model of ontogenetic development included in the °GS model, chilling decreases ontogenetic competence in the first phase of the rest period, whereas no such phase of deepening rest (Fuchigami et al. 1982) is included in the model of Leinonen (1996a). In his literature review, Hänninen (1990a) did not find such an ecophysiological assumption in any other model of bud burst, nor did he find any substantial empirical evidence for such a phase in the case of boreal trees. It is possible that the phenomenon is restricted to temperate broad-leafed trees, or, what is more probable, that the experiments where no deepening rest was found were started so late that the trees had already attained maximum rest, after which chilling increases ontogenetic competence in the °GS model as well (decreasing rest; Fuchigami et al. 1982). This disagreement between the °GS model and other ES-models of bud burst reveals the need for further experimental studies addressing the interim phase between the active growth phase and the dormant phase.

Secondly, in the °GS model the air temperature responses of the rate of development were determined by fitting polynomial functions to experimental data (Kobayashi et al. 1982, 1983, Kobayashi and Fuchigami 1983a,b). Thus, as in the ES bud burst model of Chuine (2000), no a priori assumptions about the form of the responses were made in the in the °GS model, even though the model was formulated on the basis of experimental data. Thirdly, hardening competence was not explicitly considered in the °GS model. Rather, the changes in the air temperature responses of the rate of hardening and dehardening were addressed by adopting the state of ontogenetic development, i.e. the growth stage, °GS, as an additional independent variable in the polynomial functions for the air temperature response of hardening/dehardening.

4.5 Application of the Models

Models of the annual cycle can be applied basically in two ways. They can be applied per se, when one is interested only in the corresponding ecophysiological phenomenon, i.e. the timing of bud burst (Cannell et al. 1985, Murray et al. 1989, 1994, Hänninen 1991, Linkosalo et al. 2000) or frost hardiness (Leinonen 1996a, Hänninen 2006). However, by introducing the models of the annual cycle as sub-models into models of stand or ecosystem, one can also study the implications of the ecophysiological phenomena for the development of stands and ecosystems (Hari et al. 1982, Korpilahti 1988, Kellomäki et al. 1992, 1995, Kellomäki and Väisänen 1997, Bergh et al. 1998, Kramer et al. 2000, 2002, Leinonen and Kramer 2002, Hänninen et al. 2005). The models of the annual cycle can be applied in all cases where information on the effects of climatic conditions on the growth and development of trees is needed. This is the case, for instance, in tree breeding and provenance transfers in practical forestry (Campbell 1974, Cannell et al. 1985). Most of the applications, however, have been related to predicted climatic change. During the past couple of decades, the effects of climatic change on the risk of tree frost damage have been examined in several studies using models of the annual cycle (for a review, see Hänninen et al. 2001). Recently, much attention has also been paid to the effects of the climate change on the photosynthetic production of trees and the carbon sequestration of forests. For this purpose, the model of Pelkonen and Hari (1980) has been introduced into several forest stand models (Kramer et al. 2002). Similarly, the model of Bergh et al. (1998) has been introduced into the BIOMASS stand model (McMurtrie et al. 1994, Bergh et al. 1998).

Chuine and Beaubien (2002) suggested, on the basis of models of the annual cycle of trees, that phenology is a major determinant of the geographical ranges of *Acer saccharum* and *Populus tremuloides* in North America. This suggestion shows that models of the annual cycle of trees can be applied not only to practical problems rising from the surrounding society and its need for scientific information, but also to attempts at solving the classical question of ecology, i.e. the determination of the ranges and abundances of taxa.

4.6 Concluding Remarks

Since Réaumur (1735), a large number of approaches have been suggested for modelling the timing of annually recurring phenomena in plants and animals, especially for the annual cycle of trees in the boreal and temperate zones. Reviews of models of several specified aspects of the annual cycle have also been presented previously. Rather than adding anything strictly new to this earlier work, our study contributes by comparing and explicating the ecophysiological assumptions of the different models, considering a wide variety of seasonal phenomena at one time. To this end, the classifying terminology of Chapter 2 was developed. A modelling framework with a common notation for the different phenomena and models was developed and, in order to promote further operational use of the models, the formulations of a selection of models scattered in the literature were collected in the Appendix using the unifying notation developed in this study. In this way, we hope, our study will facilitate the development and testing of new models for the annual cycle of trees with high biological realism and the derivation of parameter values for a wide range of tree species in a uniform manner. On the basis of such results, the annual development of trees and its implications for forest growth and fruit production can be analysed in a wide range of current and future environmental circumstances.

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References

Aronsson, A. 1975. Influence of photo- and thermoperiod on the initial stages of frost hardening and dehardening of phytotron-grown seedlings of Scots pine (Pinus silvestris L.) and Norway spruce (Picea abies (L.) Karst.). Studia Forestalia Suecica 128: 1–20.

Arnold, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proceedings of the American Society for Horticultural Science 74: 430–445.

Bergh, J. & Linder, S. 1999. Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. Global Change Biology 5: 245–253.

— , McMurtrie, R.E. & Linder, S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. Forest Ecology and Management 110: 127–139.

Beuker, E., Valtonen, E. & Repo, T. 1998. Seasonal variation in the frost hardiness of Scots pine and Norway spruce in old provenance experiments in Finland. Forest Ecology and Management 107: 87–98.

Campbell, R.K. 1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. Journal of Applied Ecology 11: 1069–1080.

— 1978. Regulation of bud-burst timing by temperature and photoregime during dormancy. In: Hollis, C.A. & Squillace, A.E. (eds.). Proceedings: Fifth North American Forest Biology Workshop. Forestry Department, University of Florida, Gainesville. p. 19–33.

Cannell, M.G.R. 1985. Analysis of risks of frost damage to forest trees in Britain. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Helsinki University Press, Helsinki. p. 153–166.

— 1989. Chilling, thermal time and the date of flowering of trees. In: Wright, C.J. (ed.). Manipulation of fruiting. Butterworths, London. p. 99–113.

— 1990. Modelling the phenology of trees. In: Jozefek, H. (ed.). Modelling to understand forest functions. Silva Carelica 15: 11–27.

— & Smith, R.I. 1983. Thermal time, chill days and prediction of budburst in Picea sitchensis. Journal of Applied Ecology 20: 951–963.

— Smith, R.I. 1986. Climatic warming, spring budburst and frost damage on trees. Journal of Applied Ecology 23: 177–191.

— , Murray, M.B. & Sheppard, L.J. 1985. Frost avoidance by selection for late budburst in Picea sitchensis. Journal of Applied Ecology 22: 931–941.

Chen, H.H. & Li, P.H. 1978. Interactions of low temperature, water stress, and short days in the induction of stem frost hardiness in Red Osier Dogwood. Plant Physiology 62: 833–835.

Christersson, L. 1978. The influence of photoperiod and temperature on the development of frost hardiness in seedlings of Pinus silvestris and Picea abies. Physiologia Plantarum 44: 288–294.

Chuine, I. 1998. Modélisation de la phénologie des arbres de la zone tempérée et ses implications en biologie évolutive. Ecole Nationale Supérieure Agronomique de Montpellier, France. Thèse. 83 p.

— 2000. A unified model for budburst of trees. Journal of Theoretical Biology 207: 337–347.

— & Beaubien, E.G. 2001. Phenology is a major determinant of tree species range. Ecology Letters 4: 500–510.

— , Cour, P. & Rousseau, D.D. 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. Plant, Cell and Environment 21: 455–466.

— , Cour, P. & Rousseau, D.D. 1999. Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. Plant, Cell and Environment 22: 1–13.

— , Kramer, K. & Hänninen, H. 2003. Plant development models. In: Schwartz, M.D. (ed.). Phenology: an integrative environmental science. Kluwer Academic Publishers, Dordrecht. p. 305–333.

Coville, F.V. 1920. The influence of cold in stimulating the growth of plants. Journal of Agricultural Research 20: 151–160.

Ekberg, I., Eriksson, G. & Dormling, I. 1979. Photoperiodic reactions in conifer species. Holarctic Ecology 2: 255–263.

Erez, A. & Couvillon, G.A. 1987. Characterization of the influence of moderate temperatures on rest completion in peach. Journal of the American Society for Horticultural Science 112: 677–680.

— & Lavee, S. 1971. The effect of climatic conditions on dormancy development of peach buds. I. Temperature. Journal of the American Society for Horticultural Science 96: 711–714.

— , Couvillon, G.A. & Hendershott, C.H. 1979a. Quantitative chilling enhancement and negation in peach buds by high temperatures in a daily cycle. Journal of the American Society for Horticultural Science 104: 536–540.

— , Couvillon, G.A. & Hendershott, C.H. 1979b. The effect of cycle length on chilling negation by high temperatures in dormant peach leaf buds. Journal of the American Society for Horticultural Science 104: 573–576.

Fishman, S., Erez, A. & Couvillon, G.A. 1987a. The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. Journal of Theoretical Biology 124: 473–483.

— , Erez, A. & Couvillon, G.A. 1987b. The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. Journal of Theoretical Biology 126: 309–321.

Fuchigami, L.H., Weiser, C.J., Kobayashi, K., Timmis, R. & Gusta, L.V. 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. In: Li, P.H. & Sakai, A. (eds.). Plant cold hardiness and freezing stress. Mechanisms and crop implications. Vol. 2. Academic Press, New York. p. 93–116.

Greer, D.H. 1983. Temperature regulation of the development of frost hardiness in Pinus radiata D. Don. Australian Journal of Plant Physiology 10: 539–547.

— , Leinonen, I. & Repo, T. 2001. Modelling cold hardiness development and loss in conifers. In: Bigras, F.J. & Colombo, S.J. (eds.). Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht. p. 437–460.

Grossnickle, S.C., Arnott, J.T., Major, J.E. & Tschaplinski, T.J. 1991. Influence of dormancy induction treatments on western hemlock seedlings. I. Seedling development and stock quality assessment. Canadian Journal of Forest Research 21: 164–174.

Häkkinen, R. 1999a. Analysis of bud-development theories based on long-term phenological and air temperature time series: application to Betula sp. leaves. Finnish Forest Research Institute, Research Papers 754. 59 p.

— 1999b. Statistical evaluation of bud development theories: application to bud burst of Betula pendula leaves. Tree Physiology 19: 613–618.

— , Linkosalo, T. & Hari, P. 1998. Effects of dormancy and environmental factors on timing of bud burst in Betula pendula. Tree Physiology 18: 707–712.

Hannerz, M. 1999. Evaluation of temperature models for predicting bud burst in Norway spruce. Canadian Journal of Forest Research 29: 1–11.

Hänninen, H. 1987. Effects of temperature on dormancy release in woody plants: implications of prevailing models. Silva Fennica 21: 279–299.

— 1990a. Modelling bud dormancy release in trees from cool and temperate regions. Acta Forestalia Fennica 213. 47 p.

— 1990b. Modeling dormancy release in trees from cool and temperate regions. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A. & Warren, W.G. (eds.).

Process modeling of forest growth responses to environmental stress. Timber Press, Portland. p. 159–165.

— 1991. Does climatic warming increase the risk of frost damage in northern trees? Plant, Cell and Environment 14: 449–454.

— 1995. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Canadian Journal of Botany 73: 183–199.

— 2006. Risk of frost damage to boreal forest trees under climatic warming: Identification of critical ecophysiological traits. Tree Physiology 26: 889–898.

— & Hari, P. 1996. The implications of geographical variation in climate for differentiation of bud dormancy ecotypes in Scots pine. In: Hari. P., Ross, J. & Mecke, M. (eds.). Production process of Scots pine; geographical variation and models. Acta Forestalia Fennica 254: 11–21.

— & Hari, P. 2002. Recovery of photosynthesis of boreal conifers during spring: a comparison of two models. Forest Ecology and Management 169: 53–64.

— & Pelkonen, P. 1989. Dormancy release in Pinus sylvestris L. and Picea abies (L.) Karst. seedlings: effects of intermittent warm periods during chilling. Trees 3: 179–184.

— , Beuker, E., Johnsen, Ø., Leinonen, I., Murray, M., Sheppard, L. & Skrøppa, T. 2001. Impacts of climate change on cold hardiness of conifers. In: Bigras, F.J. & Colombo, S.J. (eds.). Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht. p. 305–333.

— , Kolari, P. & Hari, P. 2005. Seasonal development of Scots pine under climatic warming: effects on photosynthetic production. Canadian Journal of Forest Research 35: 2092–2099.

— , Slaney, M. & Linder, S. 2007. Dormancy release of Norway spruce under climatic warming: Testing ecophysiological models of bud burst with a whole-tree chamber experiment. Tree Physiology 27: 291–300.

Hari, P. 1972. Physiological stage of development in biological models of growth and maturation. Annales Botanici Fennici 9: 107–115.

— & Häkkinen, R. 1991. The utilization of old phenological time series of budburst to compare models describing annual cycles of plants. Tree Physiology 8: 281–287.

— & Mäkelä, A. 2003. Annual pattern of photosynthesis in Scots pine in the boreal zone. Tree Physiology 23: 145–155.

— , Leikola, M. & Räsänen, P. 1970. A dynamic model of the daily height increment of plants. Annales Botanici Fennici 7: 375–378.

— , Kellomäki, S., Mäkelä, A., Ilonen, P., Kanninen, M., Korpilahti, E. & Nygrén, M. 1982. Metsikön varhaiskehityksen dynamiikka. Summary: Dynamics of early development of tree stand. Acta Forestalia Fennica 177. 42 p.

Heide, O.M. 1985. Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. In: Kaurin, Å., Junttila, O. & Nilsen, J. (eds.). Plant production in the north. Norwegian University Press, Tromsø. p. 1–22.

— 1993. Dormancy release in beech buds (Fagus sylvatica) requires both chilling and long days. Physiologia Plantarum 89: 187–191.

Horvath, D.P., Anderson, J.V., Chao, W.S. & Foley, M.E. 2003. Knowing when to grow: signals regulating bud dormancy. Trends in Plant Science 8: 534–540.

Hunter, A.F. & Lechowicz, M.J. 1992. Predicting the timing of budburst in temperate trees. Journal of Applied Ecology 29: 597–604.

Kellomäki, S. & Väisänen, H. 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecological Modelling 97: 121–140.

— , Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U. & Pajari, B. 1992. A simulation model for the succession of the boreal forest ecosystem. Silva Fennica 26: 1–18.

— , Hänninen, H. & Kolström, M. 1995. Computations on frost damage to Scots pine under climatic warming in boreal conditions. Ecological Applications 5: 42–52.

Kobayashi, K.D. & Fuchigami, L.H. 1983a. Modelling temperature effects in breaking rest in red-osier dogwood (Cornus sericea L.). Annals of Botany 52: 205–215.

— & Fuchigami, L.H. 1983b. Modeling bud development during the quiescent phase in red-osier dogwood (Cornus sericea L.). Agricultural Meteorology 28: 75–84.

— , Fuchigami, L.H. & English, M.J. 1982. Modeling temperature requirements for rest development in Cornus sericea. Journal of the American Society for Horticultural Science 107: 914–918.

— , Fuchigami, L.H. & Weiser, C.J. 1983. Modeling cold hardiness of red-osier dogwood. Journal of the American Society for Horticultural Science 108: 376–381.

Korpilahti, E. 1988. Photosynthetic production of Scots pine in the natural environment. Acta Forestalia Fennica 202. 71 p.

Koski, V. & Selkäinaho, J. 1982. Experiments on the joint effect of heat sum and photoperiod on seedlings of Betula pendula. Communicationes Instituti Forestalis Fenniae 105: 1–34.

— & Sievänen, R. 1985. Timing of growth cessation in relation to the variations in the growing season. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Helsinki University Press, Helsinki. p. 67–193.

Kramer, K. 1994a. Selecting a model to predict the onset of growth of Fagus sylvatica. Journal of Applied Ecology 31: 172–181.

— 1994b. A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. Plant, Cell and Environment 17: 367–377.

— 1995a. Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of temperate-zone deciduous trees. Climate Research 5: 119–130.

— 1995b. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant, Cell and Environment 18: 93–104.

— 1996. Phenology and growth of European trees in relation to climate change. Thesis Landbouw Universiteit Wageningen. 210 p.

— , Friend, A. & Leinonen, I. 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. Climate Research 7: 31–41.

— , Leinonen, I. & Loustau, D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forest ecosystems: an overview. International Journal of Biometeorology 44: 67–75.

— , Leinonen, I., Bartelink, H.H., Berbigier, P., Borghetti, M., Bernhofer, Ch., Cienciala, E., Dolman, A.J., Froer, O., Gracia, C.A., Granier, A., Grünwald, T., Hari, P., Jans, W., Kellomäki, S., Loustau, D., Magnani, F., Markkanen, T., Matteucci, G., Mohren, G.M.J., Moors, E., Nissinen, A., Peltola, H., Sabaté, S., Sanchez, A., Sontag, M., Valentini, R. & Vesala, T. 2002. Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe. Global Change Biology 8: 213–230.

Landsberg, J.J. 1974. Apple fruit bud development and growth; analysis and an empirical model. Annals of Botany 38: 1013–1023.

— 1977. Effects of weather on plant development. In: Landsberg, J.J. & Cutting, C.V. (eds.). Environmental effects on crop physiology. Academic Press, London. p. 289–307.

Leinonen, I. 1996a. A simulation model for the annual frost hardiness and freeze damage of Scots pine. Annals of Botany 78: 687–693.

— 1996b. Dependence of dormancy release on temperature in different origins of Pinus sylvestris and Betula pendula seedlings. Scandinavian Journal of Forest Research 11: 122–128.

— 1997. Frost hardiness and annual development of forest trees under changing climate. D.Sc. (Agr. and For.) thesis. University of Joensuu, Faculty of Forestry, Research Notes 60. 42 p.

— & Hänninen, H. 2002. Adaptation of the timing of bud burst of Norway spruce to temperate and boreal climates. Silva Fennica 36: 695–701.

— & Kramer, K. 2002. Applications of phenological models to predict the future carbon sequestration potential of boreal forests. Climatic Change 55: 99–113.

— , Repo, T., Hänninen, H. & Burr, K.E. 1995. A second-order dynamic model for the frost hardiness of trees. Annals of Botany 76: 89–95.

— , Repo, T. & Hänninen, H. 1996. Testing of frost hardiness models for Pinus sylvestris in natural conditions and in elevated temperature. Silva Fennica 30: 159–168.

— , Repo, T. & Hänninen, H. 1997. Changing environmental effects on frost hardiness of Scots pine during dehardening. Annals of Botany 79: 133–138.

Levitt, J. 1969. Growth and survival of plants at extremes of temperature – a unified concept. In: Woolhouse, H.W. (ed.). Dormancy and Survival, Symposia of the Society for Experimental Biology, XXIII. Cambridge University Press. p. 395–448.

Linder, S. & Lohammar, T. 1981. Amount and quality of information on CO_2-exchange required for estimating annual carbon balance of coniferous trees. In: Linder, S. (ed.): Understanding and predicting tree growth. Studia Forestalia Suecica 160: 73–87.

Linkosalo, T. 2000a. Analyses of the spring phenology of boreal trees and its response to climate change. University of Helsinki, Department of Forest Ecology Publications 22. 55 p.

— 2000b. Mutual regularity of spring phenology of some boreal tree species: predicting with other species and phenological models. Canadian Journal of Forest Research 30: 667–673.

— , Carter, T.R., Häkkinen, R. & Hari, P. 2000. Predicting spring phenology and frost damage risk of Betula spp. under climatic warming: a comparison of two models. Tree Physiology 20: 1175–1182.

Luomajoki, A. 1986. Timing of microsporogenesis in trees with reference to climatic adaptation. A review. Acta Forestalia Fennica 196. 33 p.

— 1993. Climatic adaptation of Scots pine (Pinus sylvestris L.) in Finland based on male flowering phenology. Acta Forestalia Fennica 237. 27 p.

Luoranen, J. 2000. Control of growth and frost hardening of silver birch container seedlings: growth retardants, short day treatment and summer planting. The Finnish Forest Research Institute, Research Papers 777. 67 p.

Mäkelä, A., Hari, P., Berninger, F., Hänninen, H. & Nikinmaa, E. 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. Tree Physiology 24: 369–376.

McMurtrie, R.E., Gholz, H.L., Linder, S. & Gower, S.T. 1994. Climatic factors controlling the productivity of pine stands: a model based analysis. In: Gholz, H.L., Linder, S. & McMurtrie, R.E. (eds.). Environmental constraints on the structure and productivity of pine forest ecosystems: a comparative analysis. Ecological Bulletins (Copenhagen) 43: 173–188.

Murray, M.B., Cannell, M.G.R. & Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. Journal of Applied Ecology 26: 693–700.

— , Smith, R.I., Leith, I.D., Fowler, D., Lee, H.S.J., Friend, A.D. & Jarvis, P.G. 1994. Effects of elevated CO_2, nutrition and climatic warming on bud phenology in Sitka spruce (Picea sitchensis) and their impact on the risk of frost damage. Tree Physiology 14: 691–706.

Myking, T. & Heide, O.M. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of Betula pendula and B. pubescens. Tree Physiology 15: 697–704.

Nizinski, J.J. & Saugier, B. 1988. A model of leaf budding and development for a mature Quercus forest. Journal of Applied Ecology 25: 643–652.

Partanen, J. 2004a. Dependence of photoperiodic response of growth cessation on the stage of development in Picea abies and Betula pendula seedlings. Forest Ecology and Management 188: 137–148.

— 2004b. Regulation of growth onset and cessation in Norway spruce, Scots pine and silver birch. Finnish Forest Research Institute, Research Papers 921. 39 p.

— & Beuker, E. 1999. Effects of photoperiod and thermal time on the growth rhythm of Pinus sylvestris seedlings. Scandinavian Journal of Forest Research 14: 487–497.

— , Koski, V. & Hänninen, H. 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (Picea abies). Tree Physiology 18: 811–816.

Pelkonen, P. 1980. The uptake of carbon dioxide in Scots pine during spring. Flora 169: 386–397.

— 1981a. Recovery and cessation of CO_2 uptake in Scots pine at the beginning and at the end of the annual photosynthetic period. University of Helsinki, Department of Silviculture. Research Notes 30. 95 p.

— 1981b. Investigations on seasonal CO_2 uptake in Scots pine. I CO_2 exchange in Scots pine after wintering period. II The autumn fall in CO_2 uptake in Scots pine. Communicationes Instituti Forestalis Fenniae 99(5). 40 p.

— & Hari, P. 1980. The dependence of the springtime recovery of CO_2 uptake in Scots pine on temperature and internal factors. Flora 169: 398–404.

Perry, T.O. 1971. Dormancy of trees in winter. Science 171: 29–36.

— & Wang, C.W. 1960. Genetic variation in the winter chilling requirement for date of dormancy break for Acer rubrum. Ecology 41: 790–794.

Pisek, A. & Winkler, E. 1958. Assimilationsvermögen und Respiration der Fichte (Picea excelsa Link) in verschiedener Höhenlage und der Zirbe (Pinus cembra L.) an der alpinen Waldgrenze. Planta 51: 518–543.

Pitacco, A. 1990. The ”Dynamic Model” of chilling accumulation: its structure and performance under simulated and real thermal regimes. Advances in Horticultural Science 3: 167–171.

Pop, E.W., Oberbauer, S.F. & Starr, G. 2000. Predicting vegetative bud break in two arctic deciduous shrub species, Salix pulchra and Betula nana. Oecologia 124: 176–184.

Raulo, J. & Leikola, M. 1974. Tutkimuksia puiden vuotuisen pituuskasvun ajoittumisesta. Summary: Studies on the annual height growth of trees. Communicationes Instituti Forestalis Fenniae 81(2). 19 p.

Réaumur, M. 1735. Observations du thermomètres, faites à Paris pendant l'année 1735, comparées avec celles qui ont été faites sous la ligne, à l'isle de France, à Alger et quelques unes de nos isles de l'Amérique. Académie des Sciences de Paris 545.

Repo, T. 1991. Rehardening potential of Scotch pine seedlings during dehardening. Silva Fennica 25: 13–21.

— 1992. Seasonal changes of frost hardiness in Picea abies and Pinus sylvestris in Finland. Canadian Journal of Forest Research 22: 1949–1957.

— 1993. Impedance spectroscopy and temperature acclimation of forest trees. University of Joensuu, Faculty of Forestry, Research Notes 9. 53 p.

— & Pelkonen, P. 1986. Temperature step response of dehardening in Pinus sylvestris seedlings. Scandinavian Journal of Forest Research 1: 271–284.

— , Mäkelä, A., Hänninen, H. 1990. Modelling frost resistance of trees. In: Jozefek, H. (ed.). Modelling to understand forest functions. Silva Carelica 15: 61–74.

Richardson, E.A., Seeley, S.D. & Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortScience 9: 331–332.

Rikala, R. & Repo, T. 1997. The effect of late summer fertilization on the frost hardening of second-year Scots pine seedlings. New Forests 14: 33–44.

Rinne, P.L.H. & van der Schoot, C. 2003. Plasmodesmata at the crossroads between development, dormancy, and defence. Canadian Journal of Botany 81: 1182–1197.

— , Hänninen, H., Kaikuranta, P., Jalonen, J.E. & Repo, T. 1997. Freezing exposure releases bud dormancy in Betula pubescens and B. pendula. Plant, Cell and Environment 20: 1199–1204.

Romberger, J.A. 1963. Meristems, growth, and development in woody plants. An analytical review of anatomical, physiological, and morphogenetic aspects. USDA Technical Bulletin 1292. U.S. Government Printing Office.

Sarvas, R. 1967. The annual period of development of forest trees. Proceedings of the Finnish Academy of Science and Letters 1965: 211–231.

— 1972. Investigations on the annual cycle of development of forest trees. Active period. Communicationes Instituti Forestalis Fenniae 76(3). 110 p.

— 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. Communicationes Instituti Forestalis Fenniae 84(1). 101 p.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G. & Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist 149: 369–400.

Schaber, J. & Badeck, F.W. 2003. Physiology-based phenology models for forest tree species in Germany. International Journal of Biometeorology 47: 193–201.

Sorensen, F.C. & Campbell, R.K. 1978. Comparative roles of soil and air temperatures in the timing of spring bud flush in seedling Douglas-fir. Canadian Journal of Botany 56: 2307–2308.

Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., Huttula, T., Laurila, T., Aurela, M., Grelle, A., Lindroth, A., Arneth, A., Shibistova, O. & Lloyd, J. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. Global Change Biology 9: 1410–1426.

Taiz, L. & Zeiger, E. 1998. Plant physiology, second edition. Sinauer Associates Inc., Publishers, Sunderland. 792 p.

Vaartaja, O. 1959. Evidence of photoperiodic ecotypes in trees. Ecological Monographs 29: 91–111.

Viherä-Aarnio, A., Häkkinen, R., Partanen, J., Luomajoki, A. & Koski, V. 2005. Effects of seed origin and sowing time on timing of height growth cessation of Betula pendula seedlings. Tree Physiology 25: 101–108.

Van Wijk, M.T., Williams, M., Laundre, J.A. & Shaver, G.R. 2003. Interannual variability of plant phenology in tussock tundra: modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. Global Change Biology 9: 743–758.

Viémont, J.D. & Crabbé, J. (eds.) 2000. Dormancy in plants. From whole plant behaviour to cellular control. CABI Publishing, Wallingford. 385 p.

Wang, J.Y. 1960. A critique of the heat unit approach to plant response studies. Ecology 41: 785–790.

Wareing, P.F. 1956. Photoperiodism in woody plants. Annual Review of Plant Physiology 7: 191–214.

Weiser, C.J. 1970. Cold resistance and injury in woody plants. Science 169: 1269–1278.

Winter, F. 1973. Ein Simulationsmodell über die Phänologie und den Verlauf der Frostresistenz von Apfelbäumen. Ecologia Plantarum 8: 141–152.

Zhang, G. 2001. Cold acclimation in Scots pine. D.Sc. (Agr. and For.) thesis. Finnish Forest Research Institute, Research Papers 817. 52 p.

— , Ryyppö, A., Vapaavuori, E. & Repo, T. 2003. Quantification of additive response and stationarity of frost hardiness by photoperiod and temperature in Scots pine. Canadian Journal of Forest Research 33: 1772–1784.

Total of 143 references

Appendix: Equations for a Selection of Models

Table 1. The symbols and units of the variables used in the equations. In the present study the models are applied with a time step of one day. When other time steps are used, the units of the time-related symbols have to be changed correspondingly (with the exception of the symbols $NL(t)$ and $T_{min}(t)$).

Symbol	Explanation	Unit
Basic variable of dynamic models		
t	Time	Day
Variables for phenological events		
t_{act}	Date of onset of active growth	
t_{lign}	Date of onset of lignification	
t_{quie}	Date of onset of quiescence	
t_{rest}	Date of onset of rest	
Driving variables		
$NL(t)$	Night length of day t	h
$T_{\text{min}}(t)$	Minimum air temperature of day t	°C
$T(t)$	Mean air temperature of day t	°C
Rate variables		
$R_a(t)$	Rate of active growth on day t	100 day^{-1}
$R_h(t)$	Rate of change of frost hardiness on day t	°C day^{-1}
$R_l(t)$	Rate of lignification on day t	100 day^{-1}
$R_o(t)$	Rate of ontogenetic development on day t	100 day^{-1}
$R_{o,\text{pot}}(t)$	Potential rate of ontogenetic development on day t	100 day^{-1}
$R_r(t)$	Rate of rest break on day t	100 day^{-1}
State variables		
$C_h(t)$	Hardening competence on day t	Dimensionless
$C_o(t)$	Ontogenetic competence on day t	Dimensionless
$S_a(t)$	State of active growth at the end of day t	Dimensionless
$S_h(t)$	State of frost hardiness at the end of day t	°C
$S_l(t)$	State of lignification at the end of day t	Dimensionless
$S_o(t)$	State of ontogenetic development at the end of day t	Dimensionless
$S_r(t)$	State of rest break at the end of day t	Dimensionless
Auxiliary variables		
$\Delta H_{NL}(t)$	Effect of night length on potential frost hardiness on day t	°C
$\Delta H_T(t)$	Effect of air temperature on potential frost hardiness on day t	°C
$R^a{}_h(t)$	Rate of change of asymptotic frost hardiness on day t	°C day^{-1}
$S^a{}_h(t)$	Asymptotic frost hardiness on day t	°C
$S^s{}_h(t)$	Stationary frost hardiness on day t	°C
Arbitrary developmental units		
CU	Chilling unit	
HU	High temperature unit	

Table 2. The symbols and values of the equation-specific parameters. The values of the parameters are mainly for Scots pine (*Pinus sylvestris* L.). The exceptions are indicated below the table, with references where details of the empirical background of all parameter values can be found.

Eq.	Symbol	Explanation	Value	Unit	References
A1a	$H_{\text{crit}(a)}$	High temperature requirement of growth onset	12.5 – 230	HU[a)]	16
A1a	T_1	Threshold air temperature	5	°C	16
A1b	a_1		–0.42	-	4
A1b	b_1		0.73	-	4
A1b	c_1		0.07	$°\text{C}^{-1}$	4
A1b	$H_{\text{crit}(b)}$	High temperature requirement of growth onset	139	HU[a)]	4
A1c	a_2		0.185	$°\text{C}^{-1}$	3, 17
A1c	b_2		18.4	°C	3, 17
A1c	$H_{\text{crit}(c)}$	High temperature requirement of growth onset	5.3	HU[a)]	3, 17
A1c	T_2	Threshold air temperature	0	°C	3
A2	t_0	Starting day of simulation	January 1	-	4
B1a	$C_{\text{crit}(a)}$	Chilling requirement of rest completion	30	CU[b)]	3
B1a	T_3	Lower threshold air temperature	–3.4	°C	3, 18
B1a	T_4	Optimum air temperature	3.5	°C	3, 18
B1a	T_5	Upper threshold air temperature	10.4	°C	3, 18
B1b	$C_{\text{crit}(b)}$	Chilling requirement of rest completion	12	CU[b)]	-
B1b	T_6	Threshold air temperature	5	°C	7
B1c	$C_{\text{crit}(c)}$	Chilling requirement of rest completion	30	CU[b)]	3
B2	t_{rest}	Date of onset of rest	September 1	-	3
B4b	$C_{o,\text{min}}$	Minimum ontogenetic competence	0.1	-	3
B4c	S_{r*}	Threshold state of rest	50	-	3
B6	t_{rest}	Date of onset of rest	September 1	-	3
C1	a_3		1.5	-	15
C1	b_3		–21.4	°C	15
C1	T_7	Threshold air temperature	11.3	°C	15
C2	τ	Time constant	5	Day	8, 14, 15
C3	t_0	Starting day of simulation	September 1	-	-
D1	a_4		1.5	-	15
D1	b_4		–21.4	°C	15
D1	T_8	Threshold air temperature	11.3	°C	15
D2	τ_2	Second time constant	10	Day	-
D3 & D5	t_0	Starting day of simulation	September 1	-	-
E1	$H_{a,\text{crit}}$	High temperature requirement of active growth	510	HU[a)]	8, 12
E1	T_9	Threshold air temperature	5	°C	5, 8, 12
E2	t_0	Starting day of simulation	June 1	-	-

Eq.	Symbol	Explanation	Value	Unit	References
E4	$H_{l,\mathrm{crit}}$	High temperature requirement of lignification	300	HU[a)]	8, 13
E4	T_{10}	Threshold air temperature	5	°C	8, 13
E7	$C_{\mathrm{crit}(d)}$	Chilling requirement of rest completion	28	CU[b)]	9
E7	T_{11}	Lower threshold air temperature	–13.8	°C	6, 8
E7	T_{12}	Optimum air temperature	–1.2	°C	6, 8
E7	T_{13}	Upper threshold air temperature	16.5	°C	6, 8
E10	a_5		0.11	$°C^{-1}$	6, 8
E10	b_5		37.6	°C	6, 8
E10	$H_{\mathrm{crit}(d)}$	High temperature requirement of growth onset	2.4	HU[a)]	6, 8
E10	T_{14}	Threshold air temperature	0	°C	6, 8
E13	$S_{o,\mathrm{crit}}$	Critical state of ontogenetic development for attaining zero hardening competence	187.5	-	8, 11
E16	T_{15}	Upper threshold air temperature	10	°C	1, 8
E16	T_{16}	Lower threshold air temperature	–16	°C	8, 10
E16	$\Delta H_{T\mathrm{max}}$	Maximum effect of air temperature on potential stationary frost hardiness	–47	°C	8, 10
E17	NL_1	Lower threshold night length	10	h	1, 8
E17	NL_2	Upper threshold night length	16	h	1, 8
E17	$\Delta H_{NL\mathrm{max}}$	Maximum effect of night length on potential stationary frost hardiness	–18.5	°C	2, 8, 10
E18	$S^s_{h,\mathrm{min}}$	Minimum stationary frost hardiness	–4.5	°C	8, 13
E19	τ	Time constant	5	Day	8, 14, 15
E20	t_0	Starting day of simulation	June 1	-	-
E22	α		–0.1435	$°C^{-1}$	8
E22	β		–1.4995	$°C^{-1}$	8
E22	γ		0.1071	$°C^{-1}$	8

References for the parameter values and the species represented by the values. Where no species is mentioned, the parameter value is for Scots pine.

1 Aronsson (1975)
2 Christersson (1978)
3 Hänninen (1990a) Generalized boreal species
4 Hari and Häkkinen (1991) *Betula* sp.
5 Koski and Sievänen (1985)
6 Kramer (1994b)
7 Landsberg (1974) *Malus domestica* Borkh.
8 Leinonen (1996a)
9 Leinonen (1996b)
10 Leinonen et al. (1996)
11 Leinonen et al. (1997)
12 Raulo and Leikola (1974)
13 Repo (1992)
14 Repo and Pelkonen (1986)
15 Repo et al. (1990)
16 Several boreal species Sarvas (1967)
17 Pooled data for several boreal species Sarvas (1972)
18 *Betula pubescens* Ehrhart Sarvas (1974)

[a)] High temperature unit of the model formulated in the corresponding equation.
[b)] Chilling unit of the model formulated in the corresponding equation

(A) E-models for the timing of bud burst and flowering

(Fixed-sequence development)

(A1) Air temperature response of the rate of ontogenetic development

Three alternative models:

(a) The piecewise linear 'day degree' model (Arnold 1959; Sarvas 1967)

$$R_o(t)=\begin{cases}0 & T(t)<T_1\\ \left[\dfrac{100}{H_{\mathrm{crit}(a)}}\right]\cdot\left[T(t)-T_1\right] & T(t)\geq T_1\end{cases} \tag{A1a}$$

(b) The exponential model (Hari et al. 1970)

$$R_o(t)=\left[\frac{100}{H_{\mathrm{crit}(b)}}\right]\cdot\left[a_1+b_1\exp(c_1T(t))\right] \tag{A1b}$$

(c) The sigmoidal model (Sarvas 1972; Hänninen 1990a)

$$R_o(t)=\begin{cases}0 & T(t)<T_2\\ \left[\dfrac{100}{H_{\mathrm{crit}(c)}}\right]\cdot\left[\dfrac{1}{1+\exp\left(-a_2\left(T\left(t\right)-b_2\right)\right)}\right] & T(t)\geq T_2\end{cases} \tag{A1c}$$

The state of ontogenetic development

$$S_o(t)=\int_{t_0}^{t}R_o(t)dt \tag{A2}$$

Bud burst/flowering, when

$$S_o(t)=100 \tag{A3}$$

(B) ES-models for the timing of bud burst and flowering

(Fixed-sequence development)

Air temperature response of the rate of rest break

Three alternative sub-models:

(a) The triangular sub-model (Sarvas 1974; Kramer 1994a)

$$R_r(t) = \begin{cases} 0 & T(t) < T_3 \\ \left[\dfrac{100}{C_{\text{crit}(a)}}\right] \cdot \left[\dfrac{T(t) - T_3}{T_4 - T_3}\right] & T_3 \le T(t) \le T_4 \\ \left[\dfrac{100}{C_{\text{crit}(a)}}\right] \cdot \left[\dfrac{T(t) - T_5}{T_4 - T_5}\right] & T_4 < T(t) \le T_5 \\ 0 & T(t) > T_5 \end{cases} \qquad \text{(B1a)}$$

(b) The plateau/exponential sub-model (Landsberg 1974)

$$R_r(t) = \begin{cases} \left[\dfrac{100}{C_{\text{crit}(b)}}\right] \cdot \left[\dfrac{1}{T_6}\right] & T < T_6 \\ \left[\dfrac{100}{C_{\text{crit}(b)}}\right] \cdot \left[\dfrac{1}{T(t)}\right] & T \ge T_6 \end{cases} \qquad \text{(B1b)}$$

(c) The step sub-model with rest break negation in high temperatures (Richardson et al. 1974)

$$R_r(t) = \begin{cases} 0 & T(t) < 1.4^\circ\text{C} \\ \left[\dfrac{100}{C_{\text{crit}(c)}}\right] \cdot 0.5 & 1.4^\circ\text{C} \le T(t) < 2.4^\circ\text{C} \\ \left[\dfrac{100}{C_{\text{crit}(c)}}\right] & 2.4^\circ\text{C} \le T(t) < 9.1^\circ\text{C} \\ \left[\dfrac{100}{C_{\text{crit}(c)}}\right] \cdot 0.5 & 9.1^\circ\text{C} \le T(t) < 12.4^\circ\text{C} \\ 0 & 12.4^\circ\text{C} \le T(t) < 15.9^\circ\text{C} \\ \left[\dfrac{100}{C_{\text{crit}(c)}}\right] \cdot (-0.5) & 15.9^\circ\text{C} \le T(t) < 18.0^\circ\text{C} \\ \left[\dfrac{100}{C_{\text{crit}3}}\right] \cdot (-1.0) & T(t) \ge 18.0^\circ\text{C} \end{cases} \qquad \text{(B1c)}$$

The state of rest break

$$S_r(t) = \int_{t_{\text{rest}}}^{t} R_r(t)dt \tag{B2}$$

Rest completion, when

$$S_r(t) = 100 \tag{B3}$$

Air temperature response of the potential rate of ontogenetic development

The same three alternative sub-models for $R_{o,\text{pot}}(t)$ as the three models for $R_o(t)$ in E-models: Eqs. (A1a), (A1b), and (A1c).

Dependence of ontogenetic competence on the state of rest break

Three alternative sub-models:

(a) The sub-model for abrupt rest completion (Sarvas 1972,1974; Hänninen 1990a)

$$C_o(t) = \begin{cases} 0 & S_r(t) < 100 \\ 1 & S_r(t) \geq 100 \end{cases} \tag{B4a}$$

(b) The sub-model for gradual rest completion (Landsberg 1974; Hänninen 1990a)

$$C_o(t) = \begin{cases} C_{o,\min} + \left[\dfrac{1 - C_{o,\min}}{100}\right] \cdot S_r(t) & S_r(t) < 100 \\ 1 & S_r(t) \geq 100 \end{cases} \tag{B4b}$$

(c) The sub-model for intermediate rest completion (Hänninen 1990a)

$$C_o(t) = \begin{cases} 0 & S_r(t) < S_{r*} \\ \dfrac{S_r(t) - S_{r*}}{100 - S_{r*}} & S_{r*} \leq S_r(t) < 100 \\ 1 & S_r(t) = 100 \end{cases} \tag{B4c}$$

The rate of ontogenetic development (Hänninen 1990a,1995; Kramer 1994a,b)

$$R_o(t) = C_o(t) \cdot R_{o,\text{pot}}(t) \tag{B5}$$

The state of ontogenetic development

$$S_o(t) = \int_{t_{\text{rest}}}^{t} R_o(t)\,dt \tag{B6}$$

Bud burst/flowering, when

$$S_o(t) = 100 \tag{B7}$$

(C) The first-order model of frost hardiness

(Fluctuating development, modified from Repo et al. 1990)

Stationary frost hardiness

$$S_h^s(t) = \begin{cases} a_3 \cdot T_{\min}(t) + b_3 & T_{\min}(t) \leq T_7 \\ a_3 \cdot T_7 + b_3 & T_{\min}(t) > T_7 \end{cases} \tag{C1}$$

The rate of change of frost hardiness

$$R_h(t) = \frac{1}{\tau}\left(S_h^s(t) - S_h(t)\right) \tag{C2}$$

The state of frost hardiness

$$S_h(t) = \int_{t0}^{t} R_h(t)\,dt \tag{C3}$$

(D) The second-order model of frost hardiness

(Fluctuating development, simplified from Leinonen et al. 1995)

Stationary frost hardiness

$$S_h^s(t) = \begin{cases} a_4 \cdot T_{\min}(t) + b_4 & T_{\min}(t) \leq T_8 \\ a_4 \cdot T_8 + b_4 & T_{\min}(t) > T_8 \end{cases} \tag{D1}$$

The rate of change of asymptotic frost hardiness

$$R_h^a(t) = \frac{1}{\tau_2}\left(S_h^s(t) - S_h^a(t)\right) \tag{D2}$$

Asymptotic frost hardiness

$$S_h^a(t) = \int_{t0}^{t} R_h^a(t)\,dt \tag{D3}$$

The rate of change of frost hardiness

$$R_h(t) = \frac{1}{\tau_1}\left(S_h^a(t) - S_h(t)\right) \tag{D4}$$

The state of frost hardiness

$$S_h(t) = \int_{t0}^{t} R_h(t)\,dt \tag{D5}$$

(E) The integrated model of frost hardiness

(Adopted from Leinonen 1996). Parameter values are for needles of central Finnish *Pinus sylvestris*.

The model for annual ontogenetic development

The model for active growth phase

The rate of active growth

$$R_a(t) = \begin{cases} 0 & T(t) < T_9 \\ \left[\dfrac{100}{H_{a,\mathrm{crit}}}\right] \cdot \left[T(t) - T_9\right] & T(t) \geq T_9 \end{cases} \tag{E1}$$

The state of active growth

$$S_a(t) = \int_{t_{\mathrm{act}}}^{t} R_a(t)\,dt \tag{E2}$$

At the initialization of the simulations, the onset date of active growth, t_{act}, is replaced by the starting day of simulation, t_0 (i.e., $t_{\mathrm{act}} = t_0$, see Eq. (E20)). After that, t_{act} is obtained from Eq. (E12).

Height growth cessation and onset of lignification, t_{lign}, when

$$S_a(t) = 100 \tag{E3}$$

The model for the lignification phase

The rate of lignification

$$R_l(t) = \begin{cases} 0 & T(t) < T_{10} \\ \left[\dfrac{100}{H_{l,\mathrm{crit}}}\right] \cdot \left[T(t) - T_{10}\right] & T(t) \geq T_{10} \end{cases} \tag{E4}$$

The state of lignification

$$S_l(t) = \int_{t_{\text{lign}}}^{t} R_l(t)dt \tag{E5}$$

The onset of lignification, t_{lign}, from Eq. (E3). Cessation of lignification and the onset of rest, t_{rest}, when

$$S_l(t) = 100 \tag{E6}$$

The model for the rest phase

The rate of rest break

$$R_r(t) = \begin{cases} 0 & T(t) < T_{11} \\ \left[\dfrac{100}{C_{\text{crit}(d)}}\right] \cdot \left[\dfrac{T(t) - T_{11}}{T_{12} - T_{11}}\right] & T_{11} \leq T(t) \leq T_{12} \\ \left[\dfrac{100}{C_{\text{crit}(d)}}\right] \cdot \left[\dfrac{T(t) - T_{13}}{T_{12} - T_{13}}\right] & T_{12} < T(t) \leq T_{13} \\ 0 & T(t) > T_{13} \end{cases} \tag{E7}$$

The state of rest break

$$S_r(t) = \int_{t_{\text{rest}}}^{t} R_r(t)dt \tag{E8}$$

The onset of rest, t_{rest}, from Eq. (E6). Rest completion and the onset of quiescence, t_{quie}, when

$$S_r(t) = 100 \tag{E9}$$

The model for quiescence

The rate of ontogenetic development

$$R_o(t) = \begin{cases} 0 & T(t) < T_{14} \\ \left[\dfrac{100}{H_{\text{crit}(d)}}\right] \cdot \left[\dfrac{1}{1 + \exp\left(-a_5\left(T\left(t\right) - b_5\right)\right)}\right] & T(t) \geq T_{14} \end{cases} \tag{E10}$$

The state of ontogenetic development

$$S_o(t) = \int_{t_{\text{quie}}}^{t} R_o(t)dt \tag{E11}$$

Initiation of quiescence, t_{quie}, from Eq. (E9). The onset of active growth, t_{act}, when

$$S_o(t) = 100 \tag{E12}$$

The model for the annual cycle of frost hardiness

Hardening competence, C_h, during quiescence and active growth

$$C_h(t) = \max\left[1 - \frac{S_o(t)}{S_{o,\text{crit}}}, 0\right] \tag{E13}$$

In order to use Eq. (E13), $S_o(t)$ is calculated also after it has reached the value 100, indicating the start of the active growth phase, until the critical value $S_{o,\text{crit}}$ is attained.

Hardening competence, C_h, during lignification

$$C_h(t) = \frac{S_l(t)}{100} \tag{E14}$$

Hardening competence, C_h, during rest

$$C_h(t) = 1 \tag{E15}$$

Effect of air temperature on potential stationary frost hardiness, ΔH_T

$$\Delta H_T(t) = \begin{cases} \Delta H_{T\max} & T_{\min}(t) < T_{16}, \\ \left[\dfrac{\Delta H_{T\max}}{T_{16} - T_{15}}\right] \cdot \left[T_{\min}(t) - T_{15}\right] & T_{16} \le T_{\min}(t) \le T_{15}, \\ 0 & T_{\min}(t) > T_{15} \end{cases} \tag{E16}$$

Effect of night length on potential stationary frost hardiness, ΔH_{NL}

During decreasing night length:

$$\Delta H_{NL}(t) = \begin{cases} \Delta H_{NL\max} & NL(t) > NL_2, \\ \left[\dfrac{\Delta H_{NL\max}}{NL_2 - NL_1}\right] \cdot \left[NL(t) - NL_1\right] & NL_1 \le NL(t) \le NL_2, \\ 0 & NL(t) < NL_1 \end{cases} \tag{E17}$$

During increasing night length:

$$\Delta H_{NL}(t) = \Delta H_{NL\max}$$

Stationary frost hardiness, S_h^s

$$S_h^s(t) = S_{h,\min}^s + C_h(t) \cdot \left[\Delta H_T(t) + \Delta H_{NL}(t)\right] \tag{E18}$$

The rate of change of frost hardiness

$$R_h(t) = \frac{1}{\tau}\left[S_h^s(t) - S_h(t)\right] \tag{E19}$$

The state of frost hardiness

$$S_h(t) = \int_{t0}^{t} R_h(t)dt \tag{E20}$$

The model for annual needle damage

Daily index of injury (proportion of damaged needles), I

$$I(t) = \frac{1}{1 + \exp\left[b_6 \cdot \left(S_h(t) - T_{\min}(t)\right)\right]} \tag{E 21}$$

where the slope parameter b_6 is calculated as follows:

$$b_6(t) = \alpha + \beta \cdot \exp\left(\gamma \cdot S_h(t)\right) \tag{E22}$$

The maximum of the daily values of *I(t)* is selected for the annual needle loss due to frost damage.