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Effects of temperature on dormancy release in woody plants: implications of prevailing models

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Logical structure of three simulation models and one conceptual model concerning effects of temperature on dormancy release in woody plants was examined. The three basic types of simulation models differed in their underlying assumptions. Contrasting implications of the models were inferred by deduction. With the aid of these implications, the model types can be tested using experiments with continuous and interrupted chilling. Similarly, implications of the conceptual model of rest phases were inferred, by which the model can be tested using experiments with continuous chilling and forcing in multiple temperatures. The possibilities to synthetizize the conceptual model with any of the three simulation model types, as well as the biological interpretation of the model variables, were discussed.

Työssä tutkittiin lämpötilan vaikutuksia puiden dormanssin purkautumisessa kuvaavien mallien loogista rakennetta. Yksi malleista on sanallinen, muut kolme ovat simulointimalleja. Simulointimallit edustivat kolmea tyyppiä, jotka eroavat toisistaan lähtöoletuksiensa suhteen. Simulointimalleista johdettiin toisilleen vastakkaisia seuraamuksia, joiden avulla malleja voidaan testata käyttäen erilaisia yhtäjaksoisia tai katkaistuja kylmäkäsittelyjä. Vastaavasti johdettiin lepovaiheen osavaiheita koskevan sanallisen mallin seuraamuksia, joiden avulla mallia voidaan testata käyttäen yhtäjaksoisia kylmäkäsittelyitä ja useita hyötämislämpötiloja. Lopuksi pohdittiin mallisuureiden biologista tulkintaa ja mahdollisuuksia kokonaisvaltaisen synteesin luomiseen malleista.

Keywords: annual cycle of development, bud burst, chilling requirement, rate of development, rest period, simulation models, stage of development
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1. Introduction

In the buds of woody plants, periods of active growth and dormancy generally alternate with each other. This phenomenon has given rise to many contrasting nomenclatures (eg. Doorenbos 1953, Leike 1965, Sarvas 1974, Wareing and Phillips 1978, pp. 254–256, Fuchigami et al. 1982). According to the nomenclature adopted in this study (Romberger 1963, pp. 73–76, Table 1), the concept of ”dormancy” is used in a broad sense of the word. It refers to any non-growing bud, regardless of the reason of the inactivity. Consequently, the concept ”dormancy release” is used in any case, where a previously dormant bud begins to grow. The concept ”rest” is used with special meaning. It refers to a specific physiological condition of the bud, which arrests growth regardless of the prevailing environmental conditions. Consequently, the term ”rest break” is used when referring to the removal of the growth arresting physiological conditions.

Buds of many woody plant species of the cool and temperate zones attain during autumn a state of rest. Thus, the buds will not grow at that time, even if the environmental factors were favourable for growth. In natural conditions, rest is normally broken by prolonged exposure to low temperatures. Temperatures slightly above zero have been found to be most effective (Erez and Lavee 1971, Sarvas 1974). This chilling requirement of rest break of woody plants has been documented for a great number of species (eg. Doorenbos 1953, Romberger 1963, pp. 157–161, Flint 1974). After rest break, high temperatures are required for bud burst. Thus, the buds remain usually dormant in temperate and cool climate for a long period of time after rest break has taken place.

Various models have been proposed in order to approach the role of the rest period as a part of the annual cycle (Vegis 1964, Sarvas 1972, 1974, Richardson et al. 1974, Landsberg 1974). The role of temperature in breaking the rest has been of particular interest. Descriptive models are the oldest types, but lately, also operational simulation models have been presented. Simulation models facilitate predictions concerning the bud phenology of a given tree genotype in a given climate, and thus serve as helpful tools in many fields of practical horticulture and forestry.

The prevailing models of dormancy release are in many respect contradictory to each other. An analysis of the logical structure of the models, however, is required, before the models can be experimentally tested. The purpose of this study is 1) to analyse and compare the logical structure of the prevailing models of temperature effects on dormancy release of woody plants native to the cool and temperate regions, and 2) to infer implications from the models, by which they can be experimentally tested.

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2. Deduction of the implications of models of dormancy release for experimental testing

2.1 General principle of simulation models of dormancy release

In most simulation models of plant development, the following assumptions are essential (see Hari 1968, 1972, Robertson 1968, 1973, Sarvas 1972, 1974): 1) At a given moment, the developmental stage of the plant is described by the numerical value of one variable. I will refer to this variable by the con-

Table 1. Main concepts and symbols used in the study.

Symbol	Concept	Explanation
	Dormancy	A state of a non-growing bud. In many cases, the bud has a potential to grow in favourable environmental conditions
	Dormancy release	An event, when a previously dormant bud starts to grow
	Rest	A special case of dormancy: growth of the bud is arrested due to physiological conditions inside the bud. The bud has no potential to grow even in favourable environmental conditions
	Rest break	Removal of the growth arresting conditions inside the bud
s	Stage of development	A variable, which describes numerically the phase of the annual cycle attained by a plant
M	Rate of development	A variable, which describes the rapidity of change of stage of development
f		A function describing the dependence of the rate of development on temperature
CU	Chilling unit	A unit of modelled effect of low temperatures to rest break
CU sum	Chilling unit sum	A variable describing the cumulative effects of low temperatures to rest break
FU	Forcing unit	A unit of modelled effect of high temperatures to dormancy release
FU sum	Forcing unit sum	A variable describing the cumulative effects of high temperatures to dormancy release
CH_1		Duration of first chilling period in an interrupted chilling treatment
CH_2		Duration of second chilling period in an interrupted chilling treatment
CH_{tot}		Total duration of chilling in an interrupted chilling treatment
W		Duration of an intermittent warm period in an interrupted chilling treatment
CH_{ef}		Effective duration of chilling in an interrupted chilling treatment
CH_{min}		Minimum duration of chilling, after which dormancy release occurs at least for one of the plants of a treatment group
CH_{max}		Minimum duration of chilling, after which dormancy release occurs for all of the plants of a treatment group
DRR	Dormancy release ratio	In a treatment group the proportion of the plants, for which dormancy is released, of all of the plants of the group
DRR_1		The value of dormancy release ratio in an interrupted chilling treatment after first chilling period
DRR_2		The value of dormancy release ratio in an interrupted chilling treatment after second chilling period
DBB	Days to bud burst	Time required to bud burst counted from the beginning of the forcing period
$\overline{DBB}$	Mean days to bud burst	Mean time required to bud burst counted from the beginning of the forcing period. Calculated for those plants of a treatment group, which burst bud

Table 1 cont.

Symbol	Concept	Explanation
$\overline{DBB}_{int}$		Mean days to bud burst in an interrupted chilling treatment group
Model type I_A	A sequential, non-reversible model of dormancy release	Dormancy release is simulated by the accumulation of a chilling unit sum, and a subsequential accumulation of a forcing unit sum. High temperatures have no effect to the chilling unit sum accumulated previously
Model type I_B	A sequential, reversible model of dormancy release	Dormancy release is simulated by the accumulation of a chilling unit sum, and a subsequential accumulation of a forcing unit sum. High temperatures diminish the chilling unit sum accumulated previously
Model type II	A parallel model of dormancy release	Dormancy release is simulated by parallel accumulation of a chilling unit sum and forcing unit sum. Accumulated chilling unit sum affects the rate of accumulation of the forcing unit sum
Critical CU sum	Critical chilling unit sum	A chilling unit sum, at the attainment of which the forcing unit sum begins to be accumulated (model types I_A and I_B)
Sufficient CU sum	Sufficient chilling unit sum	A chilling unit sum, after the attainment of which further accumulation of the chilling unit sum does not affect the rate of accumulation of the forcing unit sum (model type II)
Critical FU sum	Critical forcing unit sum	A forcing unit sum, at the attainment of which bud burst occurs

cept *stage of development,* and use the denotation s for it. 2) The first time derivative of s gives the rate at which the stage of development of the plant is changing. I will refer to this rate by the concept *rate of development,* and use the denotation M for it. 3) The rate of development at a given moment depends on the environmental factors prevailing at that moment.

In the simulation models considered in this study, temperature is the only environmental factor taken into account. Thus, the assumptions outlined above can be presented mathematically as follows (Hari 1972):

$$M(t) = f(T(t))$$
$$s(t) = \int_0^t M(\tau)\, d\tau \qquad (1)$$

where M(t), s(t) and T(t) give the values of the rate of development, stage of development, and temperature, respectively, at the moment t. Function f gives the dependence of the rate of development on temperature. In practical calculations, mean temperatures of short time intervals (eg. one hour) are used. Then the integration of equation (1) is carried out numerically by summing the corresponding mean values of M.

In the models of dormancy release, two types of variables are used in describing the rate of development M, and the stage of development s. 1) The effects of low temperatures on the break of rest are modelled by assuming M to have positive values in low temperatures, eg. between 0 and 10°C. The unit for these values of M is referred to as a chilling unit (CU). Correspondingly, the quantity used in describing the stage of development is referred to as a chilling unit sum (CU sum) (Sarvas 1974). 2) The effects of high temperatures on dormancy release are modelled by assuming that M increases with increasing temperatures. The unit for these values of M is referred to as a forcing unit (FU), and the corresponding quantity for s is referred to as a forcing unit sum (FU sum).

In the following hypothetical experiments two temperatures are applied. 1) A low above-0° temperature, in which chilling units are assumed to be accumulated, but not forcing units, and 2) a high temperature, in which forcing units are assumed to be accumulated, but not chilling units.

2.2 Experimental designs for testing the models

The experiments designed for the study of the chilling requirement of rest break are usually initiated during early autumn. At that time the plants have completed their active growth phase, but have not been exposed considerably to temperatures below +10°C. The classical experiment consists of two sequential parts (continuous chilling experiment, Fig. 1a). First, the plants of each treatment group are given a *chilling treatment.* The duration of the treatment is varied among the treatment groups. In the basic type of experiment, a constant temperature common to all of the treatment groups is maintained during the chilling treatments. Then, after the chilling period the plants of the group are transferred to warm *forcing* conditions, where a regrowth test is carried out by determining if the observed buds begin to grow, or not, and what is the date of starting. The purpose of the regrowth test is to measure the rest status of the plants at the time of the transfer. Thus, dormancy release during the forcing period is used as an indicator of rest break, which has taken place during the previous chilling period.

In a variant of the continuous chilling experiment, two or more treatment groups for each duration of chilling are established, and each of them is forced in a specific temperature (continuous chilling experiment with multiple forcing temperatures). In this way, both the duration of chilling, and temperature prevailing during the forcing period are varied among the treatment groups.

Interrupting the chilling period with one or more intermittent warm periods offers another possibility for testing the models (interrupted chilling experiment, Fig. 1b). The basic interrupted chilling treatment consists of three parts: first chilling period (length CH_1 days), intermittent warm period (length W days), and second chilling period (length CH_2 days). The timing and duration of the interruption, and the temperature prevailing during it can be varied between the treatment groups, within each total duration of chilling.

Two indicators are currently used for analysing the results of the chilling experiments. First, the proportion of those plants which begin to grow is calculated for each treatment group (Sarvas 1974). I will refer to this ratio by the denotation DRR (dormancy release ratio). Second, the number of days between the dates of transfer to the forcing conditions and bud burst is counted for each plant (eg. Lamb 1948, Worrall and Mergen 1967). I will refer to this quantity by the denotation DBB (days to bud burst). If a plant does not burst bud in the forcing conditions, the value of DBB is infinite for it. If only part of the plants of a given treatment group burst bud, then the value of mean DBB ($\overline{DBB}$) of the group is calculated according to the finite

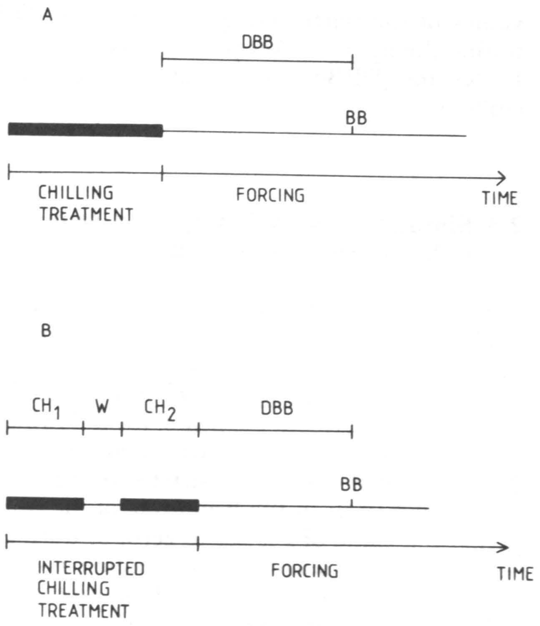


Fig. 1. Experimental designs for testing the models represented. (A) A continuous chilling experiment, and (B) an interrupted chilling experiment, both with regrowth test in forcing conditions. Thick line indicates a low (chilling) temperature, and thin line a high (forcing) temperature. BB = time instant of bud burst, DBB = time required to bud burst counted from the beginning of the forcing period, CH_1, CH_2 and W = durations of the first and second chilling period, and the intermittent warm period, respectively. Only one treatment shown for both types of experiments.

values of the particular group. In all cases, testing the models takes place by plotting the DRR- and $\overline{\text{DBB}}$-values against duration of chilling.

2.3 Simulation model type I_A: a sequential, non-reversible model

Sarvas (1972, 1974) presented a simulation model for the whole annual cycle of the trees of the cool and temperate regions (for a brief decription of the model, see Hänninen et al. 1985). For the present purposes, the following assumptions of the model are essential (Fig. 2a): 1) the rest period has strict starting and ending points; 2) in the beginning of the rest period the value of s is set to zero; 3) during rest period, the stage of development is described by the accumulated chilling unit sum (CU sum): the dependence of the rate of development M on temperature T is modelled by a convex function, which has its maximum value at +3.5°C, and the value of zero in temperatures lower than −3.5°C and higher than +10.5°C; 4) rest period comes to an end when s attains a critical value specific to the genotype (critical CU sum); 5) at the end of the rest period the value of s is set again to zero, and the stage of development is subsequently described by the accumulation of a forcing unit sum (FU sum): the function f is changed to a sigmoidal one; 6) bud burst occurs, when s subsequently attains another critical value (critical FU sum).

Consider the behaviour of the model in the case of an individual plant and continuous chilling (Fig. 3). In the constant low temperature conditions, the chilling unit sum (CU sum) increases with a constant rate. When the temperature is raised to the forcing temperature, then no more accumulation of the CU units takes place. If the temperature is raised before the attainment of the critical CU sum, then no forcing units are subsequently accumulated (Fig. 3a). In that case the critical FU sum is not attained, and no bud burst occurs. If the temperature is raised at, or after the attainment of the critical CU sum, then the FU sum begins to increase in the high temperature conditions at a constant rate (Fig. 3b,c). Thus, the critical FU sum will be reached, and bud burst will occur.

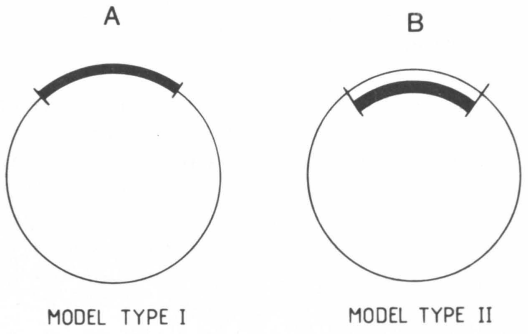


Fig. 2. Main simulation model types considered in the study. (A) A sequential model type. Development is simulated by the accumulation of a chilling unit sum during the rest period, and by the accumulation of a forcing unit sum after the end point of the rest period (Sarvas 1972, 1974, Richardson et al. 1974). (B) A parallel model type. Development is simulated all the time by the accumulation of a forcing unit sum. During rest period, the rate of accumulation of the forcing unit sum is affected also by the amount of the previously accumulated chilling unit sum (Landsberg 1974). Thin line: accumulation of a forcing unit sum, thick line: accumulation of a chilling unit sum. Rest period is indicated with bars in both (A) and (B).

In practice, the experiments are carried out at population level ie. each treatment group consists of several plants forming a sample of the whole population. Thus, genetical variation in the value of the critical CU sum may affect the results implicated by the model. During a chilling period shorter than a specific minimum, the critical CU sum is not attained for any of the plants. During successively longer periods of chilling, the critical CU sum is attained for an increasing part of the population. During a chilling period longer than a specific value, the critical CU sum is attained for the whole population. A similar pattern is expected in the subsequent values of dormancy release ratio DRR (Fig. 4a, Table 2), because according to model type I_A, rest break in the chilling conditions is always followed by dormancy release in the forcing conditions.

According to model type I_A, no sum is accumulated, when the low temperature conditions are sustained after the attainment of the critical CU sum of a given plant (Fig. 3c). Thus, duration of the chilling does not affect the value of DBB of the plant (cf. Figs. 3b,c). Accordingly, in an experiment at the population level, the mean value of DBB ($\overline{\text{DBB}}$) is independent from duration of the chilling (Fig. 4b, Table 2).

Consider the behaviour of the model in the case of an individual plant and interrupted chilling (Fig. 5). The interruption does not alter the amount of CU sum accumulated during a treatment period of a given total duration of *chilling* (cf. Figs. 3b and 5a). Thus, the interrupting period does not make any difference, whether a given plant attains its critical CU sum or not. Accordingly, in the experiment at the population level, the DRR values of the interrupted treatment groups are identical to those of the continuous groups with the same total duration of chilling (Fig. 4c, Table 2).

If the interruption occurs before the attainment of the critical CU sum of a given plant, the no forcing units are accumulated during it (Fig. 5a). Thus in this case, the value of DBB will be similar to that of the corresponding continuous treatment (cf. Figs. 3b and 5a). However, if the interruption takes place after the attainment of the critical CU sum of the plant, the FU sum begins to be accumulated during the intermittent warm period (Fig. 5b). As a result, the time required to bud burst in the forcing conditions is shortened by the length of the intermittent period, when compared with the corresponding continuous treatments (Figs. 3c and 5b).

In the case of the experiment at the population level, variation in the value of the critical CU sum among the individuals affects the implications of the model. Consider a case, when the interruption occurs after shorter duration of chilling than CH_{min} (see Fig. 4a). Then the critical CU sum has not yet been accumulated for any of the plants, and thus no forcing units are accumulated for any of them. As a result, the intermittent warm period does not affect in this case the mean time required to bud burst in the forcing conditions (Fig. 4 d, Table 2).

Consider a case, when the interruption occurs after a longer duration of chilling than CH_{max} (see Fig. 4a). In that case, the critical CU sum has been accumulated for all of the plants, so the FU sum begins to be accumulated for all of them during the intermittent

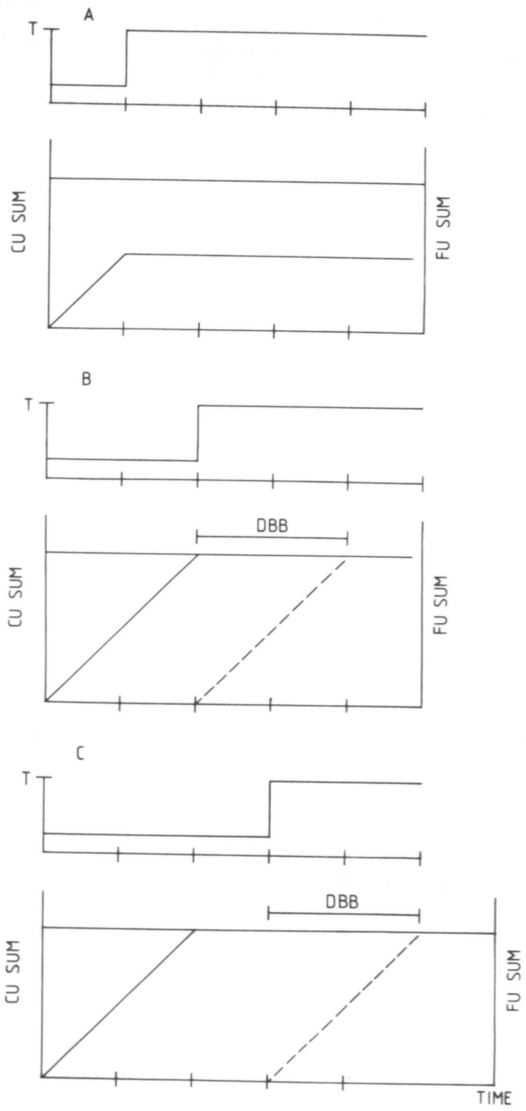
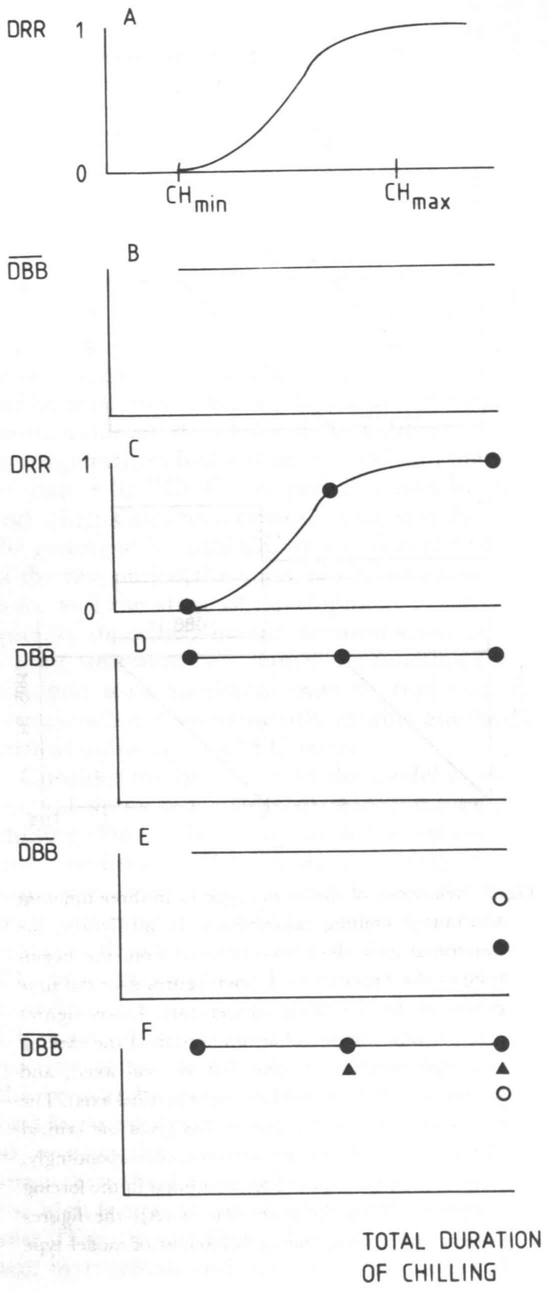


Fig. 3. Behaviour of the model type I_A in three different continuous chilling experiments. In all figures, the horizontal axis gives time counted from the beginning of the experiment. Upper figures give the time course of the prevailing temperature. Lower figures give the time courses of accumulation of the chilling unit sum (continuous line, left vertical axis), and forcing unit sum (dotted line, right vertical axis). The line parallel to the horizontal axis gives the critical chilling unit and forcing unit sums, correspondingly. DBB is the time required for bud burst in the forcing conditions. With the exception of (A), the figures present also corresponding behaviour of model type I_B.

warm period. In consequence, the bud burst of the plants of the interrupted chilling group requires less time in the forcing conditions than those of the continuous chilling group. The time difference is equal to the length of the intermittent warm period (Fig. 4 e, Table 2).



Consider finally a case, when the interruption occurs when the duration of previous chilling is longer than CH_{min}, but shorter than CH_{max} (see Fig. 4a). In that case, the FU sum begins to be accumulated for those plants, which have already attained their critical CU sum. They will behave similarly to the plants in the case, when the interruption occurred after the time instant CH_{max}: the DBB-values for them are smaller than those for the plants of the corresponding continuous treatment. The proportion of those plants increases from zero to hundred per cent, as the timing of the beginning of the interruption is delayed from CH_{min} to CH_{max}. Thus, the $\overline{DBB}$-values will decline accordingly (Fig. 4f, Table 2).

2.4 Simulation model type I_B: a sequential, reversible model

Richardson et al. (1974) presented a simulation model for the dormancy release of

Fig. 4. Implications of the model type I_A about the values of dormancy release ratio DRR, and mean days to bud burst $\overline{DBB}$ as a function of the duration of the chilling period. The curve denotes in all cases results with continuous chilling. (A) DRR, continuous chilling. CH_{min}, CH_{max} = minimum and maximum chilling requirements in the population. (B) $\overline{DBB}$, continuous chilling. (C) DRR, interrupted (circles) vs. continuous chilling. (D) $\overline{DBB}$, interrupted (circles) vs. continuous chilling, the intermittent warm period began before time instant CH_{min}. (E) $\overline{DBB}$, interrupted (circles) vs. continuous chilling, the intermittent warm period began after time instant CH_{max}. Duration of the intermittent warm period one third (open circle) or two thirds (hatched circle) of the $\overline{DBB}$-value obtained after corresponding continuous treatment. (F) $\overline{DBB}$, interrupted (circles, triangles) vs. continuous chilling. The intermittent warm period began at time instant CH_{min} (hatched circles), between time instants CH_{min} and CH_{max} (triangles), or at time instant CH_{max} (open circle). Duration of the intermittent warm period is one third of the $\overline{DBB}$-value obtained after corresponding continuous treatment. With the exception of (C), the figures present also corresponding implications of model type I_B.

Table 2. Implications of the three simulation model types concerning outcomes of continuous and interrupted chilling experiments. In the case of all interrupted treatments it is assumed that, the temperature prevailing during the intermittent warm period is similar to that prevailing during the forcing period. DRR = dormancy release ratio, $\overline{DBB}$ = mean days to bud burst, CH_{min} gives the minimum duration of chilling, after which dormancy is released at least for one plant of the treatment group, and CH_{max} the minimum duration of chilling, after which dormancy is released for all of the plants of the treatment group.

Experiment, indicator	Model type I_A	Model type I_B	Model type II
Continuous chilling, DRR as a funcion of duration of chilling	Increases from zero to unity with increasing duration of chilling	As in model type I_A	Unity for all durations of chilling
Continuous chilling, $\overline{DBB}$ as a function of duration of chilling	Independent from duration of chilling	As in model type I_A	Decreases exponentially with increasing duration of chilling
Interrupted vs. continuous chilling, DRR at each level of chilling	Identical for both treatments	Generally smaller for interrupted treatments (see Appendix 1)	Unity for both treatments
Interrupted vs. continuous chilling, $\overline{DBB}$ at each level of chilling	1) Beginning of the intermittent period before time instant CH_{min}:		Smaller for the interrupted treatments
	Identical for both treatments	Identical for both treatments, or a finite value in the continuous, and infinite value in the interrupted treatment	The difference increases as the intermittent period is delayed
	2) Beginning of the intermittent period after time instant CH_{max}:		The maximum difference is equal to the length of the intermittent period (see Appendix 2)
	Smaller for the interrupted treatments. The difference is equal to the length of the intermittent period	As in model type I_A	
	3) Beginning of the intermittent period after time instant CH_{min}, but before time instant CH_{max}:		
	Smaller for the interrupted treatments. The difference increases from zero at CH_{min} to the length of the intermittent period at CH_{max}	As in model type I_A	

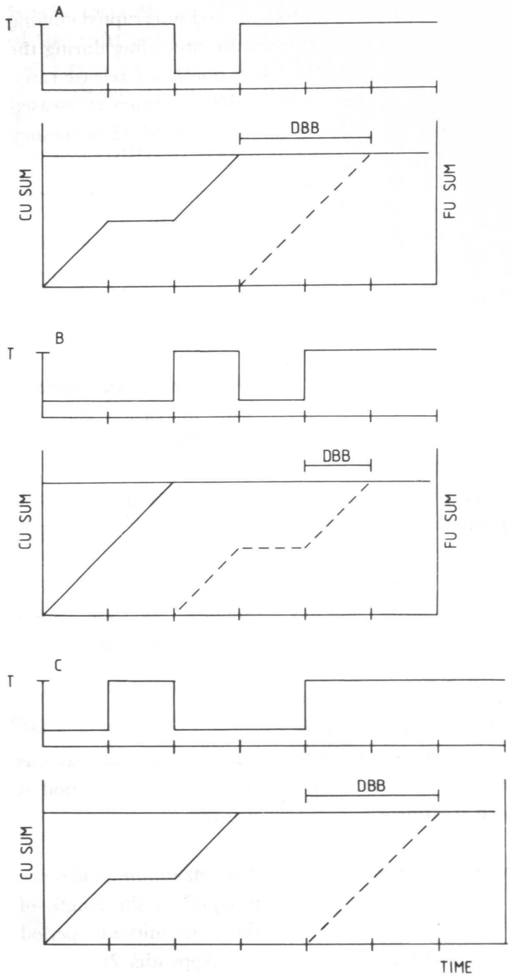


Fig. 5. Behaviour of the model type I_A in three different interrupted chilling experiments. See Fig. 3 for explanation.

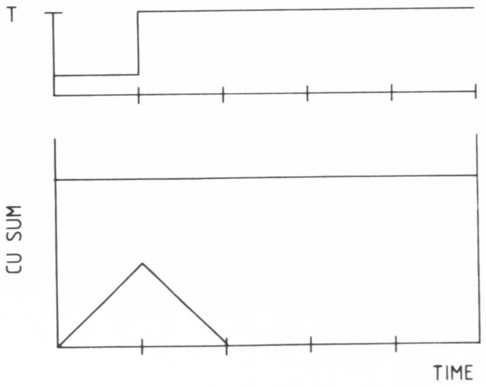


Fig. 6. Behaviour of the model type I_B in one continuous chilling experiment. See Fig. 3 for explanation.

peach (*Prunus persica*). The logical structure of the model is otherwise corresponding to that of the model of Sarvas (1972, 1974) (Fig. 2a), but in this model the function f has negative values in high temperatures during rest period. Thus before the attainment of the critical CU sum, high temperatures diminish the CU sum accumulated before. In the model, one hour in high temperature deletes the chilling effect of one hour in a low temperature.

Consider the behaviour of the model in the case of an individual plant and continuous chilling. The only difference between the model types I_A and I_B occurs, when the temperature is increased before the attainment of the critical CU sum (Figs. 3 and 6). According to model type I_B, the CU sum begins to decline after the temperature change (Fig. 6), while model type I_A implies that it remains constant (Fig. 3a). However, no FU will be accumulated in either cases. In this way, both models suggest that the plant will remain dormant, so the implications of the model type I_B as regards experiments at the population level with continuous chilling are identical to those of model type I_A (Fig. 4a,b, Table 2).

Consider the behaviour of the model in the case of an individual plant and interrupted chilling (Fig. 7). If the interruption occurs before the attainment of the critical CU sum, then the CU sum declines during the interruption. It is possible that the diminished CU sum in the interrupted treatment is not large enough to reach the critical CU sum of the plant (Fig. 7a), while the undiminished CU sum of the corresponding continuous treatment attains the critical value (Fig. 3b). Thus at the population level experimentation, the intermittent warm period generally diminishes the value of DRR, when compared with the corresponding continuous treatments (Fig. 8, Table 2, see Appendix 1 for the calculation of the value of DRR).

Assume that in the case of an individual plant and interrupted chilling, the critical CU sum of the plant was attained in spite of the interruption. This being so, the behaviour of the model as regards DBB is identical to the behaviour of model type I_A. When the chilling period is interrupted before the attainment of the critical CU sum, then according to both models, no accumulation of FU takes place during the interruption and time intervals of equal lengths in the forcing conditions are required to bud burst (cf. Figs. 5c,7b). Similarly, if the interruption takes place after the attainment of the critical CU sum, then there is again no difference between the models: FU units are accumulated during the intermittent warm period at an equal rate according to both models. Subsequently, the value of DBB is decreased in a similar manner according to both of the models, compared with the corresponding continuous treatment.

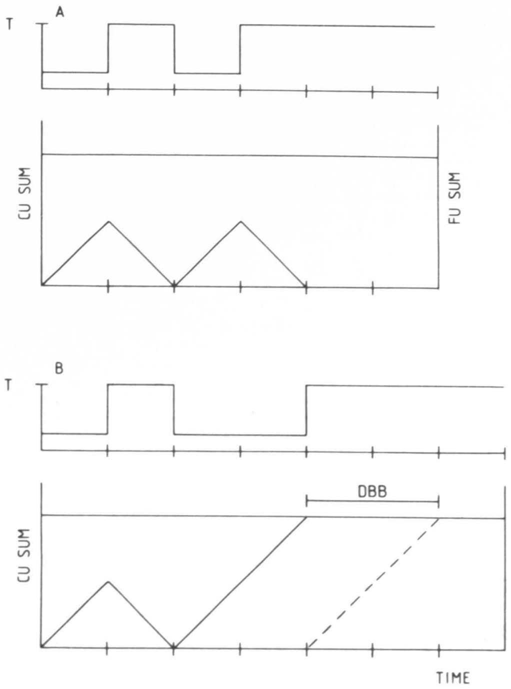


Fig. 7. Behaviour of the model type I_B in two different interrupted chilling experiments. See Fig. 3 for explanation.

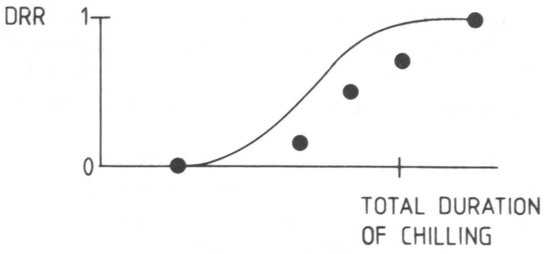


Fig. 8. Implication of the model type I_B about the values of dormancy release ratio DRR as a function of the duration of the chilling period. The curve denotes results with continuous chilling, and the circles results with interrupted chilling.

Also in an experiment at the population level, model type I_B implicates similar results as model type I_A, as regards of the value of $\overline{\text{DBB}}$ in an interrupted chilling treatment (Figs. 4d-f, Table 2). There is, however, one exception to this rule. When the intermittent warm period begins before time instant CH_{min} (see Fig. 4a), it is possible that the reduced amount of effective chilling in the interrupted treatment is not large enough to attain the critical CU sum of any of the plants, while the unreduced amount of the continuous treatment attains the critical CU sum for at least one of the plants. This being so, a finite value of $\overline{\text{DBB}}$ is obtained for the continuous group, while the value for the interrupted group is infinite (Table 2).

2.5 Simulation model type II: a parallel model

Landsberg (1974) simulated apple fruit bud development in a way differing from the approach of Sarvas (1972, 1974) and Richardson et al. (1974). In his model (Fig. 2b), no strict end point of the rest period, where the form of f abruptly changes, is calculated. Rather, the effect of chilling on the rate of accumulation of the FU sum is assumed to be gradual. This assumption is incorporated to the model by the following logical structure: 1) The stage of development is described by the accumulated FU sum all the time; 2) in addition to the FU sum, also a CU sum is calculated during rest period; 3) the rate of development M (ie. increment in the FU sum) increases with increasing temperature; 4) during rest period, the rate of development M is also dependent on the value of the CU sum accumulated before: the value of M in any given temperature increases to a certain limit with increasing CU sum. When a certain value of CU sum (sufficient CU sum) is attained, then the rate of development is regulated by prevailing temperature alone; 5) bud burst occurs, when s attains a critical value (critical FU sum).

Consider the behaviour of the model in the case of an individual plant and continuous chilling (Fig. 9). The FU sum begins to accumulate, whenever the temperature is high, thus, the critical FU sum will be attained, and the plant will burst bud in all cases. However, the rate of accumulation of the FU sum depends on the length of the previous chilling period. When the temperature is raised early, the subsequent rate of accumulation of FU sum is low, and a long forcing time will be required to bud burst (Fig. 9a). When the length of the chilling period is increased, the subsequent rate of the accumulation of the FU sum increases, and a shorter time will be required to bud burst (Fig. 9b). After the attainment of a specific CU sum (sufficient CU sum), the rate of accumulation of the FU sum can not be further increased by increasing the length of the chilling period. This being so, the time required for bud burst will stay unaltered (Figs. 9b,c).

In the experiments at the population level, all plants will attain their critical FU sum. Thus, DRR has the value of unity in all experiments with continuous treatments (Fig. 10a, Table 2). Correspondingly in the case of all of the plants, the rate of the accumulation of the FU sum increases to a certain limit with increasing duration of chilling. In consequence, the value of $\overline{DBB}$ will decline exponentially with increasing duration of previous chilling (Fig. 10b, Table 2).

Consider the behaviour of the model in the case of an individual plant and interrupted chilling (Fig. 11). The interruption does not make any difference, whether or not the critical FU sum is attained, because it will be attained in all cases. During the intermittent period, FU sum begins to be accumulated, thus, the time required to bud burst during the forcing period will be shorter in the interrupted treatment than in the corresponding continuous treatment (Figs. 9b, 11a). Additionally, the rate of accumulation of the FU sum increases, as the timing of the interruption is delayed. Thus, the reduction in the time required to bud burst will increase to a certain limit with increasing delay of the interrupting period (Figs. 11a,b).

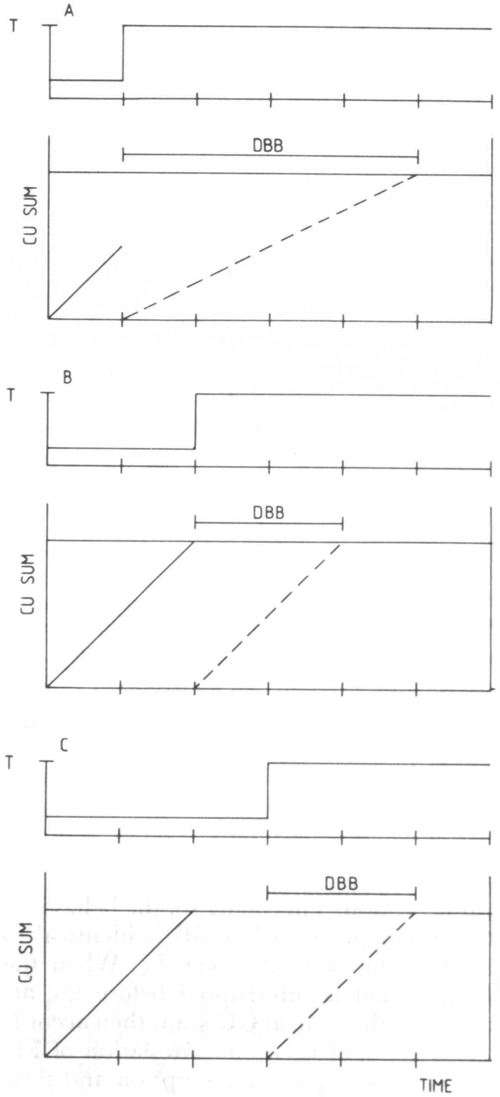


Fig. 9. Behaviour of the model type II in three continuous chilling experiments. The line parallel to the horizontal axis gives the sufficient chilling unit sum and the critical forcing unit sum, correspondingly. Otherwise see Fig. 3 for explanation.

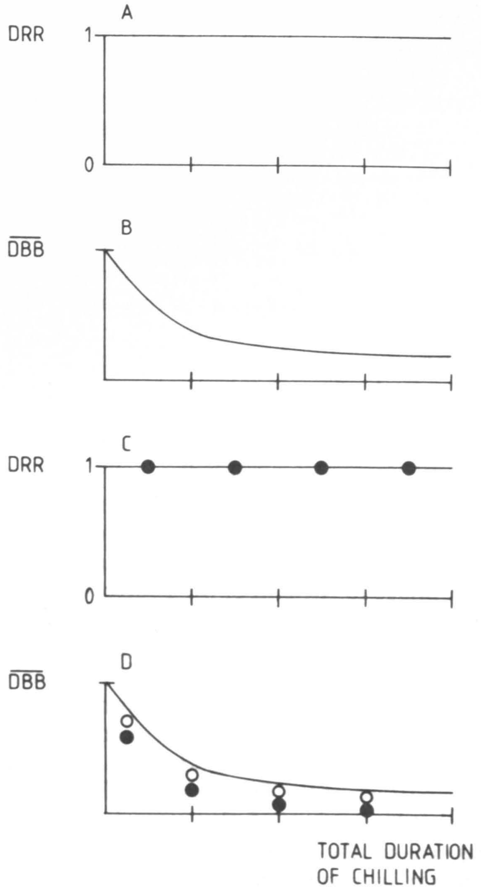


Fig. 10. Implications of the model type II about the values of dormancy release ratio DRR, and mean days to bud burst $\overline{DBB}$ as a function of the duration of the chilling period. The curve denotes in all cases results with continuous chilling. (A) DRR, continuous chilling. (B) $\overline{DBB}$, continuous chilling. (C) DRR, interrupted (circles) vs. continuous chilling. (D) $\overline{DBB}$, interrupted (circles) vs. continuous chilling. Open circles: the intermittent warm period began in an early phase of the chilling period, hatched circles: the intermittent warm period began in a late phase of the chilling period.

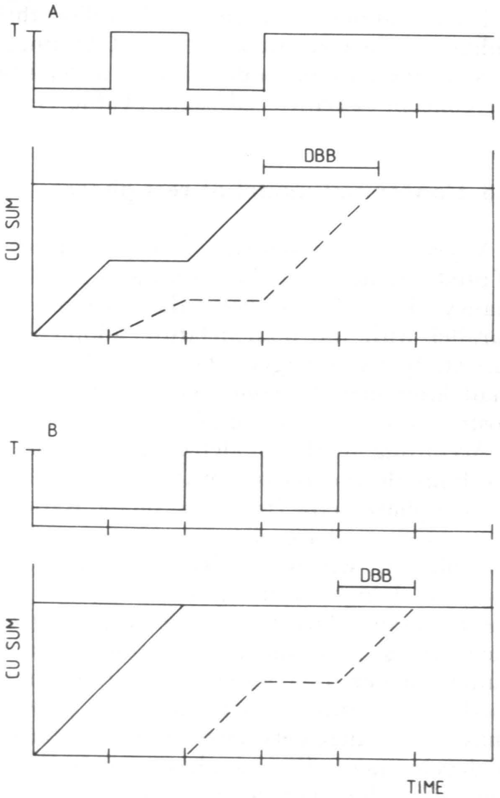


Fig. 11. Behaviour of the model type II in two interrupted chilling experiments. The line parallel to the horizontal axis gives the sufficient CU sum and the critical FU sum, correspondingly. Otherwise see Fig. 3 for explanation.

In the experiments at the population level, all plants will attain their critical FU sum also in the case of interrupted chilling. Hence, the value of DRR is unity for all of them (Fig. 10c, Table 2). The value of DBB will decline for all of the plants of an interrupted group, compared with the corresponding continuous group. Moreover, the reduction in the value of DBB increases with increasing delay of the interruption in the case of all of the plants. For this reason, the value of $\overline{DBB}$ will be smaller for the interrupted groups than for the corresponding continuous groups, and the difference in the values will increase to a certain limit with increasing delay of the intermittent period (Fig. 10d, Table 2, for the calculation of the value of $\overline{DBB}$ see Appendix 2).

In the framework of model type II, no rest period in the strict sense of model type I (Table 1) exists, because the buds have all the time potential to begin to grow in favourable environmental conditions. To reflect this difference, the concept of sufficient CU sum is used in the case of model type II instead of the concept of critical CU sum (Table 1).

2.6 Conceptual model of rest phases

Vegis (1964) presented a conceptual model of predormancy, true dormancy and postdormancy. In order to keep the terminology parallel with the nomenclature adopted in this study (Romberger 1963, pp. 73–76), I shall later use the concepts pre-, true and postrest instead of the original concepts.

According to the model of Vegis (1964), the buds do not move abrubtly from active growth phase to the (true) rest phase. Rather, there exists a phase of prerest state between the phases, which is characterized by a gradual change in the growth response to environmental factors. At the beginning of the phase, growth can take place but only in a somewhat narrowed range of environmental conditions, compared with the active growth phase. The range gets narrower in the course of development. Prerest phase comes to an end, and a phase of true rest begins, when it is not possible to bring about growth starting in any environmental conditions. Similarly, between the phases of true rest and active growth state there exists a phase of postrest, during which the growth response of the plants changes in a way opposite to the changes during the prerest phase. Thus, at the beginning of the postrest phase, it is possible to bring about growth initiation, but only in a narrow range of environmental conditions. The range widens during the course of development. Postrest comes to an end, and the growth phase begins, when the range does not widen any more.

Vegis (1964) separates various types of narrowing and widening of the range of the environmental conditions with respect to the pre- and postrest phases. He regards each type as an adaptation to the environmental conditions prevailing in the natural habitat of the plants. In the type characteristic for plants growing in a climate with regularly occurring cold season, the narrowing and widening takes place by changes in the lower limit of growth inducing temperature. During prerest phase this limit increases, and during postrest phase it decreases. Thus, according to the model, growth of woody plants of the cool and temperate regions is not induced during pre- and postrest phases in so low temperatures as during the active growth phase.

The model of pre-, true and postrest (Vegis 1964) can be tested by an experiment of continuous chilling with multiple forcing temperatures. Consider an experiment, in which two treatment groups are transferred at regular time intervals from the chilling conditions to the forcing conditions, one group to each of two forcing temperatures T_1 and T_2 ($T_1 > T_2$). Assume, that all the plants have completed their active growth phase before the experiment begins.

Let us first assume, that 1) the rate of development depends on temperature in a similar manner from the beginning of the prerest phase to the end of the postrest phase, ie. chilling is the driving force of the development during the whole rest period, and 2) there exists variation between the individuals in the chilling requirement of attainment of a given rest phase (cf. Fig. 4a). Together with these assumptions, the model generates a specific pattern of the DRR-values (Fig. 12a).

At the beginning of the experiment, all plants are in the prerest phase. Thus, they will begin to grow when transferred to the high forcing temperature T_1, but will not when transferred to the low forcing temperature T_2. After a specific duration of chilling (t_1), the first plants move from prerest to the true rest. In consequence, they will not resume growth, when transferred to either of the forcing temperatures. After that, the proportion of the plants which are in the true rest phase, increases, and thus the DRR-curve corresponding to T_1 decreases. Between time instants t_2 and t_3 all the plants are in the phase of true rest, and will not grow when transferred to either of the forcing temperatures. At time instant t_3 the first plants enter the postrest phase, and will thus begin to grow when transferred to T_1, but not when transferred to T_2. At time instant t_4 the first plants attain the active growth phase, and will consequently begin to grow when transferred to either of the forcing temperatures. At time instant t_5 the last plants move from true rest to postrest. Finally, at time instant t_6, the last plants move from postrest to the active growth phase.

It is possible that the development from prerest to true rest is caused by other environmental factors than chilling temperatures (eg. short photoperiod, cf. Nagata 1968). In that case, the chilling experiment is suitable only for testing the existence of the postrest phase. Together with this assumption, the model of rest phases generates another pattern of DRR-values (Fig. 12b).

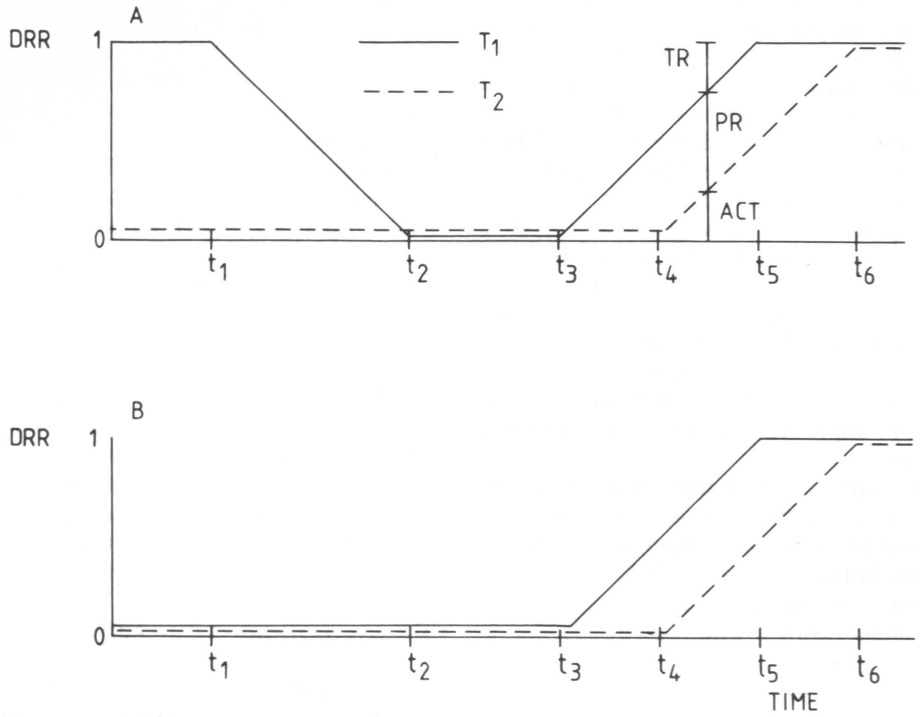


Fig. 12. Implications of the model of rest phases about the values of dormancy release ratio DRR obtained in high (T_1), and low (T_2) forcing temperature, as a function of duration of the chilling period. (A) Figure drawn assumed that, chilling is the driving force of the development from the beginning of the prerest phase until the end of the postrest phase. At a given duration of chilling, 1.) the value corresponding to T_2 gives the proportion of the plants, which are in the active growth stage (ACT), 2.) the difference between the values of the curves corresponding to T_1 and T_2 gives the proportion of the plants, which are in the state of pre- or postrest (PR), and 3.) the difference between unity and the sum of the values of the curves corresponding to T_1 and T_2 gives the proportion of the plants, which are in the state of true rest (TR). (B) Figure drawn assumed that, chilling is the driving force of the development from the beginning of the true rest to the end of the postrest.

3. Discussion

3.1 Testing of the simulation models

The three simulation model types considered in this study imply clearly contrasting consequences, with the aid of which they can be readily tested (Figs. 4,8,10, Table 2).

In this study, I have not put great emphasis on the quantitative details of the three simulation models considered. Rather, I have compared the qualitative differences between the models, in order to approach the role of the rest period as a part of the annual cycle of the trees. It is obvious that each of the original models has to be quantitatively modified, when applied for species and varieties others than for which they were originally formulated. For instance, in the case of model type I_B it is probable that the limit between "chilling" and "high" temperatures varies between genotypes.

When inferring the implications it was implicitly assumed that sample size of all of the treatment groups is large enough to detect the variation in the population. In practice this is not always the case, and thus the danger of wrong conclusions prevail.

3.2 Biological interpretation of the model variables

As such, the experimental design considered in this study (Fig. 1) does not warrant any biochemical or anatomical interpretation of the chilling unit (CU) and forcing unit (FU) concepts. Rather, these concepts refer exclusively to observations at the whole plant level. In the literature, however, some clues for the interpretation of the variables can be found.

According to prevailing understanding, chilling causes rest break by making growth promoters dominating over growth inhibitors (see Wareing and Phillips 1978, pp. 269–275). Thus, the accumulation of a chilling unit (CU) sum can be taken as to represent the cumulative effects of chilling to the balance between growth promoters and inhibitors.

Various types of temperature sums are normally used as a forcing unit (FU) sum. On the other hand, the rate of ontogenetic development (eg. cell divisions) increases with increasing temperature. Thus, the FU sum accumulation can be taken to represent the ontogenetic development of the bud, which leads to bud burst during spring (Sarvas 1972, Fuchigami et al. 1982).

In the model of Sarvas (1974), the period of accumulation of the FU sum is divided into two sub-periods, which have their own temperature response curves for the rate of maturation M. According to Sarvas, the first period is essentially a dormant one, the buds are for instance frost hardy during it (Sarvas 1974, p. 34). According to this, the buds display certain heat requirement before their ontogenetic development can begin (cf. Perry 1971). Therefore, ontogenetic development is not the only developmental phenomenon that is simulated by the accumulation of a FU sum. Changes in the concentrations of growth promoters and inhibitors are also involved.

3.3 Comparisons between the simulation models and the conceptual model

It is apparent that the logical structure of neither model type I nor II can be synthetisized as such with the model of rest phases. This is because in the model of rest phases, the forcing temperature is expected to have an effect, whether or not dormancy is released. This is not the case in any of the simulation models (Table 2).

It is, however, possible to synthetizize the model of postrest with model type I if the following two further assumptions are introduced in the model: 1) *High* temperatures are capable to augment the CU sum to the critical value, after comparatively long duration of chilling (during postrest phase). Furthermore, 2) the lower limit for a "high" temperature decreases with increasing duration of chilling. The implications of this modified model type I are consistent with the implications of the model of postrest (Fig. 12b). When interpreted physiologically this assumption would mean that during postrest phase, similar physiological changes would take place in high temperatures, as in low temperatures, but not in intermediate temperatures. According to this, the high temperatures, when prevailing in a late phase of rest, have a similar effect as long photoperiods, which have frequently been reported to promote dormancy release of non- or partially chilled plants (Nienstaedt 1966, 1967, Worrall and Mergen 1967, Garber 1983).

In the case of prerest the synthesis between the simulation models and the model of Vegis (1964) seems even more problematic. It is possible that the woody plants of the cool and temperate regions do not have any prerest phase, in the sense considered here (see Vegis 1964, pp. 191–195). Another possibility is that the hypothezized prerest phase has nothing to do with chilling (Fig. 12b). In this case, it can be related to the developmental phenomena caused by short photoperiods during late summer (eg. "summer dormancy" or "correlative inhibition", see Doorenbos 1953, Fuchigami et al. 1982).

3.4 Comparisons of the implications with previous experimental results

A model type relevant to one species or variety may not be relevant in the case of another one. However, some general observations related to the relevance of the three model types are apparent in the literature.

In the case of continuous chilling, DBB-curves like that presented in Fig. 10b have been frequently reported (eg. Lamb 1948, Worrall and Mergen 1967, Ritchie 1984). These reports do not usually contain any information of plants that have not broken dormancy. Thus, obviously, DRR-curves like that presented in Fig. 10a have been obtained. For this reason, the model type II gets support from these findings.

There are few reports concerning the effects of interrupted chilling, and furthermore, the experimental desing of these studies does not always permit a clear judgement between the model types. The most clearcut data are those of Overcash and Campbell (1955), Erez and Lavee (1971), and Erez et al. (1979), all concerning the dormancy release in peach. In all these studies, high temperatures (21°C or more) altered in a daily cycle with chilling temperatures, diminished the proportion of the buds for which dormancy was subsequently released, as compared with the continuous chilling treatments with the same amount of chilling. These findings are in agreement with model type I_B (Fig. 8, Table 2).

Weinberger (1954) found that heating the buds of peach trees during winter for three periods of the total length of 15 days caused a considerable delay in the dormancy release of the buds, compared with the unheated controls. This finding is in agreement with model type I: the intermittent warm periods delayed the attainment of the critical CU sum, and subsequently, the attainment of the critical FU sum, because during the intermittent periods, no increase in the CU sum occurred (model type I_A), or the CU sum was diminished during the intermittent periods (model type I_B).

The result of Weinberger (1954) can, however, be explained also by model type II. This is because the heating of the buds diminished the total amount of chilling, compared with the control buds. Thus according to the frame of model type II it is possible that the diminished amount of chilling caused a lowering in the subsequent rate of accumulation of the FU sum. According to this, the heated buds would reach the observed phase of development (bud burst) later, in spite of the lead in the developmental stage, which they got during the heating periods.

Erez and Lavee (1971) found that two intermittent warm periods (20°C) during the chilling period of peach increased the proportion of buds, for which dormancy was subsequently released, as compared with the continuous treatments with the same amount of chilling. Similarly, Erez et al. (1979) found that a treatment consisting of a daily cycle of 16h chilling and a further 8 h in 15°C was more effective than a continuous chilling treatment with the same amount of chilling. As such, these findings can not be explained by any of the simulation models considered (see Figs. 4c, 8, 10c).

With reference to model type II, all buds should burst after all of the chilling treatments (Fig. 10c). Thus it would seem that any results with bud burst percentages considerably below 100 are contradictory to model type II. In the studies of Erez and Lavee (1971), and Erez et al. (1979), however, the bud burst percentage was recorded at one time instant, after 14–30 days of forcing. This may have interfered with the results. According to model type II, the *mean* DBB-value decreases exponentially with increasing duration of chilling (Fig. 10b). However, there is often variation around this mean, at each duration of chilling. It is therefore possible that after a given short forcing time, not all of the buds burst that would burst after a long period of forcing. In accordance with this reasoning, accumulation of the FU sum during the intermittent warm periods caused subsequent bud burst for a larger part of the population, than that which occurred in the corresponding continuous treatment without any such accumulation before the forcing period. In this case, the results of Erez and Lavee (1971) and Erez et al. (1979) are in agreement with model type II.

However, the results of Erez and Lavee (1971), and Erez et al. (1979) can be explained also by model type I, if a further assumption is incorporated to the model type. According to this assumption, the physiological mechanism of rest break, once initiated by low temperatures, is able to function also in high temperatures, if the duration of the warm period is not long. Interpretation of this assumption suggests that chilling units can be accumulated also during periods of high temperature, which are interspersed between the chilling periods.

3.5 Effects of different chilling temperatures

When inferring the implications of the models, only chilling in a constant temperature was considered. Subsequently, the duration of chilling was used as an indicator of its amount. According to Erez and Lavee (1971), and Sarvas (1974, p. 29), the rest breaking effect is not the same for all of the chilling temperatures. Thus when considering chilling in fluctuating temperature, a weighted sum of chilling hours should be used as an index of chilling. This is in fact done in the three models considered: the rate of increment in the CU sum is dependent on temperature in all of them.

In addition to the critical (or sufficient) CU sum, there may exist genetical variation also in the dependence between rate of accumulation of the CU sum and temperature. This does not, however, affect the implications of the present study, because only chilling in one temperature was considered.

3.6 Rest period and springtime bud phenology

According to all simulation model types considered, the climatic conditions prevailing in autumn may have an effect on the bud phenology during the following spring. In the case of a habitat of a maritime climate, lack of chilling might cause a delay in the timing of bud burst (Cannell and Smith 1983, Cannell 1985). This is especially the case, when species or varieties native to more continental areas are cultivated in maritime regions. On the other hand, in the case of a habitat of a continental climate, lack of chilling is hardly affecting the springtime phenology of the buds. In this case it is, however, possible that part of the forcing units are accumulated during autumn (Sarvas 1974). This might be the case especially when the advent of winter is delayed. This being so, the time required to bud burst during spring is shortened.

The rest period is a key factor in the climatic adaptation of the woody plant species native to the cool and temperate regions. Thus, a sound ecophysiological understanding of the rest period is needed, especially for horticultural and forestry practices. This is further emphasised by the great climatic changes which are predicted to occur during the next decades (Cannell and Smith 1986).

Mathematical modelling has proved to be a useful tool in studying the rest period as a part of the annual cycle of trees. Before the models can be effectively tested, however, it is necessary to analyse and compare the logical structure of the models. After experimental testing, the models can then be used in computer simulations, in order to assess the adaptiveness of any tree species or provenance in any climatic conditions (Cannell and Smith 1983, 1986, Cannell 1985).

References

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. pp. 153–166.

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

— & Smith, R. I. 1986. Climatic warming, spring budburst and frost damage on trees. J. Appl. Ecol. 23: 177–191.

Doorenbos, J. 1953. Review of the literature on dormancy in buds of woody plants. Meded. Landbouwhogeschool Wageningen/Nederland 53(1): 1–23.

Erez, L. & Lavee, S. 1971. The effect of climatic conditions on dormancy development of peach buds. I. Temperature. J. Amer. Soc. Hort. Sci. 96(6): 711–714.

— , Couvillon, G. A. & Hendershott, C. H. 1979. Quantitative chilling enchancement and negation in peach buds by high temperatures in a daily cycle. J. Amer. Soc. Hort. Sci. 104(4): 536–540.

Flint, H. L. 1974. Phenology and genecology of woody plants. In: Lieth, H. (ed.). Phenology and seasonality modeling. Springer-Verlag, Berlin. pp. 83–97.

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, vol. 2. Academic Press, New York. pp. 93–116.

Garber, M. P. 1983. Effects of chilling and photoperiod on dormancy release of container-grown loblolly pine seedlings. Canad. J. For. Res. 13: 1265–1270.

Hari, P. 1968. A growth model for a biological population, applied to a stand of pine. Commun. Inst. For. Fenn. 66(7): 1–16.

— 1972. Physiological stage of development in biological models of growth and maturation. Ann. Bot. Fenn. 9: 107–115.

Hänninen, H., Kanninen, M. & Smolander, H. 1985. The annual cycle of forest trees: The Sarvas approach revisited. In: Tigerstedt, P. M. A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Helsinki University Press, Helsinki. pp. 195–201.

Lamb, R. C. 1948. Effect of temperatures above and below freezing on the breaking of rest in the Latham raspberry. Proc. Amer. Soc. Hort. Sci. 51: 313–315.

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

Leike, H. von. 1965. Neuere Ergebnisse über die Ruheperiode (Dormancy) der Gehölzknospen. Wiss. Zeitschrift Univ. Rostoc 14: 475–492.

Nagata, H. 1968. Studies on the photoperiodism in the dormant bud of Pinus densiflora SIEB. et ZUCC. (IV) Thermo-sensitivity of the terminal buds in the stage of predormancy. J. Jap. For. Soc. 50: 211–216.

Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. For. Sci. 12(3): 374–384.

— 1967. Chilling requirements in seven Picea species. Silvae Genet. 16: 65–68.

Overcash, J. P. & Campbell, J. A. 1955. The effects of intermittent warm and cold periods on breaking the rest period of peach leaf buds. Proc. Amer. Soc. Hort. Sci. 66: 87–92.

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

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(4): 331–332.

Ritchie, G. A. 1984. Effect of freezer storage on bud dormancy release in Douglas-fir seedlings. Canad. J. For. Res. 14: 186–190.

Robertson, G. W. 1968. A biometeorological time scale for a cereal crop involving day and night temperatures and photoperiod. Intern. J. Biometeorol. 12(3): 191–223.

— 1973. Development of simplified agroclimatic procedures for assessing temperature effects on crop development. In: Slatyer, R. O. (ed.). Plant response to climatic factors. Unesco, Paris. pp. 327–343.

Romberger, J. A. 1963. Meristems, growth, and development in woody plants. U.S. Department of Agriculture, Forest Service. Technical Bulletin No. 1293: 1–214.

Sarvas, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. Tiivistelmä: Tutkimuksia metsäpuiden kehityksen vuotuisesta sykluksesta. Aktiivi periodi. Commun. Inst. For. Fenn. 76(3): 1–110.

— 1974. Investigations on the annual cycle of development of forest trees II. Autumn dormancy and winter dormancy. Tiivistelmä: Tutkimuksia metsäpuiden kehityksen vuotuisesta syklistä. Syys- ja talvihorros. Commun. Inst. For. Fenn. 84(1): 1–101.

Vegis, A. 1964. Dormancy in higher plants. Ann. Rev. Pl. Phys. 15: 185–224.

Wareing, P. F. & Phillips, I. D. J. 1978. The control of growth & differentiation in plants. 2nd ed. Pergamon Press, Oxford. 347 pp.

Weinberger, J. H. 1954. Effects of high temperatures during the breaking of the rest of Sullivan Elberta peach buds. Proc. Amer. Soc. Hort. Sci. 63: 157–162.

Worrall, J. & Mergen, F. 1967. Environmental and genetic control of dormancy in Picea abies. Physiol. Plant 20(3): 733–745.

Total of 31 references

Appendix 1. Determination of the value of dormancy release ratio DRR according to model type I_B in the case of an interrupted chilling treatment

In the model type I_B, the diminishing effect of high temperatures to the accumulated CU sum is gradual: one hour in a high temperature deletes the chilling effect of one hour in a low temperature. This rule makes it possible to calculate the *effective duration of chilling*, CH_{ef}, according to which the value of DRR is determined using the DRR curve of the continuous chilling experiment (see figure below).

1) At the end of the first chilling period CU sum has a specific value DRR_1 determined according to the length of the first chilling period CH_1. If DRR_1 is greater than zero, then the critical CU sum is attained during the first chilling period for the part of the population indicated by DRR_1. The subsequent intermittent warm period does not affect the rest break of these plants. Thus, the minimum value of CH_{ef} is equal to CH_1.

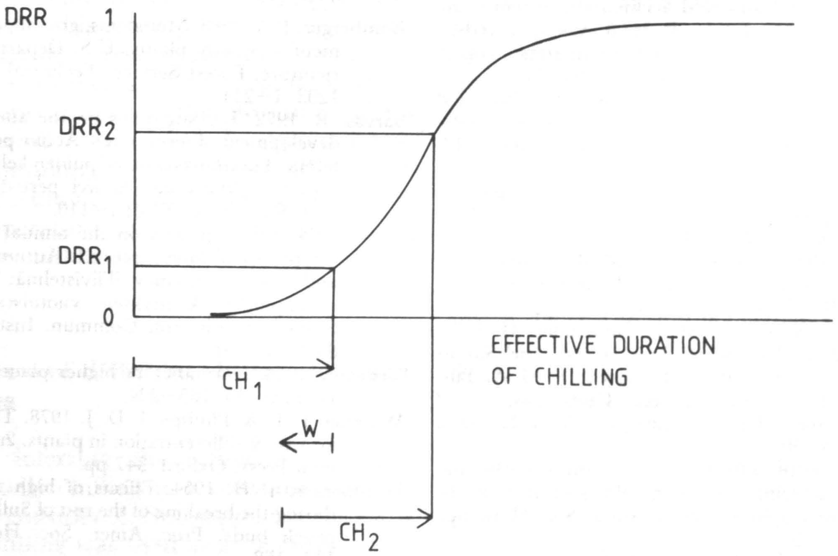
2) During the intermittent warm period the CU sum begins to decline for *the rest of the population*. The corresponding decline in the value of CH_{ef} is equal to the length of the warm period W, as far as W is smaller that CH_1. If W is greater than CH_1, then the decline is equal to CH_1. This is because the value of the CU sum can not be smaller than zero, and correspondingly, the effective duration of chilling can not be negative. 3.) During the second chilling period the value of the CU sum begins again to increase. If length of the second chilling period CH_2 is greater than length of the intermittent warm period W, then the critical CU sum is attained for other plants in addition to those, for which it was attained during the first chilling period. Thus in this case, the value of effective duration of chilling CH_{ef} is obtained by summing CH_1 and CH_2, and subtracting W from the sum.

According to model type I_B, the value of dormancy release ratio DRR in the case of an interrupted chilling treatment is obtained from the DRR curve of a continuous chilling treatment, as the ordinate corresponding to the effective duration of chilling, which is calculated according to the following rule:

$$R = \begin{array}{l} W, \ (W \le CH_1) \\ CH_1, \ (W > CH_1) \end{array}$$

$$CH_{ef} = \begin{array}{l} CH_1, \ (CH_2 < R) \\ CH_1 - R + CH_2, \ (CH_2 \ge R) \end{array}$$

where R = effect of the intermittent warm period to the effective duration of chilling



The principle of determining the value of dormancy release ratio according to model type I_B in the case of an interrupted chilling treatment. Horizontal axis gives the effective duration of chilling (CH_{ef}). The curve gives the dependence between DRR and duration of chilling in a continuous chilling treatment (in that case the effective duration of chilling is equal to the total duration of the chilling). CH_1, CH_2, and W give the durations of the first and second period of chilling, and the intermittent warm period, respectively. DRR_1 gives the value of DRR at the end point of the first chilling period, and DRR_2 the final value of DRR.

Appendix 2. Determination of the value of mean days to bud burst $\overline{DBB}$ according to model type II in the case of an interrupted chilling treatment

Consider a given value of $\overline{DBB}$. The ratio $1/(\overline{DBB})$ gives the proportion of the total development to bud burst, which takes place during one day. According to model type II, the value of $\overline{DBB}$ is dependent on the duration of previous chilling (Fig. 10b). Thus, the proportion of the development taking place during the intermittent warm period is given by $W * 1/\overline{DBB}(CH_1)$, where W = duration of the intermittent warm period in days, CH_1 = duration of the first chilling period in the interrupted chilling experiment, and $\overline{DBB}(CH_1) = \overline{DBB}$-value obtained in the continuous chilling experiment after CH_1 days of chilling. Let us denote by $\overline{DBB}_{int}$ the time, which is required to bud burst in the forcing conditions after an interrupted chilling treatment. Then the proportion of development occurring in the forcing conditions is given by $\overline{DBB}_{int} * 1/\overline{DBB}(CH_{tot})$, where CH_{tot} is the total duration of chilling, and $\overline{DBB}(CH_{tot}) = \overline{DBB}$ value obtained in the continuous chilling experiment after CH_{tot} days of chilling.

By definition, the total proportion of development equals unity:

$$W * 1/\overline{DBB}(CH_1) + \overline{DBB}_{int} * 1/\overline{DBB}(CH_{tot}) = 1$$

Thus the $\overline{DBB}$-value of the interrupted group is given by the following formula

$$\overline{DBB}_{int} = \overline{DBB}(CH_{tot}) * (1 - W * (1/\overline{DBB}(CH_1)))$$