The Temperature Dependence of Dormancy Breaking in Plants: Mathematical Analysis of a Two-Step Model Involving a Cooperative Transition

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A two-step model describing the thermal dependence of the dormancy breaking phenomenon is developed. The model assumes that the level of dormancy completion is proportional to the amount of a certain dormancy breaking factor which accumulates in plants by a two-step process. The first step represents a reversible process of formation of a precursor for the dormancy breaking factor at low temperatures and its destruction at high temperatures. The rate constants of this process are assumed to be dependent upon the temperature according to the Arrhenius law. The second step is an irreversible cooperative transition from the unstable precursor to a stable dormancy breaking factor. The transition is assumed to occur when a critical level of the precursor is accumulated. The two-step scheme is analysed mathematically. This model explains qualitatively the main observations on dormancy completion made under controlled temperature conditions and relates the parameters of the theory to the measurable characteristics of the system.

1. Introduction

Buds of many deciduous tree species commonly enter into a rest state and exhibit no growth during the cold part of the year. This state of rest (or dormancy) is completed when the plants are exposed to an extended period of low temperature. Erez & Lavee (1971) observed under controlled conditions that the dependence of the rest completion of peach buds on the temperature has a maximum, with a temperature of 6-8°C contributing to the rest break more than any other temperature. Using these data and the results of their own observations, Richardson *et al.* (1974) developed a model of dormancy completion. The model represents a summation of chill-units where one chill-unit is equal to one hour of exposure to 6-8°C and chilling-contribution becomes less as the temperature rises above or drops below that range. Studies by Gilreath & Buchanan (1981) indicate that there are cultivar- as well as climatic condition-dependent differences in the chilling temperature effectiveness and accumulated chill-unit requirements. Shaltout & Unrath (1983) used the chill-unit concept for prediction of rest completion by apples grown in North Carolina.

The concept of effective chilling hours accumulation assumes that 2 hours at equal temperatures recorded at different times in a long-term observation contribute

equally to the breaking of dormancy. This assumption contradicts results obtained by Erez *et al.* (1979*a*) in experiments with periodically changed temperatures. The cycles of 1, 3, 6 and 9 days were examined with $\frac{2}{3}$ of the cycle length at temperature of 4–6°C and the remaining $\frac{1}{3}$ at 24°C. Each cycle was repeated until the plants were exposed to a fixed number of chilling hours. The experiment shows a remarkable dependence of the dormancy breaking on the cycle length: the longer the cycle, the smaller the chilling negation by high temperatures. Data presented by Gilreath & Buchanan (1981) also substantiate the importance of the cycle length. These results indicate the influence of the dynamics of the temperature conditions on the contribution of a chilling-hour to dormancy completion.

An additional effect, which points up the necessity of taking into account the system's dynamics for the description of the phenomenon, was observed by Couvillon & Erez (1985) in experiments with diurnal cycles, in which the high temperature was 20° for 0, 2, 4, 6 or 8 hours and 4°C for the remainder of the cycle. The cycles were continued until all plants were exposed to 1200 hours at 4°C. Plants exposed to cycles with the high temperature of 20°C for a short time (2 and 4 h) showed chilling enhancement instead of negation. Longer exposures to 20°C led to chilling negation which gradually increased with the length of the exposure. A specific effect of moderate temperatures on the completion of the rest in peach buds was recorded by Erez & Couvillon (1987). When 13, 15 or 17°C was cycled with 6°C (8 and 16 h, respectively) and compared with a continuous 6°C regime, an enhanced effect by moderate temperatures was observed only with 13°C, while 6–15°C acted similarly to continuous 6°C, and 6–17°C had a negative effect.

To take into account the influence of the history of the temperature conditions on the rest completion, a dynamic model has to be analysed. Salisbury & Ross (1969) suggested a schematic description of the phenomenon in terms of enzymatic reactions. The rate of reaction increases with the rise in temperature, but the increasing temperature results also in an increased rate of the enzyme denaturation. These two opposing reactions may result in a bell-shaped thermal dependence. Purvis & Gregory (1957) used similar consideration in their study of vernalization of rye plants. They suggested a multistage scheme which includes a thermally unstable substance. In order to understand the dual effect of the temperature on dormant peach buds, Erez & Couvillon (1987) proposed a two-step scheme, with the first step being a reversible formation–destruction of a thermally unstable substance and the second step being a fixation of this substance. The dynamics and thermal behaviour of the system were not yet analysed mathematically.

The temperature relations of seed germination and other biological processes have been considered by Hegarty (1973). He points out that "several biological processes, whether seemingly governed by individual chemical reactions or whether describing gross physiological processes", do seem to obey the Arrhenius law.

In the present study a phenomenological theory for dormancy breaking caused by low temperatures is developed. It assumes the occurrence of a thermally unstable precursor, which leads to the accumulation of a factor(s) in the buds resulting in the completion of dormancy. The Arrhenius law is used to describe the thermal dependence of the rates of the reversible processes. The transition from the precursor

to the active dormancy breaking factor is assumed to be an irreversible cooperative process in biological macromolecules or membranes. The objective of this work is to develop a simple model with a minimal number of parameters, which will be able to explain qualitatively three main observations concerned with the temperature effects: the bell-shaped dependence of bud rest completion on the temperature; the dependence of the chilling negation by high temperatures on the cycle length; and the promotion of the chilling effect by short periods of high temperatures or by longer periods of exposure to moderate temperatures.

2. Description of the Model

Let the dormancy completion be proportional to an accumulated amount of some changes in plants. It may be an accumulation of some chemical substance, like an enzyme, or an accumulation of changes in physical structures on the cellular or subcellular level, like changes in permeability of biological membranes, etc. The dynamics of accumulation of this dormancy breaking factor (DBF) is presented by the following scheme

$$\underset{k_1}{\overset{k_0}{\rightleftarrows}} PDBF \rightarrow DBF \tag{1}$$

where PDBF is a precursor of DBF, and k_0 and k_1 are the rate constants for formation and destruction of PDBF, respectively. These two rate constants are assumed to obey the Arrhenius law

$$k_{0,1} = A_{0,1} \exp\left(-E_{0,1}/\Theta\right) \tag{2}$$

where Θ is the temperature in absolute degrees ($^\circ K$), $E_{0,1}$ are the energies of activation for the processes of PDBF formation and destruction (in the temperature units), respectively, and $A_{0,1}$ are the rate coefficients, independent of the temperature.

The transition PDBF $\rightarrow$ DBF is assumed to be a cooperative process: when the amount of PDBF reaches a critical level, the whole portion undergoes an irreversible transition (fixation) to the state DBF. Henceforth, the amounts of PDBF and DBF are denoted as x and y, respectively. They are designed as dimensionless variables measured in the units of the critical portion. Therefore, the transition point is $x = 1$.

The model contains two dynamic variables: x and y, and four parameters: A_0, A_1, E_0 and E_1.

3. Dynamics Under Constant Temperatures

The changes of x with the time within the interval between two consecutive threshold transitions are described by the linear equation

$$dx/dt = k_0 - k_1 x. \tag{3}$$

If the temperature is constant within the time interval under consideration, the parameters k_0 and k_1 are constants and the solution of eqn (3) is

$$x(t) = x_s - (x_s - x_0) \exp(-k_1 t) \tag{4}$$

where x_0 is the initial value of x and $x_s = k_0/k_1$ is its steady-state value.

The variable x reaches its critical value $x = 1$ for the first time at the instant $t = \tau_0$. Using eqn (4) one obtains

$$\tau_0 = (1/k_1) \ln [(x_s - x_0)/(x_s - 1)]. \tag{5}$$

At this moment the value of y receives a portion which is equal to 1, while the value of x drops to zero; so, the next threshold state will be reached after time interval

$$\tau = (1/k_1) \ln [x_s/(x_s - 1)]. \tag{6}$$

Continuation of this process during time $T > \tau_0$ leads to the total number N of thresholds which can be calculated as

$$N = \text{FLOOR} [(T - \tau_0)/\tau + 1]. \tag{7}$$

Now the value of $y(T)$ is

$$y(T) = N \tag{8}$$

and the value of $x(T)$ is

$$x(T) = x_s\{1 - \exp[-k_1(T - \tau_0 - (N-1)\tau)]\}. \tag{9}$$

Surely, if $x_s \leq 1$, the critical level will never be obtained (see Fig. 1).
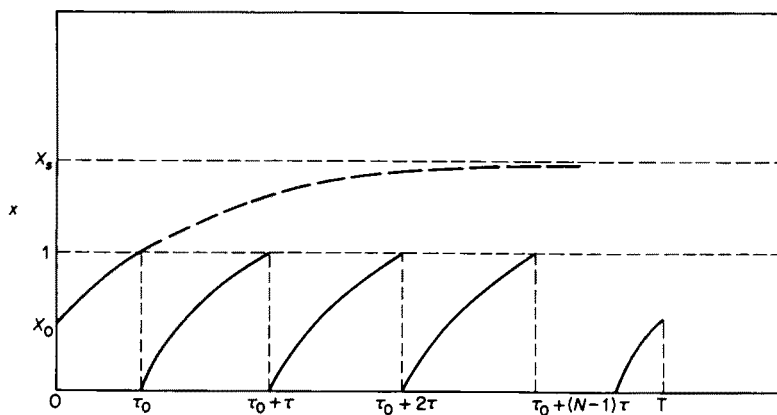

FIG. 1. Dynamics of variable x under condition of constant temperature. The steady-state value, x_s, is greater than one. The dashed extrapolation of the curve $x(t)$ over the line $x = 1$ shows the dynamics without thresholds. x_0 is the initial value and τ_0 is the first threshold interval. τ is the threshold interval when the accumulation of x starts from 0.

4. The Thermal Dependence of Dynamic Variables

At the early time course of accumulation of DBF, when $t \ll k_1^{-1}$ and $x_0 \cong 0$, it can be seen from eqn (4) that $x(t) \approx k_0 t$. Then, using eqn (2), one obtains

$$x(t) \approx A_0 t \exp(-E_0/\Theta). \tag{10}$$

At this stage x increases monotonically with temperature increase. For the case of steady-state ($t \gg k_1^{-1}$), the situation may be different. According to the definition

$$x_s = (A_0/A_1) \exp[-(E_0 - E_1)/\Theta]. \tag{11}$$

Equation (11) represents a monotonically increasing function x_s on Θ if $E_1 < E_0$, and a decreasing one if $E_1 > E_0$. Henceforth, only the latter case will be considered. For each pair of those E_1 and E_0, a critical temperature Θ_c may be found which leads to the equality $x_s(\Theta_c) = 1$. As stated above, the threshold line will never intercross the curve $x(t)$ at this temperature as well as at all higher temperatures, $\Theta > \Theta_c$.

One can conclude from eqns (10) and (11) that in the two limiting situations, $t \ll k_1^{-1}$ and $t \gg k_1^{-1}$, x is a monotonic function of the temperature. Therefore, if the fixation occurs at these time intervals, $y(\Theta)$ should not have a bell-shaped form. The thermal maximum for $x(t, \Theta)$ and $y(t, \Theta)$ may appear at intermediary t's only.

According to eqns (7) and (8), the temperature which leads to a minimal time interval between the two consecutive cooperative transitions, provides a maximum of the function $y(T, \Theta)$. The common condition for extremum $(d\tau/d\Theta = 0)$ applied to eqn (6) gives the following implicit equation for the variable Θ, hidden in x_s, as defined in eqn (11)

$$\ln[x_s/(x_s - 1)] = (E_1 - E_0)/[E_1(x_s - 1)]. \tag{12}$$

Let us introduce a new variable, σ, which is related to Θ through x_s as follows

$$\sigma = x_s/(x_s - 1). \tag{13}$$

For the new variable eqn (12) converts to

$$\ln \sigma = p(\sigma - 1) \tag{14}$$

where

$$p = (E_1 - E_0)/E_1 \tag{15}$$

Figure 2 graphically represents the solution of eqn (14) as an intercept of the logarithmic curve $\ln \sigma$ with the line $p(\sigma - 1)$. The solution depends on the single parameter p. One can see that there is a single solution, σ^*, and the parameter has to obey the inequality

$$0 < p < 1 \tag{16}$$

i.e., $E_1 > E_0$. This is the case under consideration which implies unstable PDBF at high temperatures. (The higher the temperature, the lower the steady-state level of PDBF.) It can also be seen that, at the point $\sigma = \sigma^*$, the slope of $\ln \sigma$ has to be less than the slope of the line $p(\sigma - 1)$, which means
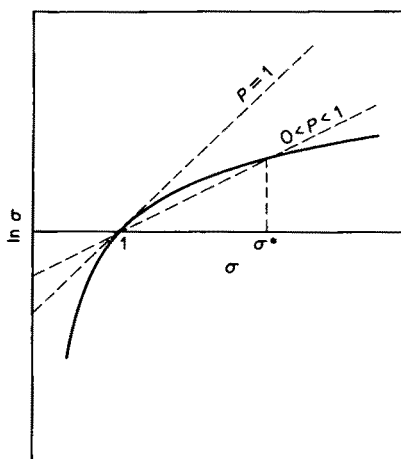
$$1/\sigma^* < p. \tag{17}$$

FIG. 2. The graphical solution of eqn (14).

To check what kind of extremum is given by eqn (14), the second derivative $d^2\tau/d\Theta^2$ is calculated at the extremum point $\sigma = \sigma^*$

$$d^2\tau/d\Theta^2|_{\sigma=\sigma^*} = k_1^{-1}\Theta^{-4}E_1(E_1 - E_0)\sigma^*(\sigma^* - 1)(p - 1/\sigma^*). \tag{18}$$

Taking into account eqn (17), one can conclude that the second derivative in eqn (18) is positive. Therefore, $\tau(\Theta)$ has a minimum at the point $\sigma = \sigma^*$.

The temperature Θ^*, which corresponds to the minimum of τ, may be obtained using eqns (11) and (13)

$$\Theta^* = (E_1 - E_0)\ln^{-1}[A_1\sigma^*/A_0(\sigma^* - 1)]. \tag{19}$$

This analysis reveals the conditions of existence of the threshold temperature and of the bell-shaped thermal dependence of the dormancy completion in the constant temperature conditions.

5. Two-temperature Cycles

When the temperature changes continuously with time, eqn (4) no longer represents the solution of eqn (3). In the general case the equation cannot be integrated analytically, but when the temperature changes stepwise, eqn (4) gives the solution inside each step with the proper constants $k_0(\Theta)$ and $k_1(\Theta)$.

In the experiments with the two-temperature cycles, a dual effect of high temperatures was observed: the chilling enhancement when the high temperature was applied for a short period in each cycle, and the chilling negation when the high-temperatute periods became longer.

The chilling enhancement by high temperatures may be explained qualitatively using Fig. 3. Two one-temperature curves started at $t = 0$ are represented by a solid line for $x(t, \Theta_1)$ and by a dashed one for $x(t, \Theta_2)$. According to eqns (10) and (11),
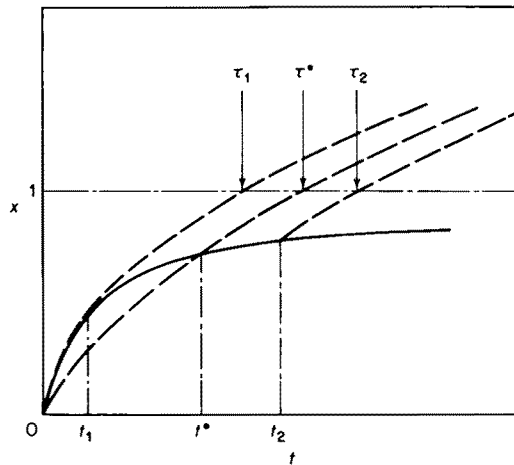
FIG. 3. Enhancement of the domancy break by application of high temperature during a short period. The solid curve represents dynamics under high temperature. The dashed curves represent dynamics under low temperature applied from the starting point or after some period of exposure to high temperature (t_1 or t_2). If the period of heating is short enough (t_1), the time interval needed for reaching the critical level is shorter than in the condition of the constant low temperature ($\tau_1 < \tau^*$).

the curve representing a higher temperature ($\Theta = \Theta_1$) has a higher initial slope but a lower asymptote as compared with the curve for lower temperature ($\Theta = \Theta_2$). One can see that the curve $x(t, \Theta_2)$ crosses the threshold line at the instant τ^*, whereas the curve $x(t, \Theta_1)$ does not reach the threshold because its asymptote is lower than one. The curves intersect at point t^*.

Let us now consider the situation where the system was exposed to temperature Θ_1 during period $(0, t_1)$ with $t_1 < t^*$ and then the temperature changed stepwise to Θ_2. The dashed curve started at $t = t_1$ represents the dynamics of the system in this case. It reaches the threshold line earlier than the curve $x(t, \Theta_2)$, i.e., $\tau_1 < \tau^*$. Hence, more portions of DBC can be fixed for the same chilling time if such a two-temperature period is repeated in the long-term observations. This enhancement is effective for short warming periods only. The dashed curve started at $t = t_2$, shows the dynamics of the system exposed to the temperature Θ_1 during the period $(0, t_2)$ with $t_2 > t^*$. This curve reaches the threshold later than the curve $x(t, \Theta_2)$, which results in chilling negation by exposure to the high temperature.

It is understood from Fig. 3 that the maximal enhancement is achieved if the temperature switch is made at point $x = x_e$, where $dx(t, \Theta_1)/dt = dx(t, \Theta_2)/dt$. The higher the temperature Θ_1, the earlier the intersection point t^* and the shorter is the interval where the enhancement can be observed. This is in accordance with the observations of Couvillon & Erez (1985) and Erez et al. (1979b).

The second reason for the observed enhancement of the dormancy break may be an "artifact" of experiments which are designed in order to give a constant number of hours which the system spent at the chill temperature, assuming that the time under high temperatures is not effective.

The role of cycle length on the chilling negation may be described analytically. Let us consider the situation when the temperature is changed stepwise and periodically, denoting the length of the period as π. At the first part of each period $(0 \le t < \eta\pi)$ the system is exposed to the temperature Θ_1 and during the rest of the period $(\eta\pi < t \le \pi)$ the temperature equals Θ_2. The behaviour of the system may be analysed when such periods are repeated before the critical level is reached. For a period number i the solution of eqn (3) is

$$x_i(t, \Theta_1) = x_s(1)\{1 - \exp[-k_1(1)t]\} + x_i(0, \Theta_1) \exp[-k_1(1)t], \qquad (0 \le t < \eta\pi)$$

$$x_i(t, \Theta_2) = x_s(2)\{1 - \exp[-k_1(2)(t - \eta\pi)]\}$$

$$+ x_i(\eta\pi, \Theta_2) \exp[-k_1(2)(t - \eta\pi)], \qquad (\eta\pi \le t \le \pi) \tag{20}$$

where $k_1(1) = k_1(\Theta_1)$, $k_1(2) = k_1(\Theta_2)$, $x_s(1) = x_s(\Theta_1)$, and $x_s(2) = x_s(\Theta_2)$. Equations (20) are subject to the following boundary conditions

$$x_i(0, \Theta_1) = x_{i-1}(\pi, \Theta_2)$$

$$x_i(\eta\pi, \Theta_1) = x_i(\eta\pi, \Theta_2). \tag{21}$$

Let α and β stay for the following expressions

$$\alpha = x_s(1)\{1 - \exp[-k_1(1)\eta\pi]\} \exp[-k_1(2)(1 - \eta)\pi]$$

$$+ x_s(2)\{1 - \exp[-k_1(2)(1 - \eta)\pi]\}$$

$$\beta = \exp[-k_1(1)\eta\pi - k_1(2)(1 - \eta)\pi]. \tag{22}$$

Using eqns (20)-(22) one can obtain the recurrent equation

$$x_i(\pi, \Theta_2) = \alpha + \beta x_{i-1}(\pi, \Theta_2). \tag{23}$$

Application of the recurrent equation (23) i timess leads to

$$x_i(\pi, \Theta_2) = \alpha/(1 - \beta) - [\alpha/(1 - \beta) - x_0]\beta^i \tag{24}$$

where $x_0 = x_1(0, \Theta_1)$.

In the long-term considerations eqn (24) represents a discrete function of i, which is similar to the continuous function of t given by eqn (4), with $L = \alpha/(1 - \beta)$ being the asymptote and $\zeta_1 = k_1(1)\eta + k_1(2)(1 - \eta)$ playing the role of k_1

$$x_i(\pi, \Theta_2) = L - (L - x_0) \exp(-\zeta_1\pi i). \tag{25}$$

The function increases or decreases monotonically when $x_0 < L$ or $x_0 > L$, respectively. The dependence of the function $x_i(\pi, \Theta_2)$ on the cycle length may be studied from the derivative

$$dx_i/d\pi = (dL/d\pi)(1 - \exp(-\zeta_1\pi i)) + (L - x_0)\zeta_1 i \exp(-\zeta_1\pi i). \tag{26}$$

For $L > x_0$ the derivative is positive if $dL/d\pi > 0$.

Denoting

$$q_1 = \exp[-k_1(1)\eta\pi] \quad \text{and} \quad q_2 = \exp[-k_1(2)(1 - \eta)\pi] \tag{27}$$

the following representation of L may be obtained

$$L = x_s(1) + [x_s(2) - x_s(1)](1 - q_2)/(1 - q_1 q_2). \tag{28}$$

It is worth noting that two discrete functions may be considered: one, built up by the end-points of the chill part of cycles, and the other, formed by the end-points of the high temperature parts. Here the first one is of interest because it is the higher and reaches the critical level earlier. For $x_s(1) < x_s(2)$, it follows from eqn (28) that

$$x_s(1) < L < x_s(2) \tag{29}$$

The dependence of L on the cycle length may be studied from analysis of the derivative

$$dL/d\pi = (x_s(2) - x_s(1))(1 - q_1 q_2)^2$$
$$\times q_1 q_2 [k_1(2)(1-\eta)(1-q_1)/q_1 - k_1(1)(1-q_2)\eta]. \tag{30}$$

The sign of the derivative depends on the sign of the expression in the squared brackets, which is the difference of two increasing functions of π

$$f_1 = k_1(2)(1-\eta)\{\exp[k_1(1)\eta\pi] - 1\}$$
$$f_2 = k_1(1)\eta\{1 - \exp[-k_1(2)(1-\eta)\pi]\}. \tag{31}$$

The slopes of these functions are

$$df_1/d\pi = k_1(1)k_1(2)\eta(1-\eta)\exp[k_1(1)\eta\pi]$$
$$df_2/d\pi = k_1(1)k_1(2)\eta(1-\eta)\exp[-k_1(2)(1-\eta)\pi]. \tag{32}$$

One can see from eqns (31) and (32) that the functions f_1 and f_2 both start from zero but f_1 increases more strongly. Hence, $f_1 > f_2$ and $dL/d\pi > 0$. This means that, according to eqn (26), $x_i(\pi, \Theta_2)$ increases with the increase in cycle length, which results in a reduction in the threshold time and leads to an increase in the value of y.

If $L = 1$ the threshold will never be reached in the two-temperature regime. This means that for given Θ_1, Θ_2 and η a critical cycle length $\pi = \pi_c$ may be found, which leads to complete chilling negation.

6. Relation of the Parameters of the Theory to the Experimentally Observable Characteristics

The theory developed here for explanation of the dormancy break phenomena contains four parameters: E_0, E_1, A_0 and A_1. The mathematical analysis of the behaviour of the system at constant temperatures relates these parameters with the values which could be estimated from experiments. The critical temperature, Θ_c, corresponds to the case when the steady-state value $x_s(\Theta)$ is equal to one. Using eqn (11), one obtains

$$\Theta_c = (E_1 - E_0)\ln^{-1}(A_1/A_0). \tag{33}$$

The optimal chilling temperature, Θ^*, is given by eqn (19). The time interval for threshold occurrence at the optimal temperature, τ^*, may be expressed in the following form, using eqn (11)

$$\tau^* = -A_1^{-1}\exp(E_1/\Theta^*)\ln\{1 - \exp[(E_0 - E_1)q\} \tag{34}$$

where $q = 1/\Theta^* - 1/\Theta_c$.

Using eqns (14), (19) and (33) one obtains

$$E_1 = (E_0 - E_1)/\{\exp[(E_1 - E_0)q] - 1\} \ln\{1 - \exp[(E_0 - E_1))q]\}. \tag{35}$$

Inserting eqn (33) into eqn (6), gives after algebraic transformations for $\Theta = \Theta^*$

$$A_1 = -\exp(E_1/\Theta^*)\tau^{-1}(\Theta^*) \ln\{1 - \exp[(E_0 - E_1)q]\}. \tag{36}$$

The parameter A_0 is defined from eqn (33) as

$$A_0 = A_1 \exp[(E_0 - E_1)/\Theta_c]. \tag{37}$$

The condition for the complete chilling negation in the two-temperature cyclic regime $(L = 1)$ allows to obtain, using eqns (11), (27), and (28), the following relationship

$$\{\exp[(E_1 - E_0)/\Theta_c] - \exp[(E_1 - E_0)/\Theta_1]\}/\{\exp[(E_1 - E_0)/\Theta_2] - \exp[(E_1 - E_0)/\Theta_1]\}$$

$$= \{1 - \exp[-k_1(\Theta_2)(1 - \eta)\pi_c]\}/\{1 - \exp(-[k_1(\Theta_1)\eta + k_1(\Theta_2)(1 - \eta)]\pi_c)\}. \tag{38}$$

Equations (35)–(38) represent a system of non-linear algebraic equations with theoretical parameters E_0, E_1, A_0 and A_1 as unknown variables related to the experimentally measurable charactreristics: Θ^*, Θ_c, $\tau(\Theta^*)$, and π_c with corresponding set of Θ_1, Θ_2, and η. If the listed experimental data are available, the system of the equations may be solved numerically, leading to the estimation of the parameters of the theory. As may be estimated approximately from experiments under controlled temperature conditions, $\Theta^* = 279$ K, $\Theta_c = 287$ K, $\tau(\Theta^*) = 28$ h, $\pi_c = 26$ h, $\Theta_1 = 297$ K, $\Theta_2 = 279$ K, and $\eta = \frac{1}{3}$. Inserting these values into eqns (35)–(38) and solving numerically the non-linear system, results in the following set of theoretical parameters: $E_0 = 2874{\cdot}364$ (K), $E_1 = 11441{\cdot}415$ (K), $A_0 = 1{\cdot}386 \times 10^3$ (1/h), and $A_1 = 1{\cdot}275 \times 10^{16}$ (1/h).

Discussion

The theory for the dormancy break phenomenon developed here assumes some basic features of kinetics of the transformations: the rate constants of formation and destruction of the DBF-precursor obey the Arrhenius law and the fixation of the precursor to DBF is a cooperative transition. These assumptions are sufficient to explain the observations: the bell shape of the thermal dependence of the rest break, the dual effect of warm temperatures (enhancement and negation of the chilling depending on the time interval to application of the high temperature), and the diminishing of chilling negation when the cycle length increases.

A commonly accepted basis for comparing the temperature relations of rates of biological processes is to evaluate the temperature coefficients (Q_{10}). The activation energies, E_0 and E_1, estimated above for the processes of formation and destruction of PDBF correspond to Q_{10} values of $1{\cdot}4$ and $3{\cdot}7$, respectively. These magnitudes are realistic ones, because Q_{10} values of many chemical reactions obeying the Arrhenius law range from 2 to 3 (see, e.g., Hegarty, 1973). This justifies the model assumed above. The real mechanism of bud dormancy break is probably more sophisticated, but the main rate-limiting reactions involved in the complex process

may be, apparently, described by the scheme used in this analysis. To develop a more exact fundamental model of the phenomenon, more experimental information is required.

It is worthwhile pointing out that, apart from the breaking of dormancy in the buds of perennial woody plants, a few other biological processes with positive responses to low temperatures are of importance, e.g. breaking of seed dormancy, induction of the growth of underground storage organs, and vernalization. Salisbury & Ross (1969) indicated that similarities in mechanisms underlying these phenomena seem reasonable. In the earlier publication by T. Morinaga (1926) it was pointed out the necessity "to learn in the main mechanism, or perhaps the various sorts of mechanisms, by which alternating temperatures and their substituting factors promote germination". The model developed here for bud dormancy break may be applicable to the analysis of mechanisms of other low-temperature responses.

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