

The Temperature Dependence of Dormancy Breaking in Plants: Computer Simulation of Processes Studied Under Controlled Temperatures

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Experimental studies of breaking of peach bud dormancy under controlled temperature conditions are used for estimation of parameters of a dynamic two-step model involving a cooperative transition. The parameters are installed into an adequate computer program for simulation of the dormancy breaking at cycled temperature regimes. The calculated results are compared with available experimental data obtained for constant temperatures and for two-temperature cycles. In accordance with experimental observations, the simulations show the bell-shaped dependence on temperature for dormancy completion; negation of the chilling effect by high temperatures; dependence of the effect on the cycle length; and the enhancement of the effect by short applications of high temperatures.

1. Introduction

In the course of their development, buds of many deciduous trees enter into a state of dormancy (or rest), which is accompanied by growth cessation. Normal bud growth in the spring is resumed only after the buds have been subjected to an extended period of low temperature during the preceding winter. Dormancy completion is found to be a bell-shaped function of temperature, with a maximum within the range 6 to 8°C, as found by Erez & Lavee (1971) and Erez & Couvillon (1987) in peach buds. A similar function with the maximum at 4 to 6°C was reported recently by Seeley & Damavandy (1985) for the response of seed of 7 deciduous fruit species to stratification temperatures.

A model counting the effective chilling hours in the winter season and relating the accumulated chilling units to dormancy completion was developed by Richardson *et al.* (1974) for two peach cultivars. A similar rest completion prediction model for a low-chilling cultivar of nectarine was built by Gilreath & Buchanan (1981) and for apples by Shaltout & Unrath (1983). In all those models the contribution to the rest completion from each chilling hour was considered to be independent of the temperatures during the preceding period, i.e. the dynamics of the process was not taken into consideration.

Experiments under controlled temperature conditions, performed by Erez, Couvillon and co-workers (Erez *et al.*, 1979*a, b*; Couvillon & Erez, 1985; Erez &

Couvillon, 1987) reveal the interdependence of temperatures experienced throughout the observations on the process of dormancy breaking in peach buds. In the study of moderate temperature effect, Erez & Couvillon (1987) suggested that the effect may be explained by means of a two-stage scheme; the first step being a reversible process which has to explain the action of chilling and high temperatures, and the second step is the moderate temperature reaction that fixes the chilling effect.

In the recent study by Fishman *et al.* (1987), a dynamic model was analysed which gives a qualitative explanation to the experimental observations. According to this theory, a two-step process is responsible for the changes in the buds leading to the dormancy breaking. The first step is considered to be a reversible process of formation and destruction of a thermally labile precursor for the dormancy breaking factor (PDBF). When a critical portion of the precursor is amassed, the whole accumulated quantum of PDBF is transferred irreversibly to a quantum of stable dormancy-breaking factor (DBF). The rate constants for formation (k_0) and destruction (k_1) of the PDBF are assumed to obey the Arrhenius law

$$k_{0,1} = A_{0,1} \exp(-E_{0,1}/\theta) \quad (1)$$

where θ is temperature in absolute degrees (K); E_0 and E_1 are energies of activation for formation and destruction processes, respectively, in absolute temperature units (K); and A_0 and A_1 are coefficients independent of the temperature, having the same dimensions as k_0 and k_1 , respectively. The theory contains four parameters: E_0 , E_1 , A_0 , A_1 . To use the dynamic model as a basis for simulation, it is necessary to estimate the parameters mentioned above. The mathematical analysis given in the previous communication (Fishman *et al.*, 1987) relates the theoretical parameters with experimentally measurable values: the temperature, leading to a maximal chilling effect, θ^* ; the highest temperature which still gives a positive response, θ_C , the time needed to accumulate one critical portion of DBF under optimal temperature conditions, $\tau(\theta^*)$; and the length of the cycle in a two-temperature regime, which leads to complete chilling negation, π_c (for given alternated temperatures, θ_1 and θ_2 , and for a fixed relation of periods of application of these two temperatures, η).

The objective of this study was to perform computer simulations of the processes studied experimentally by Erez, Couvillon and co-workers under controlled temperatures. The simulations are preceded by an analysis of the experimental data, which allows us to estimate the measurable characteristics of the system. These characteristics are used for evaluation of the parameters of the model. The simulations enable us to calibrate the parameters and to check the main assumptions of the theory. The verified model may be used to simulate dormancy break in other controlled temperature regimes as well as under field conditions.

2. Study of the Basic Characteristics of the System from Experimental Data

The observations performed under constant temperatures by Erez & Lavee (1971) and Erez & Couvillon (1987) led to the conclusions that (i) the maximal response to chilling of dormancy breaking in the peach buds is obtained under temperature

of 6–8°C; and (ii) a zero chilling response appears at temperatures of 13–14°C and higher.

In the experiments by Erez *et al.* (1979a), peach plants were exposed to cyclic temperature regimes, with chilling (4–6°C) and warm (20–24°C) temperatures being alternated. To compare the effects of different cycle lengths, four regimes were examined experimentally, with cycles of 1, 3, 6 and 9 days. During each cycle the plants were exposed to 4–6°C for 2/3 of the cycle length and to 24°C for the remaining 1/3 of the cycle, with all cycles repeated until the plants were exposed to a designated number (1200) of chilling hours. No lateral bud break occurred with variety “Redskin” in the 1-day cycle, a low level was obtained in the 3-day cycle and good bud break occurred in the continuous chilling control and in the 6- and 9-day cycles. With variety “Redhaven” no break was evident in the 1-day cycle, while in the 3-, 6-, and 9-day cycles it responded similarly to the continuous chilling control. Percent of chilling negation (z) was calculated from the formula: $z = 100(1 - r)$, where r is the ratio of the level of bud break in the chilling cycle treatment to the corresponding level in continuous chilling. The degree of chilling negation decreased with cycle length.

In experiments by Couvillon & Erez (1985) on peaches with diurnal cycle, the high temperature (20 or 24°C) was applied 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 h at 4°C. An increased negation effect was observed with increased time of exposure to 24°C. In experiments where the high temperature was 20°C for 2–4 h, a slight enhancement of chilling effect, instead of the negation, was observed. With elongation of the high temperature period a gradual increase in chilling negation occurred. An effect of moderate temperatures on the completion of the rest in the peach buds was recorded by Couvillon & Erez (1985). When 15°C was cycled with 4°C (8:16 h) and compared with a continuous 4°C regime, an enhanced effect by moderate temperature was observed with leaf buds.

These data show that the influence of the dynamics of the temperature conditions on rest release is noticeable and point up the necessity of including temperature dynamics in any model developed to predict rest completion. The model has to describe four major observations relating to temperature effects on rest, namely: (i) the bell shaped dependence of the bud rest break on the temperature; (ii) the dependence of the degree of chilling negation by high temperatures on cycle length; (iii) the promotion of the chilling effect by short periods of high temperature or longer periods of moderate temperature in a daily cycle; and (iv) the dependence of the level of chilling negation by high temperature on the duration of the high temperature application in a daily cycle.

3. Relation of the Theoretical Parameters to the Experimentally Observable Characteristics

The dynamic two-step model involving a cooperative transition developed by Fishman *et al.* (1987) to describe rest completion as influenced by low temperatures, describes qualitatively the four major observed effects. The analysis performed in

the theoretical study results in a system of nonlinear algebraic equations. The equations which relate the parameters of the theory to the values, which can be estimated from experiments, are presented in Appendix 1. This set of nonlinear equations can be solved numerically with theoretical parameters E_0 , E_1 , A_0 and A_1 as unknown variables, and the measurable values θ^* , θ_c , $\tau(\theta^*)$ and π_c (with fixed θ_1 , θ_2 and η) as given constants. The theoretical parameters, obtained in this way, can be used for computer simulations of the processes described by the model under different temperature regimes.

Two basic thermal characteristics can be estimated from observations obtained at constant temperatures (Erez & Lavee, 1971): the optimal temperature ranges from 6 to 8°C and the critical temperature is 13–14°C. In absolute degrees this means $\theta^* = 279$ –281 K and $\theta_c = 286$ –287 K.

The dynamic characteristics of the system can be studied from experiments performed at the cycled temperature regimes (Erez *et al.*, 1979a). From the one-day cycles where 24°C antagonized former chilling at 6°C during 16 hours, it can be deduced that the lack of rest completion means that this interval is insufficient for accumulation of the portion of PDBF which can be fixed at the cool temperature. The appearance of bud break at 3-day cycles means that 1 to 2 days of chilling may be enough to collect at least one critical portion of PDBF. Therefore, $16 < \tau(\theta^*) < 48$ h.

On the other hand, the cycled temperature experiments provide information about the length of the period which results in complete chilling negation. The negation occurs when the cycle length drops from 3 to 1 day, with 24°C for 1/3 and 6°C for 2/3 of the cycle. This means that for $\theta_1 = 297$ K, $\theta_2 = 279$ K and $\eta = 1/3$, the critical period, π_c , is approximately equal to or slightly exceeds 24 hours.

Using an iterative method for numerical calculations (Carnahan *et al.*, 1969), the solution of the system of equations presented in Appendix 1 was found for about 40 sets of constants taken from the analysis of experimental data. Some of the results are presented in Table 1. Columns 2 to 4 in Table 1 represent the sets of constants taken from experiments, while the next four columns give the theoretical parameters

TABLE 1

Parameters of the theory, $E_0(K)$, $E_1(K)$, A_0 and A_1 , evaluated by numerical solution of eqns (A1)–(A4) with the use of $\theta^(K)$, $\theta_c(K)$ and $\pi_c(h)$ listed in columns 2 to 4; the other experimental characteristics used in the calculations were $\tau(\theta^*) = 28(h)$, $\eta = 0.3333$, $\theta_1 = 297(K)$ and $\theta_2 = 279(K)$ except for set No. 1, where $\tau(\theta^*) = 30(h)$.*

No.	θ^*	θ_c	π_c	$E_0 \times 10^{-4}$	$E_1 \times 10^{-5}$	A_0	A_1
1	281	287	24	0.4458	0.1016	0.4197×10^6	0.1797×10^{15}
2	279	286	28	0.3531	0.1114	0.1572×10^5	0.5597×10^{16}
3	279	287	26	0.2874	0.1144	0.1386×10^4	0.1275×10^{17}
4	280	286	26	0.4395	0.1055	0.3703×10^6	0.8083×10^{15}
5	280	287	26	0.3516	0.1153	0.1405×10^{15}	0.1875×10^{17}
6	281	286	24	0.5384	0.1008	0.1375×10^8	0.1868×10^{15}
7	281	287	25	0.4377	0.1120	0.3185×10^6	0.6764×10^{16}

which resulted from the numerical solutions. In addition to the experimental characteristics listed in Table 1, the following constants were used in each set of calculations: $\tau(\theta^*) = 30$ h, $\eta = 0.3333$, $\theta_1 = 297$ K and $\theta_2 = 279$ K for the first line and the same but $\tau(\theta^*) = 28$ h for the rest of the lines. It can be seen that from the four theoretical parameters, the energies, E_0 and E_1 , are less sensitive to the variation of the constants, while the coefficients A_0 and A_1 change the order of magnitude. This is because the energy is involved in the exponential part of the rate constant; so, the nonexponential factor has to be changed markedly to compensate for a small change in the energy, which results in a reasonable variability of the rate constants as a whole.

Simulations performed using the parameters estimated describe qualitatively the four basic effects revealed by the system. However, with all these sets of parameters, the quantitative description of the bell-shaped response curve in the region of temperature lower than 4°C showed a systematic decline: the calculated response was greater than the one observed experimentally. To fit the response curve more accurately, a correction to the first approximation of the theory was made here. The transition from PDBF to DBF was considered in the first theoretical treatment (Fishman *et al.*, 1987) as the temperature-independent one. Now a dependence of this cooperative process on the temperature is taken into account. The probability, P , of transition from PDBF to DBF is included; it depends on the temperature as a sigmoidal curve, like the one used by Tanford (1970) to describe a cooperative phenomenon of protein denaturation

$$P = \frac{\exp(-\Delta G/\theta)}{1 + \exp(-\Delta G/\theta)} \quad (2)$$

where ΔG is the free energy changes caused by transition from PDBF to DBF for the whole group of subunits performing the cooperative transition. As pointed out by Thornley (1981), this form of equation may be used for adequate description of threshold or sigmoidal response exhibit by certain biophysical processes, especially ones related to development phenomena. Due to the thermodynamic relationship $\Delta G = \Delta H - \theta \Delta S$ (with ΔH and ΔS being the enthalpy and entropy portions of ΔG , correspondingly) the transition temperature is defined from $\Delta G = 0$ and is equal to $\theta_f = \Delta H/\Delta S$. Now eqn (2) may be expressed as

$$P = \frac{\exp(\Delta H/\theta_f - \Delta H/\theta)}{1 + \exp(\Delta H/\theta_f - \Delta H/\theta)} \quad (3)$$

The slope, F , of the curve (3) at the point $\theta = \theta_f$ equals to $\Delta H/4\theta_f^2$. The probability approaches 1 at $\theta \gg \theta_f$ and 0 at $\theta \ll \theta_f$. Therefore, if the transition temperature is approximately 4°C ($\theta_f = 277$ K) and the slope is sharp enough, the correction (3) leads to nearly the same results as in the first approximation, but it diminishes the response at $\theta < 277$ K. The slope is chosen as $F = 0.4$ (in K) to fit the observations.

4. Description of the Simulation Procedure

The method used for simulation of the process of DBF accumulation in periodic temperature regimes is valid for each temperature regime, when the temperature

could be assumed to be constant in a given time interval, Δt . According to the model, the dynamics of PDBF accumulation is approximated by the linear differential equation in the time interval where the temperature is constant. The simulation starts with input of the temperature for each Δt followed by calculation of the PDBF amount which is accumulated during this interval according to the linear equation

$$dx/dt = k_0 - k_1 x \quad (4)$$

where x is the level of the PDBF. The level of DBF is designated as y . When x reaches a critical value, the accumulated portion of the PDBF is transferred to the fixed state, DBF, with probability P given by eqn (3); the process described by eqn (4) starts again from $x = x(1 - P)$. Henceforth, x and y will be measured in units of the critical portions. So, the critical (threshold) level of x is $x = 1$. Intervals of one hour are used for simulations. The solution of eqn (4) in the case of constant temperature is

$$x = x_s - (x_s - x_0) \exp(-k_1 t) \quad (5)$$

where x_0 is the value of x at the beginning of the hourly interval. If x_s for the given temperature is less than or equal to one, the critical level is not reached at the end of the first hour, x is calculated according to eqn (5) with $t = 1$, and nothing is added to y . If $x_s > 1$, the threshold occurs during the first hour, which leads to $x_1 = x(1 - P)$ and $y_1 = xP$. At the second hour the procedure is repeated starting from x_1 and y_1 and so on. If a season of 100 days is studied, 2400 data of the hourly temperatures are to be given as the input and the computation is to be repeated 2400 times. For periodic changes of the temperature, an additional loop can be built for the recurrent cycles with identical temperature conditions. The computer program written in FORTRAN language according to this algorithm is given in Appendix 2.

5. Results

To simulate processes observed under conditions of constant temperatures, different sets of the theoretical parameters were checked. Henceforth, the results obtained using the parameters of set No. 1 from Table 1 (which results in the best fitting to the experimental data) are reported. The computerized model was applied for 1200 periods at temperatures from 0 to 16°C. The results of simulation are presented in Fig. 1 as points, connected by a solid line, and compared with the chilling contributions by the respective temperatures recorded by Erez & Couvillon (1987) for "Redhaven" peach leaf buds (circles).

The negation of chilling by high temperatures follows automatically from the dynamic model, as can be seen from simulations of the processes under two-temperature regimes. Similarly to the experimental conditions (Erez *et al.*, 1979a), the cycles of 1, 3, 6 and 9 days were investigated. Chilling constituted 2/3 of each cycle, while warming constituted 1/3. The warming temperature was 24°C ($\theta_1 = 297$ K); the chilling was applied at 6°C for 1-day cycles and at 4°C for the other cycles ($\theta_2 = 279$ or 277 K, respectively). The number of cycles, P , was calculated from the equation

$$2\pi P/3 = 1200 \quad (9)$$

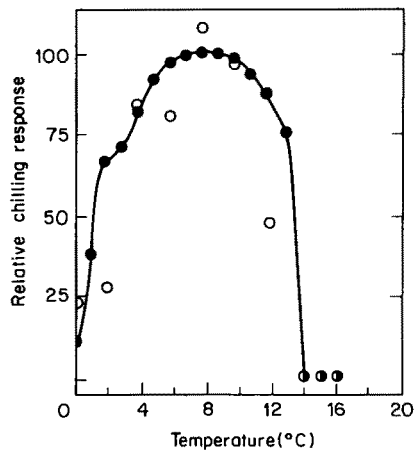


FIG. 1. The temperature-response curve. The number of portions of DBF obtained after 1200 hours of application of constant temperature vs the temperature predicted by the dynamic model (points and solid line), as compared with the chilling contributions by the respective temperatures recorded by Erez & Couvillon (1987) for "Redhaven" peach leaf buds (circles).

which guarantees 1200 hours of chilling time in each run. In the control run, continuous application of 4°C for 1200 h was simulated. With the use of set No. 1 of the parameters from Table 1, the results of the simulation are as follows. The value of y equals 0, 25.4, 30.5, 28.4 and 31.4 for the 1-, 3-, 6-, 9-day cycles and control, respectively. Calculating the chilling negation, z , as defined above, shows that the chilling negation by high temperature drops from 100% to zero with the increase of the cycle length from 1 to 9 days. The results are presented in Fig. 2, which coincides satisfactory with the experimental results obtained by Erez *et al.* (1979a).

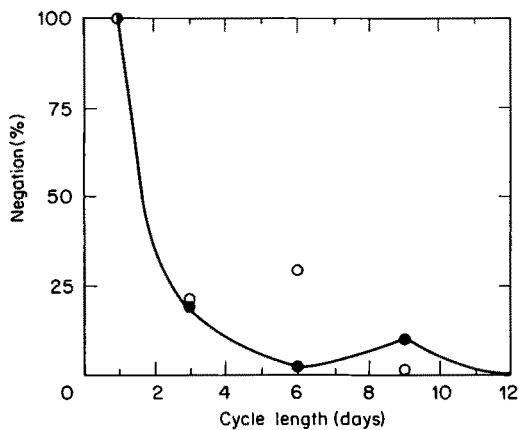


FIG. 2. Influence of cycle length on chilling negation. Percent of chilling negation by high temperature in cycled temperature regime vs cycle length, calculated by the dynamic model (solid line) and observed experimentally by Erez *et al.* (1979a) (circles).

The third set of simulations, performed for the diurnal ($\pi = 24$ h) cycles with different ratios of chill and warm parts of the period, was designed to demonstrate the enhancement of the chilling effect by short applications of high temperatures. The simulations with 2, 4, 6, ..., 22 hours were run each under various temperatures $\theta_1 = 286, 288, 290, 293$, and 297 K with the "optimal" temperature 279 K as θ_2 . The results, obtained using set No. 1 of the theoretical parameters, are presented in Fig. 3. The obtained y -curves show that the level of dormancy completion is greater than in the control (continuous chilling at 6°C) if the applications of high temperatures are not too long. Longer applications lead to negation of the chilling effect. The higher the temperature, the lower the promotion effect and the shorter the interval where it appears. This is in accordance with observations by Couvillon & Erez (1985).

In addition to the simulations reported, calculations are performed which may help in choosing an economically optimal regime in the case where the chilling is applied under controlled temperature conditions. Let us consider a situation where the chilling exposure demands energy, whereas the application of the moderate temperature does not. A simulation was undertaken to compare the diurnal cycled regimes where long exposure (12, 16 and 20 h) to the moderate temperature of 14°C was alternated with chilling at 6°C . Each run was designed for 40 cycles. As a control, a 20 days' run was made with the temperature of 6°C continuously applied during 24 h. The control run results in 14.5 portions of DBF after 20 days. The

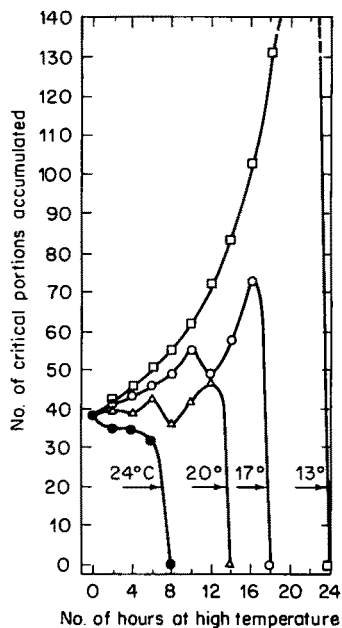


FIG. 3. Dual effect of moderate temperatures on the level of dormancy completion. The level of dormancy completion predicted by the dynamic model vs the number of hours the system spent daily at high (moderate) temperature (arrows), with chilling at 6°C applied during the rest of the day.

number of days needed to reach this level of DBF ($y = 14.5$) at different temperature regimes, as well as the number of chilling hours accumulated during those periods, are given in Table 2, which demonstrates that the regime with long application of moderate temperature may become economically preferable to the continuous chilling. The optimal regime can be evaluated using an optimization program if the costs of chilling and the whole treatment are given.

TABLE 2

Number of days needed to accumulate 14.5 portions of DBF, and chilling hours accumulated during those periods, for different proportions of low (6°C) to moderate (14°C) temperature intervals in diurnal cycle

Treatment (h/day)		Chilling hours accumulated	Number of days needed for $y = 14.5$
Low temp.	Moderate temp.		
24	—	480	20
12	12	276	23
8	16	240	30
4	20	128	32

6. Discussion

The computerized two-step model is used for simulation of the process of dormancy completion under different temperature regimes. In considering the results of simulation, it is necessary to keep in mind that the accuracy of quantitative predictions depends on the accuracy of the parameters, estimated from the major experimentally obtained characteristics which, in turn, are measured with certain variability. For instance, the maximal temperature ranges from 6 to 8°C and the critical one from 13 to 14°C . Taking three maximal temperatures and two critical ones results in six possible combinations of parameters. The kinetic characteristics, τ and π_c , also have ranges, which increases the number of possible sets of the parameters. Therefore, it is useful to compare the orders of magnitude of the theoretically evaluated parameters with independently recorded values. Of the four parameters two are energies of activation of some biochemical or biophysical processes. The energies of activation of the processes involved in the model can be used for calculation of the respective temperature coefficients, Q_{10} 's. The temperature coefficient, evaluated for the minimal energy from those presented in Table 1, is equal to 1.4 , and for the maximal energy $Q_{10} = 3.7$. For the usual chemical reactions the temperature coefficients are known to range from 2 to 3 (Hegarty, 1973). The apparent activity energy estimated by Washitani & Takenaka (1984), for seed germination rates is approximately 100 kJ/mol , which is equal to $12\,028^{\circ}$ in absolute temperature units and is comparable to the energies E_1 reported above in Table 1. Purvis & Gregory (1952), who proposed a multi-stage scheme in their studies of vernalization, estimated a Q_{10} of 2.3 for the rate of the temperature dependent stage.

Therefore, the interval from 1.4 to 3.7 for Q_{10} 's, obtained here for the complicated biochemical processes, may be considered as realistic. The enthalpy changes by the fixation process can be calculated from the slope: $\Delta H = 4FQ_f^2 = 122\,766.4\text{ K}$ for $F = 0.4$. This is equivalent to $\sim 1000\text{ kJ/mol}$. Cooperative transitions in globular proteins are known to result in ΔH of the order of hundreds of kJ/mol. So $\Delta H \sim 1000$ as a rough estimate of the phenomenon observed on the plant level seems to be reasonable.

Simulation of the processes of dormancy breaking, studied before experimentally under controlled conditions, can serve as a verification of the model. Therefore, four effects, mentioned above as major experimental observations, are now studied on the computer model. The No. 1 set of parameters from Table 1 is used for the calculations. Theoretical results of the calculations performed for constant temperatures are presented in Fig. 1 and compared with the relative chilling contributions by the respective temperatures recorded experimentally by Erez & Couvilton (1987) for "Redhaven" peach leaf buds. To describe the chilling negation by high temperatures, the negative chilling units were introduced into the chilling-unit model (Richardson *et al.*, 1974). In the dynamic model (Fishman *et al.*, 1987), the variable y has the meaning of the value of the dormancy breaking factor and cannot be negative. Its dependence on temperature is bell-shaped, but for each temperature equal to or higher than the critical one, the dynamic model predicts $y = 0$.

The negation of the chilling by high temperatures is demonstrated by a simulation of processes at periodically changed temperatures. The biophysical mechanism underlying this phenomenon is the destruction of the thermally unstable precursor by comparatively long exposure of the system to high temperatures. When the intervals of application of high temperatures are short, the precursor is accumulated rapidly, but has not enough time to be destroyed, thereby resulting in the recorded enhancement of dormancy completion.

Simulation of the processes with longer applications of high temperatures results not only in chilling negation, but also in dependence of the effect on the cycle length (see Fig. 2), as recorded previously by Erez *et al.* (1979a). The results of simulations with the shorter applications of high and moderate temperatures are presented in Fig. 3. The experimental data, which are adequate for these calculations, were reported by Couvillon & Erez (1985). The curves predicted by the model are not smooth, but have an oscillation shape. This may be due to a complicated relationship between the inherent dynamic parameters of the system and the dynamics of the externally applied cycled temperature regime. It must be taken into account that, in addition to the biophysical mechanism, which causes the enhancement—there is a specific experimental design which demands a constant time of exposure of the system to low temperature, independent of the level of the high temperature in the cycle.

Evaluations of the regimes where the moderate temperature of 14°C is alternated with chilling at 6°C show the way for search of the optimal conditions for dormancy completion at controlled temperatures. Dormancy completion in buds of deciduous trees is an example of the phenomenon of positive response of plants to low temperature. The communication by Seeley & Damavandy (1985) supports the

concept that the model which describes the role of temperature in breaking of bud dormancy may be useful to describe the response of seed of deciduous fruits to stratification temperature. When the dynamic model is justified for stratification and/or other phenomena of this group (such as induction of the growth of underground storage organs and vernalization), the optimization of chilling conditions will become very important for agricultural practice, because in such cases the chilling is under control.

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APPENDIX 1

The mathematical analysis of the dynamic two-step model involving a cooperative transition was reported recently (Fishman *et al.*, 1987). It relates the theoretical

parameters of the model (E_0 , E_1 , A_0 , and A_1) to the values, which may be estimated from experiments (θ^* , θ_c , $\tau(\theta^*)$, π_c , θ_1 , θ_2 , and η) by means of the following system of nonlinear algebraic equations

$$E_1 = (E_0 - E_1) / \{\exp[(E_1 - E_0)q] - 1\} \ln \{1 - \exp[(E_0 - E_1)q]\} \quad (A1)$$

$$A_1 = -\exp(E_1/\theta^*) \tau^{-1}(\theta^*) \ln \{1 - \exp[(E_0 - E_1)q]\} \quad (A2)$$

$$A_0 = A_1 \exp[(E_0 - E_1)/\theta_c] \quad (A3)$$

$$\{\exp[(E_1 - E_0)/\theta_c] - \exp[(E_1 - E_0)/\theta_1]\} / \{\exp[(E_1 - E_0)/\theta_2] - \exp[(E_1 - E_0)/\theta_1]\} \\ = \{1 - \exp[-k_1(\theta_2)(1 - \eta)\pi_c]\} / \{1 - \exp(-[k_1(\theta_1)\eta + k_1(\theta_2)(1 - \eta)]\pi_c)\} \quad (A4)$$

where $q = 1/\theta^* - 1/\theta_c$.

APPENDIX 2

program cycles

```

dimension tet(250)
open(unit = 1, file = 'enhanjnd.dat', status = 'old')
open(unit = 2, file = 'cycljnd.lis', status = 'new')
n = 0
e0 = 0.44578e+04
e1 = 0.101619e+05
a0 = 0.4197e+06
a1 = 0.1797e+15
e = e1 - e0
tetmlt = 277.
slp = 1.6
do while (n .eq. 0)
  read(1, *, end = 50) np, tet, tet1, nwarm, nhr
  x0 = 0.
  y = 0.
  do 5 l = 1, nhr
5    tet(l) = tet
  do 7 l = 1, nwarm
7    tet(l) = tet1
  do 20 j = 1, np
  do 10 i = 1, nhr
    ftmprt = slp * tetmlt * (tet(i) - tetmlt) / tet(i)
    sr = exp(ftmprt)
    xi = sr / (1. + sr)
    xs = (a0/a1) * exp(e/tet(i))
    ak1 = a1 * exp(-e1/tet(i))
    x = xs - (xs - x0) * exp(-ak1)
    x0 = x
  if (x.ge.1.) then
```

```
delt = x*xi
xo = x - delt
y = y + delt
end if
10 continue
20 continue
   write(2,40) y,teta1, nwarm
40 format (1x,f5.1,3x,f5.1,3x,i5)
   end do
50 stop
end
```