THE DYNAMIC MODEL FOR REST COMPLETION IN PEACH BUDS

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Abstract

A model describing the response of dormant buds in deciduous fruit trees to temperature was developed. The model is based on observations on dormancy breaking under controlled conditions. It assumes that the level of dormancy completion depends on the level of a certain dormancy breaking factor which is accumulated in buds by a two-step process. The first step is assumed to be a reversible process of formation and destruction of a thermally labile precursor. When a critical portion of the precursor is amassed, it is transferred irreversibly in the second step to one portion of a stable factor. The dynamics of this process simulate development during dormancy and agree with the complex effects of temperature on rest completion. The following effects were described by the model: 1. The optimum bell shaped curve of the rest breaking dependence on temperature with maximum efficiency at 6°C and zero effect at -2°C and 14°C. 2. Negation of the chilling effect by high temperatures depending on their level, duration and cycle length when alternating with lower temperatures. 3. Enhancing effect of moderate temperatures on chilling when they alternate with chilling temperatures.

A computer program for simulation of the dormancy completion process was developed. The program is written in FORTRAN and is easily accessible with most computers. Simulation of dormancy breaking under cycled temperature condition was carried out using the STELLA program (High Performance Systems, Inc. developed for simulation of dynamic phenomena for the Apple Macintosh). The graphs generated during the simulations are presented in this communication.

The Dynamic model was compared with the Chill-Units model, developed in Utah, for five locations in South Africa during winter 1988. A good correlation of the two models was found for the coldest region whereas in warmer ones the results of the two models diverge; the warmer the location the greater the difference. The

Dynamic model gives the best indication of effective winter chilling in both cold and warm areas.

1. Introduction

The field of modelling rest development and completion attracted considerable attention during the last 25 years [Erez et al. (1988), Fishman et al. (1987 a and b), Gilreath and Buchanan (1981), Richardson et al. (1974), Seeley and Damavandy (1985) and Shaltout and Unrath (1983)]. The reason for this was the need to know the actual stage of rest completion prior to bud break in order to decide on corrective measures in orchard management.

Rest development and completion is an isolated process controlled by temperature in a rather complicated way. In order to fully simulate the response of the dormant bud, one has to consider all the main factors that are affecting the process.

The Utah model, the most commonly used model today, is based on 3 elements [Richardson et al. (1974)]:

1. Chill units are accumulated and must reach a certain level for each cultivar and species in order to allow a high level of budbreak.
2. The chilling effect that advances rest completion has an optimum at 6°C and is lost at 0°C and 12.5°C.
3. Temperatures higher than 16°C have negative values depending on temperature level.

The Dynamic model adds another important element viz. timing of exposure to temperatures in a cycle which markedly influences rest advancement. It also incorporates more detailed responses of the bud to temperature based on experimental data with peach plants [Erez and Lavee (1971), Couvillon and Erez (1985), Erez and Couvillon (1987), Erez et al. (1979a and b)]:

1. The optimum bell shaped curve for dependence of rest breaking on temperature shows maximum efficiency at 6 to 8°C and zero effect at -2°C and 13°C.
2. Negation of the chilling effect by high temperatures depends on their level, duration and cycle length when alternating with lower temperatures.
3. Moderate temperatures, while having no rest breaking effect, will enhance the chilling effect when occurring alternately with chilling temperatures.

In the Dynamic model it is assumed that the level of dormancy completion depends on the level of a certain dormancy breaking factor which is accumulated in buds by a two-step process. The first step is a reversible process of formation and destruction of a thermally labile precursor. When a critical portion of the precursor is amassed, it is transferred irreversibly in the second step, to one portion of a stable factor. The dynamics of this process simulate rest development and agree with the complex effects of temperature on rest completion.

2. The Dynamic model - theory

Rest completion is assumed to be dependent on the accumulation of some chemical (enzyme) or physical (structure) changes in plants. We have termed this factor "Product". On the basis of experimental evidence this factor is assumed to have a thermally labile intermediate ("Intermediate"). Following Erez and Couvillon's [1987] suggestions, a two-step process is thus considered to be responsible for the changes in the buds leading to rest breaking:

$$\text{Precursor} \underset{k_1}{\overset{k_0}{\rightleftharpoons}} \text{Intermediate} \dashrightarrow \text{Product} \qquad (1)$$

The first step is a reversible process of formation and destruction of the intermediate. The second step is suggested to act as a cooperative transition: when a critical level (quantum) of the intermediate is amassed, it is transferred irreversibly to a quantum of stable product. The rate constants for formation (k_0) and destruction (k_1) of the Intermediate are assumed to obey the Arrhenius law [France and Thornley, 1984]:

$$k_{0,1} = A_{0,1} \exp(-E_{0,1}/T) \qquad (2)$$

where T is temperature in absolute degrees (^{o}K); E_0 and E_1 are energies of activation for formation and destruction of the intermediate respectively, in absolute temperature units (^{o}K); and A_0 and A_1 are coefficients independent of the temperature, having the same dimensions as k_1 and k_1, respectively. All temperature effects may be described by using only the parameters E_0, E_1, A_0, and A_1 as was shown before [Fishman et al. 1987 a and b]. The simplest dynamic equation adequate to the first step of the scheme (1) is the linear one:

$$db/dt = k_0 - k_1 b \qquad (3)$$

where b is the level of the Intermediate. If the temperature is constant, the solution for b is a smooth curve:

$$b = b_s - (b_s - b_0) \exp(-k_1 t) \qquad (4)$$

where b_s is the steady state level ($b_s = k_0/k_1$) and b_0 is the initial value of b. If the steady state exceeds a critical level b_c (Fig.1 T_1,T_3 or T_4), one portion of intermediate (b) is passed to one portion of the product (c), while b drops to zero and the dynamic curve exhibits a periodic form (Fig 2 a and b). If the steady state is below the critical level b_c, the transition from b to c will never occur and rest will not be completed (Fig1 T_2, Fig 2 c).

Analysis of the solution of eq. (4) shows that, early on the time scale, the initial slope of the b curve is greater, the higher the temperature independent of the parameter values (Fig 1). On the other hand, the level of the asymptotic lines for different temperatures depends on the parameters E_0 and E_1. Since E1 is involved in the destruction of the intermediate which occurs at high temperatures, then $E_1 > E_0$. As a result, the higher the temperature, the lower the steady state will lie in agreement with the pattern of behavior of the dormant bud. The dependence of accumulation of b on temperature is not monotonous, but has a maximum [Fig 3 in Erez et al. 1988]. It is important to note that according to the Dynamic model, any change of temperature will cause a shift from one steady state to another, corresponding with the other temperature. This explains the negation of the chilling effect by high temperatures. Using the model to compare short cycles of low and high temperatures shows that the critical level has not been reached during the cold portion of the cycle, and the accumulated 'b' level drops when temperature is elevated, to follow the dynamic steady state of its temperature [Fig 4 in Erez et al. 1988]. Analysis of the resulting curve shows that as this combined asymptote is lower than the critical level, no product is accumulated and hence no rest breaking is obtained, in spite of a long exposure to chilling temperatures. When a moderate temperature, T_2, is applied during time t_1 (Fig. 1) and then the temperature changes to the chill one, T_1, the chilling regime starts now from the point $b = b_1$ which may be higher than the respective point in the case of continuous chilling (b_2). The dynamic curve for T_2 does not intersect with the critical line bc , which means that continuous application of this temperature results in zero accumulation of product and hence in no rest breaking. The curve for T_1 intersects with the critical level at time t_3, which means that the time t_3 is needed for production of one portion of product. The combined dynamic curve T_3 crosses the critical line at t_2 earlier than the curve of the continuous chilling, which means that more portions of product are produced during the same period of time in the combined regime than with the continuous chilling. The enhancing effect is amplified when the length of the cycle is close to the time needed for achieving the critical level and when the exposure to moderate temperature is short enough. During the cycle, longer exposure period to moderate temperature leads to a reduced chilling effect, as the respective dynamic curve crosses the critical line later (Fig. 1 at t_4) than the curve for the continuous chilling (Fig. 1 at t_3). However, per unit of chilling, this is the most efficient combination.

With all these sets of parameters, the calculated quantitative bud break response of the bell-shaped curve in the region of temperatures lower than 4^{o}C was greater than the one observed experimentally. Thus a correction to the first approximation of the theory that the transition from intermediate to the product is temperature-independent has to be limited to temperatures $\geq$ 4^{o}C. Below this temperature, it seems that temperature has a positive effect on the transition from intermediate to product. To estimate this effect, we adopted the dependence of a sigmoidal curve, like the one used by Tanford [1970] to describe a cooperative phenomenon of protein denaturation.

If the transition temperature is approximately 4^{o}C and the slope of the sigmoid curve is sharp enough, the correction leads to nearly the same results as in the first approximation, but the response diminishes at temperatures lower than 277^{o}K. The slope value was chosen as 0.4 (in ^{o}K) to fit the observations [Fishman et al. 1987b]

Simulation of the dynamic changes in the level of intermediate and product in the course of 240 hours under various continuous temperatures with the Stella program (Fig 2) illustrates the work of the model. While at 6^{o}C 8 portions where accumulated in 10 days, 6 only were accumulated at 12^{o}C and none at 14^{o}C. In the last case the steady state level never reached the critical level.

3.Comparison of field observations with the Dynamic and the Utah models

Climatic and phenological data were collected from 5 locations in the Cape Province of South Africa in 1988. These locations were quite different in their winter climate and in the level of bud break which the 3 nectarine cultivars examined exhibited (Table 1).

It is clear there is a series of increasing exposure to chilling from Robertson to Esperanto. Vegetative bud break for Fantasia and Flavortop were the lowest for Robertson with maximum levels obtained at Zeekovlei. The chilling needed by these two cultivars was supplied already in this location. Sunlite on the other hand had its chilling requirements fulfilled in the warmer Robertson so that no further improvement was observed in the cooler locations.

When comparing the two models, it is obvious that the Utah model accentuates the differences among locations compared to the Dynamic model. Chill units accumulated in Robertson reached only 202 CU against Esperanto with 1071 an increase of 430% while chilling portions did not vary as much among locations with an increase of only 72% between the extremes. Percent vegetative bud break with Fantasia and Flavortop showed a relatively small difference among locations which points to the Dynamic model as a better simulator of the actual effective rest breaking conditions.

Furthermore, The number of CU accumulated in Robertson are far below the requirement for dormancy release according to the Utah model and cannot explain the level of bud break obtained. Under constant low temperature of 6^{o}C, 42 days were required for a medium level of bud break in the Fantasia nectarine (unpublished results). This amounts to 1008 CU and to 36 portions with the Dynamic model. The latter value is similar to what was obtained in Bien Donne and a little higher than what was accumulated in Robertson whereas the number of CU is five times greater than that actually recorded at Robertson.

Comparison of the accumulation of CU and Chill portions x 20 throughout the winter in these 5 locations (Fig 3) shows a very good agreement in Esperanto, the coldest location, small divergence in the next 2 coldest locations (Theewaterskloof and Zeekoevlei) and strong divergence in the 2 warmest locations (Bien Donne and Robertson). The Utah model seems not to work in relatively warm winter locations as has previously been reported [Del Real Laborde (1986)] and as can be seen from the levelling off of the CU number at Robertson after 90 days due to the high negative CU accumulation. On the other hand, the number of Dynamic model portions increased steadily upto 140 days from May 1. Thus the Dynamic model seems an improvement on the chill-unit model as it simulates better the effect of winter temeratures in warm areas .

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Table 1. Chill units (Utah model) and chilling portions (Dynamic model) accumulated in 5 locations in South Africa in the period May 1 till August 31 as compared to the % vegetative bud break with 3 nectarine cultivars in these locations.

Location	Utah M. CU	Dynamic M. Portions	% vegetative bud break Fantasia	Flavortop	Sunlite
Robertson	202	32.6	46.0	32.9	52.4
Bien Donne	475	38.5	58.1	58.4	58.1
Zeekoevlei	677	39.4	77.0	72.5	48.3
Theewaterskloof	779	47.8	70.4	59.2	44.2
Esperanto	1071	56.0	69.0	55.0	53.0

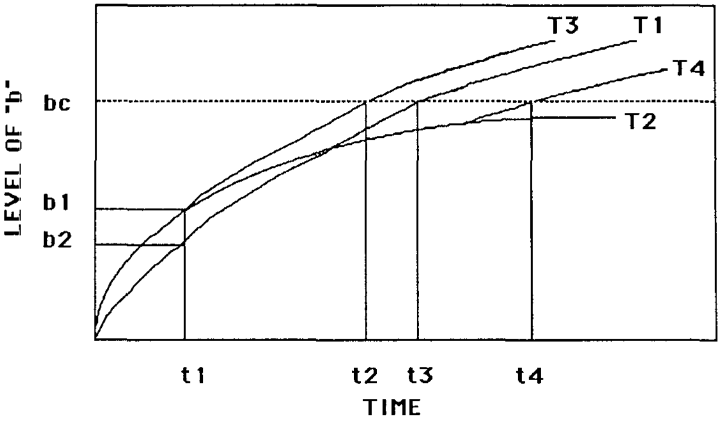

FIG. 1 The effect of moderate temperature alternating with chilling on the dynamics of the accumulation of the intermediate rest breaking factor 'b'.

T_1 = chilling temperature e.g. 6°C, T_2 = moderate temperature e.g. 15°C, T_3 and T_4 = T_2 then T_1.

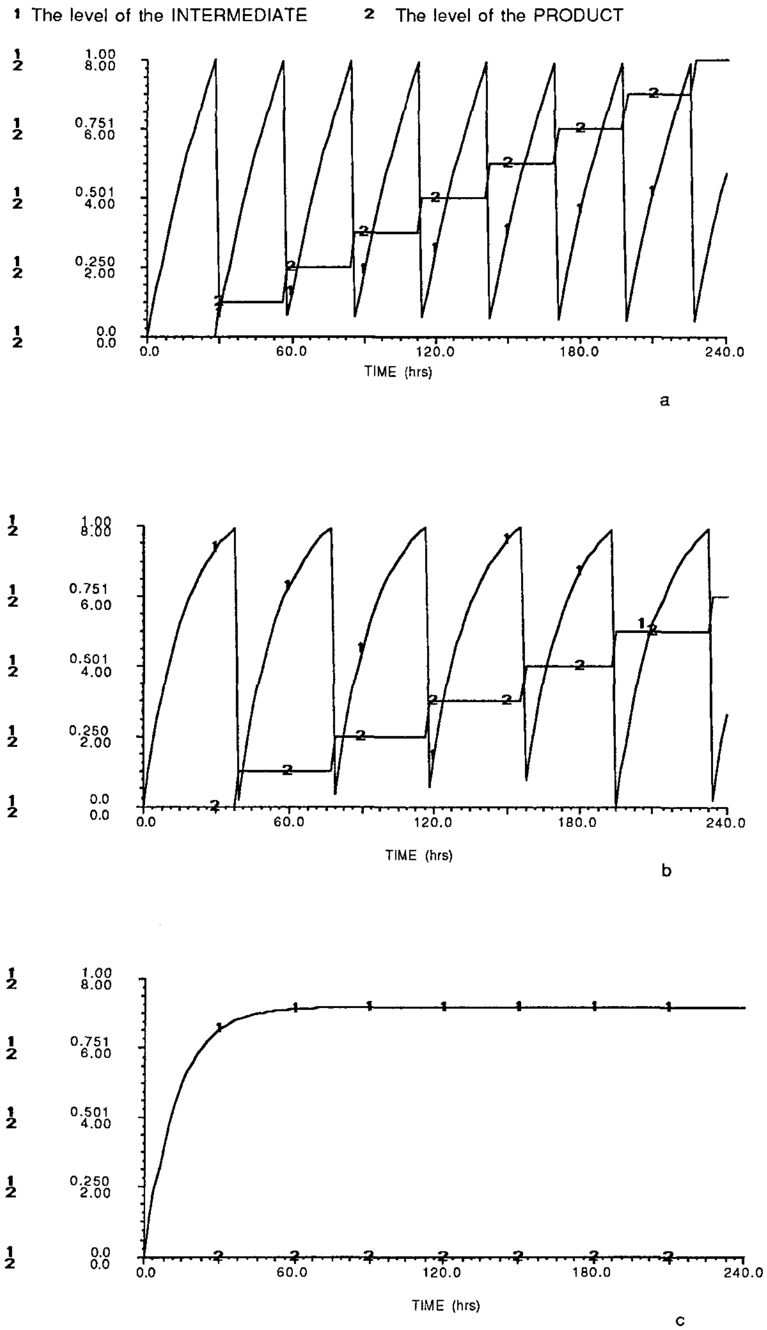

Fig. 2: The dynamics of the changes in the level of the intermediate (Curve 1) and the product (curve 2) in the course of 240 hours at 6^{o}C-a; 12^{o}C-b; and 14^{o}-c

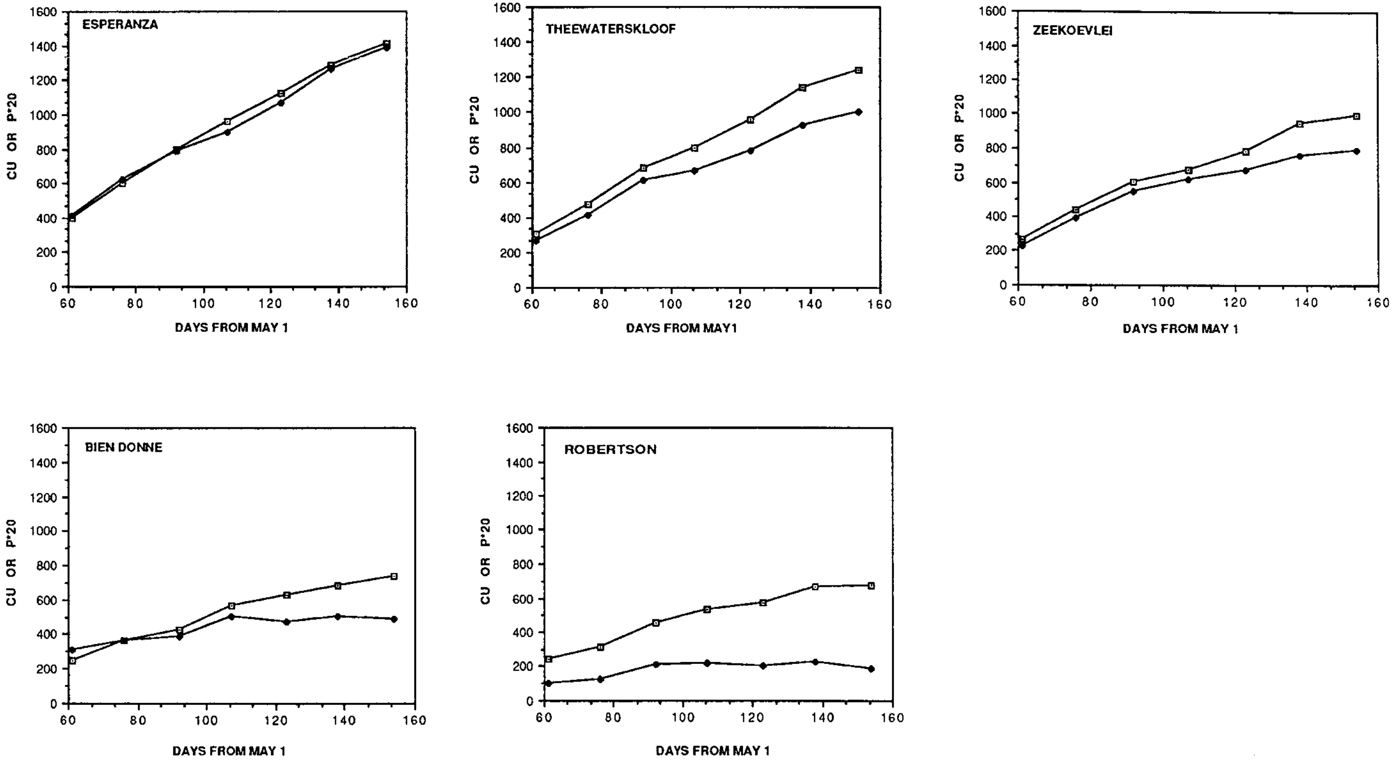

Fig. 3: Accumulation of chilling in 5 locations in South Africa according to the Utah chill-unit model and the dynamic model. Chill unit model (CU) = circles; Dynamic model (Portions x 20) = open squares.