Optimization of Endodormancy Release Models, Using Series of Endodormancy Release Data Collected in France

M. Bonhomme, R. Rageau and A. Lacointe
Unité Mixte de Recherche (UMR) 547
Physiologie Intégrée de l'Arbre Fruitier et Forestier (PIAF)
Institut National de la Recherche Agronomique (INRA)
site de Crouël, 234 avenue du Brézet, F-63100, Clermont-Ferrand
France

Keywords: endodormancy, peach, *Prunus persica*, optimization, chilling, one-node-cutting test, endodormancy release models

Abstract

Evaluation of endodormancy release models in temperate fruit tree species has generally been indirect, as a component of the global evaluation of bud break-date models that include an endodormancy release module. Due to the lack of data, their direct evaluation based on the knowledge of the dynamics of bud dormancy states has been very succinct. Consequently, these models have not been optimized, except for the 'amount of chill units required to break endodormancy' taken as the genotype specific parameter. As part of different studies on bud state during the rest period, near 30 yearly dynamics of the dormancy state of 'Redhaven' peach vegetative buds under natural conditions have been recorded, based on the biological 'one node cuttings' test under standard conditions (25°C). These data were used to optimize classic models (Weinberger-W; Utah-U, etc.) of endodormancy release in fruit tree species with temperature as the only input variable, in order to compare their goodness of fit and their predictive capacity. The fitted parameters were the 'amount of chill units required to break endodormancy', those of the temperature functions f(T) describing the rate of endodormancy development and, when relevant, the starting date of endodormancy release. The results and practical conclusions for predicting dormancy release date are presented. The optimization method used was the minimization of the mean square error (MSE) between the observed (biological test) and the computed dates of endodormancy release and was carried out using the *nls* module of R software. As main results: the optimization of the W model resulted in an increase of the standard threshold temperature; the endodormancy release effect of negative temperatures (up to freezing injury) in the optimized form of U model that was not taken into account in the standard form; the sharp transition from positive to negative f(T) values for the temperatures above 12°C , in the optimized U model; and the fact that the model of Weinberger is a particular form of smoothed Utah model.

INTRODUCTION:

It is known that lack of chilling occuring under mild winter conditions results in abnormal pattern of budbreak and development in temperate fruit trees (Jacobs et al., 1981; Couvillon and Erez, 1985; Erez and Couvillon, 1987; Dennis, 1985, 1987; Mauget and Rageau, 1988; Lam Yam, 1989; Balandier et al., 1993; Cook and Jacobs, 1999; Améglio et al., 2000). Usually a drastic chilling deprivation provokes an erratic bud break and only few buds break, mainly at the base of the twigs. Moreover, in contrast to vegetative buds, 'strictly floral' buds (their primordia are only floral), as those of peach tree, are well known to die under prolonged mild winter temperature. Monet and Bastard (1971) and Bonhomme et al. (1997) observed that all the floral primordia died within 6 months in peach trees under a total cold deprivation treatment. When chilling deprivation is less drastic, terminal buds break as well as buds at the base of the twigs, with a zone with poor bud break between these two portions of stem.

Chilling requirements are considered as always satisfied during the winter period under temperate climates. But this could change in the global warming context and some predictions obtained by models explicitly point out the possible occurrence of dormancy release problems (Honjo, 2007). In these conditions setting more accurate dormancy release models will be of interest also for temperate zones.

In fruit tree species evaluation of models of endodormancy release has generally been indirect, as part of the global evaluation of bud break/blooming models that include an endodormancy release sub-model. Data suitable for the direct evaluation based on the dynamic state of bud dormancy have been very limited. Due to the lack of data, models in the literature have not been optimized, except for the 'amount of chill units required to break endodormancy' taken as the genotype specific parameter. Nevertheless, optimization involving all relevant parameters would likely improve the endodormancy release models.

Since the late 1960s, as part of different studies on bud state evolution during the rest period, near 30 yearly dynamics of the dormancy state of 'Redhaven' vegetative buds under natural conditions have been recorded. Main datasets were based on the results of 'one node cuttings' test which yields the delay to bud breaking under standard conditions (25°C) allowing then to determine the bud dormancy status.

In the present study, these data were used to optimize and compare classic models of endodormancy release in fruit tree species with temperature as the only input variable. The predictive value of the optimized models obtained was checked on independent datasets.

MATERIALS AND METHODS

Plant Material

Experiments were mainly carried out in an orchard located in Clermont-Ferrand (45°N;3°E, France). 'Redhaven' peach trees grafted on GF305 were fertilized with 150 U of nitrogen and normally protected against insects and fungi. The soil is a deep chalky clay with ground water located ca. 2 meters in depth.

Data from orchards in the mid-Rhone valley (5 years between autumn 1973 and spring 1978) were used as independent series in testing the optimized forms of the models.

Test of Endodormancy

The "one node cuttings" test (Rageau, 1978) was applied to the vegetative buds. This test reveals whether the growth of a bud is (or is not) inhibited by endodormancy, paradormancy or ecodormancy. The longer the duration of the action of a forcing temperature (25°C) needed to obtain budbreak (TB) on cutting, the stronger the intensity of the endodormancy or longer the remaining growth path until bud break (i.e., ecodormancy). At each sampling date and for each treatment, 25 cuttings randomly sampled were used and the mean time to budbreak (MTB) calculated from the individual TB.

Previous studies made it possible to determine the threshold level of MTB at 12 days (MTB12) as corresponding to the transition endo/ecodormancy in 'Redhaven' peach tree (Balandier et al., 1993; Bonhomme et al., 2000).

Dormancy Release Models Used

In all models, the common idea is that any bud has to pass from an initial maximum endodormancy state to a second (endodormancy released) through the action of chilling temperatures. The form of the response curve to the temperature differs from one model to another as shown at Figure 1. The parameters of these different curves of chilling response by buds regarding the temperature received could be optimized.

As example, only 3 of the classical models found in the literature will be presented here.

1. Weinberger (1950) (Fig. 1A). For this ancient model, three parameters are used and could be optimized: the starting date (t0) for chilling accumulation, the threshold temperature (T1) of chilling effect, and the level of chilling requirements (R).
2. Utah (Richardson et al., 1974). In the original form (Fig. 1B), the starting date t0 is determined by the model as the date where chilling accumulation reaches the absolute minimum in autumn. Then six thresholds of increasing temperature are used and could be optimized (Tmin the temperature for a 0.5 positive effect, T1 the temperature for a 1.0 positive effect, T2 the temperature for a 0.5 positive effect, T3 the temperature for zero positive effect, T4 the temperature for a 0.5 negative effect and Tmax the temperature for a 1.0 negative effect) and the level of chilling requirements (R).

We used also a smoothed form of Utah (SU – Fig. 1C). The slope at Topt and T3 is null, T3 is determined by the slope at T2. So, only three temperatures (T1, Topt for the maximum positive effect and T2 the temperature where the chilling effect returns to zero) are used and could be optimized, with the slope at T2, the chilling requirement level (R) and the maximum of negative effect resulting from warm temperatures.
3. Dynamic Model (Fishman et al., 1987a, b). This model is based on the analogy with a double biochemical reaction, the first one reversible and the second one non reversible (Fig. 1D). It takes into account a reversible effect of warm temperatures at the daily step, then, when a critical level of chilling effect is reached, a 'portion' of the chilling requirement is considered as definitively obtained. The starting date (t0) is determined by the model, 5 specific parameters (e0, e1, a0, a1 resulting of the non linear system of equations of the model and slp, a coefficient correcting the influence of temperature below 4°C) and R could be optimized.

Method for Optimization

The optimization method consisted in minimizing the mean squared error (MSE) between the actual given by the cuttings test (through date of MTB12) and computed dates of dormancy release. The fitted parameters were the 'amount of chill units required to break endodormancy', those of the temperature functions describing the rate of endodormancy development and, when relevant, the starting date of endodormancy release.

This was made by running non linear regression for the considered parameter of the model using the *nls* module of R software.

RESULTS

Standard Form of the Models and Optimization

1. Weinberger. The relationships between the date of endodormancy release obtained with the one node cutting test and with the classical and the optimized parameterization of the model are given in Figure 2. The threshold temperature raised 11.1°C and consequently the requirements were modified (1466 hours below 11.1°C vs. 900 hours below 7.2°C).
2. Utah. For the original form (U) and the smoothed form of the model (SU), the relationships between the date of endodormancy release obtained with the one node cutting test and with the optimized parameterization of the model, compared to the results with standard U configuration, are given in Figure 3. For both forms, the negative temperature has to be considered as having a real chilling effect. The threshold temperature between positive and negative effects was around 12°C. The negative effect of temperature occuring above 12°C was lower than in standard form. The chilling requirement was increased (from 870 to 1450 chilling units) in the optimized model compared to the standard form. The residual error was divided by 2.
3. Dynamic Model. The relationship between the date of endodormancy release obtained with the one node cutting test and (i) the classical or (ii) the model with optimized parameterization are given in Figure 4. Only the slp parameter and the requirements were modified in the optimized form, but the residual error was greatly decreased.

Predictive Value of the Optimized Forms of the Models

A second series of DMD12 data corresponding to 6 different years and site (5 from the mid-Rhone valley and 1 from Clermont-Ferrand) were used to assess the predictive value of the optimized models. As example, the predictive value of the optimized Smoothed Utah model and the optimized Dynamic model can be evaluated through the relationship between predicted dates of endodormancy release and observed DMD12 dates (Fig. 5A and B, respectively).

DISCUSSION

Parameters Values

All the optimized models were obtained with an increase of the threshold temperature for effective chilling action compared to the standard values. Temperatures up to 12°C have a positive effect on chilling satisfaction. Above this value, a negative temperature effect was confirmed as in U and SU, but weaker than in the original form of the model. This is in agreement with agronomical observations in mild winter areas where budbreak was observed whereas classical models (Weinberger mainly) did not accumulate any chilling effect (Lam Yam, 1989; Balandier et al., 1993). The threshold temperature in the Dynamic model is close to this level (13°C) and this point could partly explain the better results obtained with this model in subtropical areas (Erez et al., 1988, 1990).

It is known that mild or high temperature during fall and winter could provoke developmental problems or necrosis independently to the chilling requirement satisfaction (Legave et al., 1982). So, the weaker negative effect of the temperatures above 12°C for the endodormancy release process in vegetative peach buds revealed by this study does not concern the sensibility of the floral buds and the possibility of developmental problems.

As concerns the dynamics of chilling accumulation during fall and winter (data not presented), the dates of endodormancy release predicted by the Utah or Dynamic models (in our conditions) appeared generally very early induced. These observations point out the real influence of the first fresh temperatures received by buds at fall and the impact of the starting date for chilling accumulation found in the models. Theoretically, the chilling accumulation should start once the maximum endodormancy has been reached. This corresponds to early October concerning peach vegetative buds in temperate climate but it could be very different in mild winter conditions. This maximum of endodormancy is rarely determined by accurate biological observations (except in Cook and Jacobs, 2000) so it is difficult to optimize the models for subtropical areas regarding the starting date parameter.

Weinberger as a Particular Case of Utah Model

The Weinberger model could be considered as one particular form of the more general smoothed-Utah model. It is the form obtained when low temperatures (including freezing temperature up to damage threshold) have to be considered as effective regarding chilling requirements satisfaction in the Utah formalism. This is the case in our optimization, in opposition with Sugiura et al. (2002) who found that negative temperatures should not be considered as effective for flower buds of Japanese pear.

The Best Model for French Situation

The best results were obtained with the optimized smoothed Utah model with positive chilling effect of freezing temperatures and a threshold temperature at 12.2°C between positive and negative effect of temperature in chilling (Fig. 6).The maximum negative effect of warm temperature is weaker than in the original model (-0.4 action vs. -1 action). As a result, the optimized smoothed Utah model looks like a Weinberger model. The optimized Dynamic model, which needs heavier parameterization gives results close to the optimized smoothed Utah.

CONCLUSIONS

In our conditions (Centre of France) the temperature should be considered effective in releasing endodormancy up to freezing negative values and up to 12°C. The negative effect of warmer temperatures should be introduced in models. Between 12° and 18°C an increasing negative effect should be considered but weaker than given in the literature. This could have a particular influence during October.

The best optimized model for French conditions is given by a simplified smoothed Utah model.

Further study will consist in testing a larger panel of data and also assessing the introduction of the optimized endodormancy release model as sub-model into budbreak/bloom phenological model. This will likely improve them and could be very interesting for phenological predictions in the global change context.

Literature Cited

Améglio, T., Alves, G., Bonhomme, M., Cochard, H., Ewers, F., Guillot, A., Julien, J.L., Lacointe, A., Petel, G., Rageau, R., Sakr, S. and Valentin, V. 2000. Winter functioning of Walnut: involvement in branching processes. p.230-238. In: L'Arbre, Biologie et développement. Isabelle Quentin, Montréal (CAN).

Balandier, P., Bonhomme, M., Rageau, R., Capitan, F. and Parisot, E. 1993. Leaf bud endodormancy release in peach trees: evaluation of temperature models in temperate and tropical climates. Agric. For. Meteor. 67:95-113.

Bonhomme, M., Rageau, R. and Gendraud, M. 2000. Influence of temperature on the dynamics of ATP, ADP and non-adenylic tri-phosphate nucleotides (NTP) in vegetative and floral peach buds during dormancy. Tree Physiol. 20:615-621.

Bonhomme, M., Rageau, R., Richard, J.P. and Gendraud, M. 1997. Dormancy of peach floral buds: biological and tentative biochemical approaches. Acta Hort. 441:167-174.

Cook, N.C. and Jacobs, G. 1999. Suboptimal winter chilling impedes development of acrotony in apple shoots. HortScience 34:1213-1216.

Cook, N.C. and Jacobs, G. 2000. Progression of apple (*Malus* × *domestica* Borkh.) bud dormancy in two mild winter climates. J. Horticult. Sci. Biotechnol.75:233-236.

Couvillon, G.A. and Erez, A. 1985. Effect of level and duration of high temperatures on rest in the peach. J. Amer. Soc. Hort. Sci. 110:579-581.

Dennis, F.G., Jr. 1985. Temperate zone fruits in the tropics: problems and prospects. Acta Hort. 158:41-46.

Dennis, F.G., Jr. 1987. Producing temperate-zone fruits at low latitudes: an overview. HortScience 22:1226-1227.

Erez, A. and Couvillon, G.A. 1987. Characterization of the influence of moderate temperatures on rest completion in peach. J. Am. Soc. Hort. Sci. 112:677-680.

Erez, A., Fishman, S., Gat, Z. and Couvillon, G.A. 1988. Evaluation of winter climate for breaking bud rest using the dynamic model. Acta Hort. 232:76-89.

Erez, A., Fishman, S., Linsley Noakes, G.C. and Allan, P. 1990. The dynamical model for rest completion in peach buds. Acta Hort. 276:165-174.

Fishman, S., Erez, A. and Couvillon, G.A. 1987a. The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. J. Theor. Biol. 126:309-321.

Fishman, S., Erez, A. and Couvillon, G.A. 1987b. The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. J. Theor. Biol. 124:473-483.

Honjo, H. 2007. Effects of global warming on dormancy and flowering behavior of temperate fruit crops in Japan. Hortic. Res. 6:1-5.

Jacobs, G., Watermeyer, P.J. and Strydom, D.K. 1981. Aspects of winter rest of apple trees. Gewasprod., Crop Prod. 10:103-104.

Lam Yam, L. 1989. Contribution à l'étude de la croissance et de la fructification du pêcher (*Prunus persica* L. Batsch) dans les conditions climatiques de type tropical de l'île de la Réunion. Fruits 44:669-680.

Legave, J.M., Garcia, G. and Marco, F. 1982. Some descriptive aspects of drops process of flower buds, or young flowers observed on apricot tree in south of France. Acta Hort. 121:75-83.

Mauget, J.C. and Rageau, R. 1988. Bud dormancy and adaptation of apple tree to mild winter climates. Acta Hort. 232:101-108.

Monet, R. and Bastard, Y. 1971. Effets d'une température modérément élevée: 25 degrés C, sur les bourgeons floraux du pêcher. Physiol. Vég. 9:209-226.

Rageau, R. 1978. Croissance et débourrement des bourgeons végétatifs de pêcher (*Prunus persica* L. Batsch) au cours d'un test classique de dormance. C.R. Acad. Sci. Paris, Série D: 287:1119-1122.

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

Sugiura, T., Kuroda, H., Honjo, H. and Ito, D. 2002. Temperature dependence of endodormancy development in flower buds of 'Kousui' Japanese pear and a model for estimating the completion of endodormancy. Acta Hort. 587:345-351.

Weinberger, J.H. 1950. Chilling requirements of peach varieties. Proc. Amer. Soc. Hortic. Sci. 56:122-128.

Figures

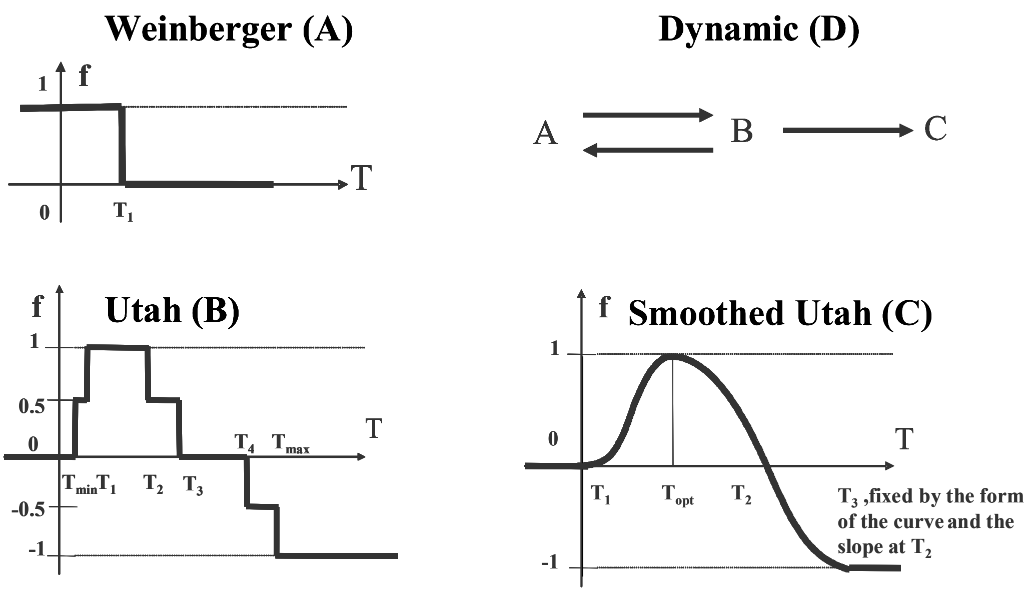
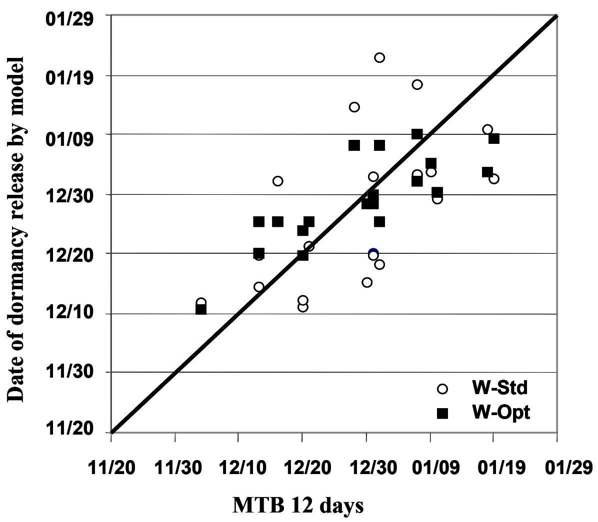
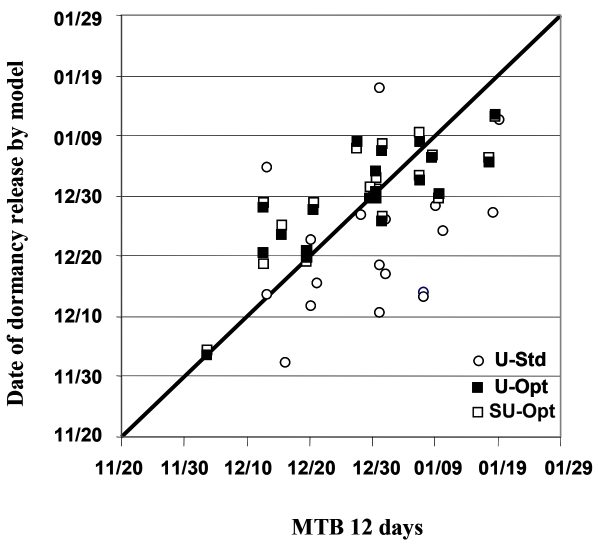


Fig. 1. Standard forms of the chilling response of buds f(T) to the temperatures for the models used.



W	standard	optimized
Starting date	10/01	10/01
T1(°C)	7,2	11,1
Requirement (h)	900	1466
Mean date	25 Dec	27 Dec
std dev (days)	12,7	7,4
SCE	2575	1106
Resid error (days)	11,3	7,4

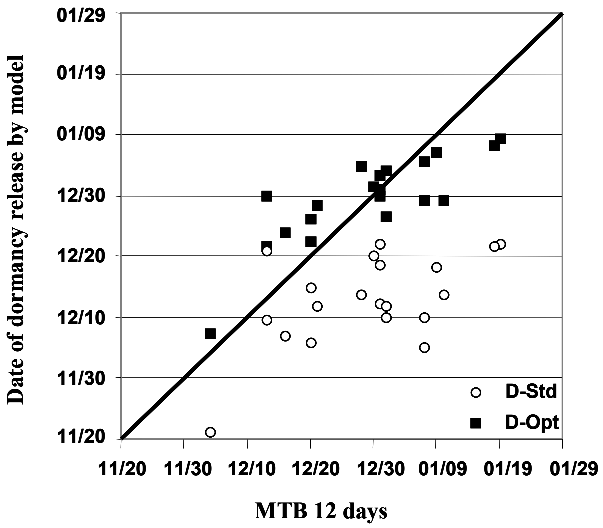
Fig. 2. Standard and optimized parameters of the Weinberger model and the relationships between MTB 12 days and the date of endodormancy release given by the model in standard form (Std) and optimized form (Opt).



U original	standard	optimized
T min (°C)	1,5	-200
T1(°C)	2,5	-100
T2 (°C)	9,2	10,9
T3 (°C)	12,5	11,8
T4 (°C)	16	16
Tmax (°C)	18	18
Requirement (CU)	870	1452
Mean date	18 Dec	27 Dec
Std dev (days)	15,1	9,0
SCE	4867	963
Resid error (days)	15,6	6,9

SU	standard	optimized
Heat Action	-1	- 0,4
T opt (°C)		12
T1 (°C)		-700
T2 (°C)		12,2
Requirement (CU)	870	1482
Mean date	18 Dec	30 Dec
Std dev (days)	15,1	9,0
SCE	4867	964
Resid error (days)	15,6	6,9

Fig. 3. Standard and optimized parameters of the Utah model (original form U and smoothed form SU) and the relationships between MTB 12 days and the date of dormancy release given by the two form of the model in standard form (Std) and optimized form (Opt).



D	standard	optimized
e0	4,154E+03	4,154E+03
e1	1,289E+04	1,289E+04
a0	1,395E+05	1,395E+05
a1	2,567E+08	2,567E+08
slp	1,6	0
Requirement (portions)	45	48
Mean date	11 Dec	28 Dec
Std dev (days)	7,5	7,2
SCE	7284	1214
Resid error (days)	19,1	7,4

Fig. 4. Standard and optimized parameters of the Dynamic model and the relationships between MTB 12 days and the date of dormancy release given by the model in standard form (Std) and optimized form (Opt).

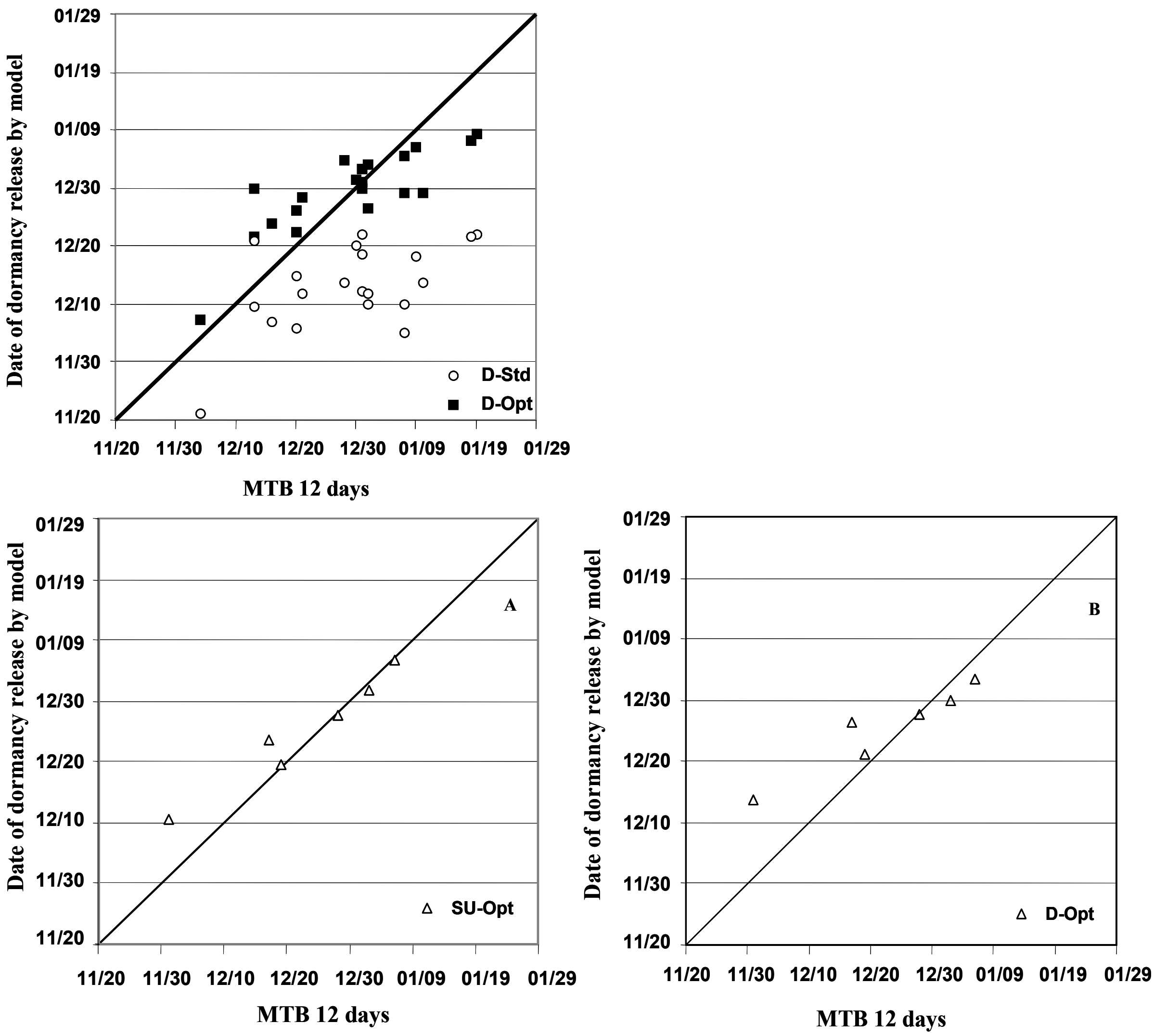


Fig. 5. Predictive values of the endodormancy release date from the optimized smoothed Utah model (A) and the optimized dynamic model (B) compared to the observed MTB 12 days.

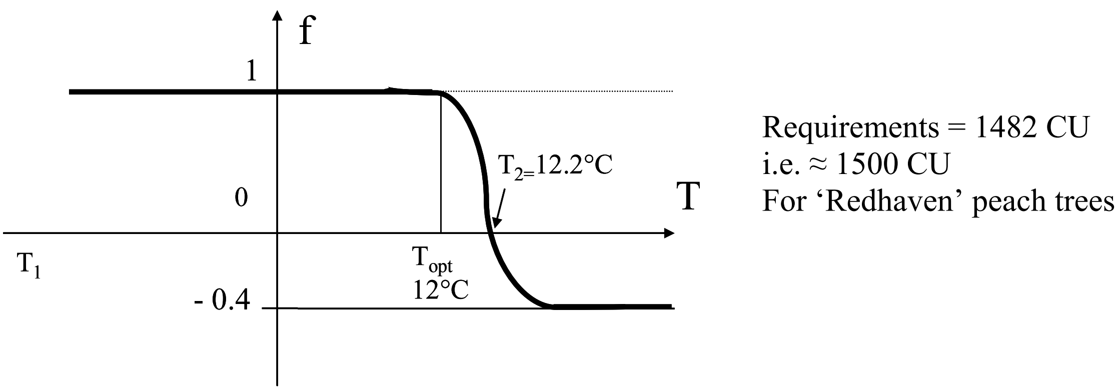


Fig. 6. Optimized form of the smoothed Utah model.