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Predicting the timing of budburst in temperate trees

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Summary

1. Four models for predicting budburst in northern hardwood trees, based on response to spring warming alone, or with the response to spring warming modified by winter chilling and photoperiod, were compared. An historical, 18-year budburst record, and artificial datasets with budburst dates generated according to each of four conceptual models, were used to analyse the abilities of the models to predict budburst dates.

2. The four models all gave better predictions than could be obtained by taking the average date of budburst of a species. The historical budburst dates were most accurately predicted by models based only on spring warming from a fixed start date, or from a start date determined by the satisfaction of a chilling requirement. A photothermal model was only useful for species with late budburst dates, and gave relatively little improvement over the average date of budburst as a predictor.

3. Analysis of artificial datasets, in which budburst dates were generated according to the biological assumptions of each conceptual model, reveals little connection between the ability to predict budburst with accuracy and the underlying biological response to temperature. This should be a general caveat to modellers; even biologically incorrect models can give reasonably good predictions of budburst phenology.

Key-words: modelling tree phenology, thermal sum, photoperiod, chilling.

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Introduction

An ability to predict tree budburst has many applications: insect–host phenological interactions (Valentine 1983), assessing the consequences of climatic change (Cannell & Smith 1986), and modelling energy and mass exchange (Nizinski & Saugier 1988). Warming in the spring, winter chilling and photoperiod can all influence budburst timing but there is no consensus on the relative importance of these factors. Here four approaches to predicting tree budburst are analysed and compared. In this paper we avoid creating new models or over-specifying some models which have many potential parameters, and compare the models simply as they are typically used.

We deal with records of budburst dates from several years at a single site and emphasize the abilities of the different models to predict budburst dates accurately, rather than which model more closely follows the unknown, underlying biological responses of trees. We will show that in fact good predictions can be obtained using the wrong biological response model, and in some cases the appropriate causal model may not give good predictions. To this end, analysis of the historical record of budburst was complemented by analysis of budburst dates simulated from climatic records under the biological responses assumed in the four models.

CURRENT APPROACHES TO MODELLING THE ENVIRONMENTAL CONTROL OF BUDBURST PHENOLOGY

Spring warming

The degree-day approach, focusing on spring warming, dates back to the work of Réaumur in 1730 (Wang 1960). Spring warming has continued to be identified as the major determinant of the timing of budburst (BB) (Hickin & Vittum 1976; Thomson & Moncrieff 1982; Castonguay, Boisvert & Dubé 1984). Degree-day (DD) models, assume (i) that there is a linear relation between temperature and rate of development, and (ii) that an event occurs when a certain number of 'heat units' above a base or threshold temperature have accumulated (Fig. 1a). Three parameters must be estimated: the date from which to begin accumulations, the threshold temperature, and the required heat sum. An arbitrary start date is used for trees, or a suitable

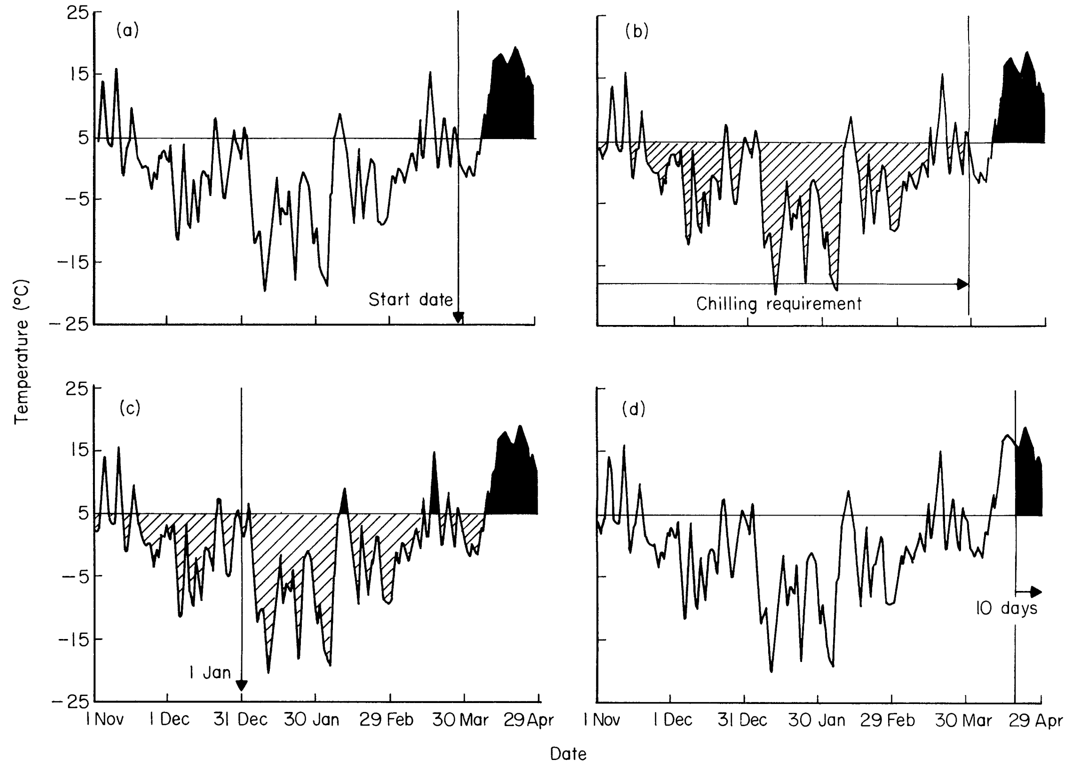

Fig. 1. Determination of the date of budburst by the models. Shaded areas contribute to heat accumulation towards budburst (■) or chilling duration (▨). Vertical lines represent constants in (a) and (c), variables in (b) and (d). (a) The spring warming model assumes a constant degree-day sum to budburst from a constant start date. (b) The sequential chilling model also has a constant degree-day sum to budburst, but the start date varies depending on when the constant chilling requirement is met. (c) The parallel chilling model assumes that there is a variable heat sum to budburst from 1 January which depends upon the chilling duration over the entire winter. (d) In the photothermal model the heat sum to budburst is a variable dependent upon the photoperiod. (Daily mean temperatures from Wauseon, Ohio in 1885–86.)

phenological stage. Threshold temperatures may be determined by regressing development rate against temperature (Arnold 1959), but this is not a practical approach for trees. Instead, the DDs to BB are calculated for a range of possible thresholds and start dates to find the combination that gives the minimum standard error of prediction of BB date (Lindsey & Newman 1956; Boyer 1973; Hickin & Vittum 1976; Castonguay, Boisvert & Dubè 1984).

Winter chilling and spring warming

Most dormant trees will not break bud in warm temperatures except after exposure to cool temperatures, in the order of 10 °C or less (Perry 1971; Cannell & Smith 1983). Two models of tree phenological dependence on such chilling exist, called sequential and parallel chilling (Hänninen 1987).

In the sequential chill model, trees are assumed to have fixed chilling requirements of a certain number of hours below a threshold temperature (Richardson, Seeley & Walker 1974). Fulfilment of the chilling requirement determines the start for DD summations. The heat sum for BB is fixed. There is no response to warm temperatures before dormancy release, and no effect of additional chilling on the amount of heat required for BB, i.e. responses to chilling and warming follow in sequence (Fig. 1b). Several alternative calculations of chilling hours have been proposed to accommodate the variable contribution of different temperatures to dormancy release (Ashcroft, Richardson & Seeley 1977). To specify the sequential chill model, the chilling requirement and the DDs to BB from dormancy release must be determined; the chilling and warming thresholds are taken as fixed (Richardson *et al.* 1974). As with the spring warming model, the standard error of BB prediction is minimized, but in this case over different chilling requirements rather than different thresholds and start dates (Richardson *et al.* 1974).

In the alternative parallel chill model, trees are assumed to respond to increasing durations of chilling with decreasing heat sum requirements for BB (Fig. 1c). When seedlings were exposed experimentally to different durations of chilling followed by warm temperatures, BB occurred sooner with longer chilling (for review see Cannell & Smith 1983). To use this model a curve must be fitted to data on the relationship between chilling duration and DDs to BB; the parameters of the fitted function define the model (Cannell & Smith 1983).

Photothermal model

A purely photoperiodic model would be a calendar date model at a single site; inter-annual variations at a site indicate that photoperiod alone cannot control tree phenology (Lechowicz 1984). In experimental conditions, long days can bring on BB in spite of cool temperatures or can substitute for chilling (Farmer 1968; Campbell & Sugano 1975). However, photoperiod seems to be unimportant in natural conditions for most species; rising temperatures bring about BB before lengthening days have any effect (Perry 1971; Campbell & Sugano 1975). A few species do use photoperiod to cue BB (e.g. *Fagus sylvatica* L., which has no chilling requirement; Wareing 1953).

In other species photoperiod interacts with temperature; the longer the photoperiod the cooler the temperatures required for BB (Campbell & Sugano 1975; Nizinski & Saugier 1988). Nizinski & Saugier (1988) found that BB of *Quercus petraea* could be predicted from the relationship between cumulative temperatures 10 days prior to BB and photoperiod on the day of BB (Fig. 1d). Like the parallel chilling model, in the photothermal model a curve is fitted to the photoperiod–temperature relationship observed in an historical dataset.

Methods

HISTORICAL PHENOLOGICAL RECORD

The historical dataset is a 30-year record of weather and plant phenology collected by Thomas Mikesell in Wauseon, Ohio (41·3°N 84·1°W) between 1883 and 1912 (including the unusually cold year following the explosion of Krakatau in August of 1883; Smith 1915). However, BB dates were only recorded in at most 18 years, for 26 species of native hardwood trees (Table 1). Nothing is known about the number of trees of each species that were observed. Mikesell's observations were made on the woodlots and hedgerows remaining after clearing for agriculture (Smith 1915; Boerner & Cho 1987). Variation in altitude and aspect in this region are too limited to introduce strong local variation in climate.

Degree-days were calculated by the sine wave method from Mikesell's records of daily maximum and minimum temperatures (Allen 1976; Higley, Pedigo & Ostlie 1986). The standard basis for comparing the predictive abilities of the models is the difference between the observed and predicted day of BB (standard error of prediction in days; Hickin & Vittum 1976). This standard error measures the

Table 1. Standard errors of prediction in days for models used to predict date of budburst of tree species in an historical dataset from Ohio. Species are ordered by mean date of budburst from earliest to latest. Bold entries show the lowest standard error for prediction of a species; useful models must have a lower standard error than the null model (average date). Errors of prediction were not calculated for the photothermal model when there was not a significant negative correlation between mean temperature and photoperiod on the day of budbrust

Species	Average date	Spring warming	Sequential chill	Parallel chill	Photothermal
Salix nigra L.	5·3	3·2	**3·1**	3·2	·
Acer saccharinum L.	3·9	**2·1**	3·5	3·9	·
Ulmus americana L.	4·2	4·5	**3·7**	5·5	·
Populus tremuloides Michx.	5·9	**4·9**	5·0	5·8	·
Acer negundo L.	4·1	**3·3**	3·5	5·2	·
Aesculus glabra Willd.	5·1	**3·2**	4·1	3·4	·
Ostrya virginiana (Mill.) K. Koch.	4·6	4·6	**4·5**	5·7	·
Acer saccharum Marsh.	4·6	**3·5**	3·6	3·8	·
Populus deltoides Marsh.	5·9	**5·2**	5·9	5·5	·
Sassafras albidinum (Nutt.) Nees.	7·5	4·4	**4·0**	4·7	·
Hamamelis virginiana L.	9·2	7·0	7·2	**6·8**	·
Cornus florida L.	7·4	**4·2**	4·7	4·9	7·1
Quercus bicolor Willd.	7·3	**3·3**	4·1	4·5	5·7
Carya ovata (Mill.) K. Koch.	6·1	3·7	**3·1**	4·2	5·4
Quercus macrocarpa Michx.	6·9	4·6	**3·2**	4·4	6·5
Fraxinus americana L.	7·6	**4·2**	4·3	5·5	6·2
Rhus typhina L.	9·3	5·7	**5·7**	6·8	6·0
Quercus velutina Lam.	6·5	2·8	**2·7**	3·9	4·5
Fraxinus nigra Marsh.	6·5	**4·2**	4·9	5·9	·
Juglans nigra L.	6·6	3·5	**3·3**	4·1	5·2
Quercus alba L.	6·0	**2·9**	3·1	4·2	5·4
Carya glabra (Mill.) Sweet.	6·1	**3·3**	3·5	4·7	5·3
Gymnocladus dioica (L.) K. Koch.	8·4	**4·2**	4·5	5·3	5·4
Maclura pomifera (Raf.) Schneid.	8·8	5·3	**4·5**	4·9	7·0
Diospyros virginiana L.	8·2	4·5	**3·7**	4·1	7·5
Platanus occidentalis L.	7·1	4·4	4·5	**4·3**	6·2

precision of the models, but not their accuracy: the predicted dates could all be far from the observed BBs and still have a low standard error because they did not vary greatly. Therefore, we also tested accuracy by calculating the chi-squared value between predicted and observed BB dates.

ARTIFICIAL BUDBURST DATASETS

Budburst dates for each of the 18 years in the historical dataset were created based on responses to environmental cues exactly as assumed in the four models. Artificial BB dates based on the assumptions of the spring warming model used threshold temperatures of −5, 5, and 15 °C, and start dates of 1 January, 30 January, and 1 March (Table 2). The heat sum for BB was the average DDs on 30 April, which is in the middle of the BB period in Ohio. The sequential chilling artificial data had chilling requirements of 2800, 3000 and 3100 hours less than 10 °C. Nested within each of these chilling requirements were subsequent warming requirements of about 100, 150 and 200 DDs above 5 °C (Table 2). The data created under the parallel chilling model used the equations for groups of tree species with varying chilling requirements from Murray, Cannell & Smith (1989). Group 1 had the highest requirement and the steepest decline in DDs required for BB with increased chilling duration and group 5 had the lowest chilling requirement, while the other groups were intermediate. Artificial BB dates based on photothermal responses were constructed from mean temperature–photoperiod relations observed for five species in the Ohio dataset: two species which showed fairly strong photothermal responses, two which

Table 2. Standard errors of prediction in days for models when applied to artificial budburst datasets generated under the assumptions of the phenological models. Bold entries show the model giving the best prediction

	Method of analysis applied				
Generating model	Day of year	Spring warming	Sequential chill	Parallel chill	Photothermal
Spring warming					
Base (°C) Start					
−5 1 Jan	8·7	**1·3**	5·4	4·6	NC
−5 30 Jan	6·2	**1·0**	3·3	2·3	NC
−5 1 Mar	5·1	**1·0**	2·5	2·9	NC
5 1 Jan	7·5	**1·5**	3·3	1·5	NC
5 30 Jan	6·3	**1·0**	1·5	1·7	NC
5 1 Mar	5·9	1·1	**0·9**	2·4	NC
15 1 Jan	8·5	**0·9**	6·5	5·5	7·2
15 30 Jan	8·6	**0·6**	6·4	5·7	7·1
15 1 Mar	8·6	**0·9**	6·4	4·9	7·1
Sequential chill					
Chill (h) Heat requirement (D D above 5 °C)					
2800 96	7·3	2·2	**0·4**	4·2	NC
155	5·7	1·3	**0·6**	2·0	7·2
200	5·9	1·3	**0·8**	2·2	6·7
3000 100	4·6	1·8	**0·5**	3·0	NC
185	5·4	2·1	**0·6**	2·8	5·3
245	5·8	1·6	**0·5**	2·1	2·5
3100 99	3·9	1·2	**0·7**	2·5	5·2
140	4·0	1·6	**0·6**	3·1	4·0
198	5·2	1·1	**0·6**	2·2	2·9
Parallel chill					
Group (cf. Murray, Cannell & Smith 1989)					
1 High chill	4·9	2·9	2·6	**1·7**	NC
2	6·0	2·1	**2·0**	2·5	NC
3	9·3	**2·4**	4·5	4·0	NC
4	11·2	**3·5**	7·5	4·7	NC
5 Low chill	14·8	**1·8**	14·5	4·1	NC
Photothermal					
No response	6·1	1·8	3·9	4·2	**1·0**
No response	7·0	3·9	6·1	4·3	**3·8**
Intermediate	9·5	4·7	5·0	5·8	**0·5**
High response	7·2	3·4	2·8	4·1	**1·0**
High response	7·1	3·9	3·3	4·3	**2·8**

NC, no correlation between temperatures prior to budburst and photoperiod on the day of budburst.

showed no response, and one with an intermediate photothermal response.

ESTIMATING PARAMETERS FOR EACH PHENOLOGICAL MODEL

The simplest method for predicting the time of budburst is to use the average date of BB over several years. This is a null model which we use as our base reference for comparison; any useful model must have a lower standard error in days than this average date.

Spring warming

For each threshold and start date combination the DDs to BB were calculated in each year (Thomson & Moncrieff 1982). Base temperatures at 1 °C intervals between −10 °C and 10 °C were tried, and start dates at 4-day intervals. The mean DD sum between each start date and BB was used to predict BB in each year, for each combination. The threshold and start date combination that gave the smallest standard deviation of the difference between predicted and actual BB was chosen as the best model.

Chilling and degree-days to budburst

Usually the starting point for chilling accumulation is chosen in late autumn, after leaf senescence and as temperatures begin to drop below 5 °C regularly. Here, 1 November was used, since deciduous trees in Ohio have lost their leaves by this time (Smith 1915). To estimate parameters in the sequential chill model, several chilling requirements were tried. The chilling requirement that gave the minimum standard deviation of the warming DDs to BB was selected (Ashcroft, Richardson & Seeley 1977). Here chilling is the number of hours below 10 °C, and values at 25 chilling hour intervals from 2850 hours were used. The threshold for DD accumulation was 5 °C. In the parallel model, the relationship between DDs to BB (above 0 °C from 1 January) and the number of chilling days (mean temperature below 5 °C) was determined (Cannell & Smith 1983). To predict dates of BB, the observed chilling durations were used to calculate the DDs required for BB from this relationship.

Photothermal model

The method of Nizinski & Saugier (1988) was followed. First, each set of BB dates was screened for a relationship between photoperiod and mean temperature in the 10 days before BB. Only datasets showing a significant negative correlation were retained to fit a curve of the form:

$$S = aD/(bD - 1)$$

where S is the sum of the mean temperatures in the 10 days before BB, and D is the day length on the day of BB; a and b are constants. Daylengths were calculated after Brock (1981).

Results

In both the historical and artificial datasets, the chi-squared analysis matched the standard error of prediction results. More precise predictions were also more accurate. The chi-squared values are not reported.

Historical phenological record

All of the models except the photothermal model predicted BB more precisely than did use of the average day of the year model (Table 1). The spring warming model provided the most accurate predictions for 13 of the 26 species. Sequential chilling was next best, giving the best predictions for 11 species. The parallel chilling model was only best for two species, and was worse than the average day model for several early flushing species (Table 1). The photothermal model usually offered only a slight improvement over the average date model, and several species, particularly those with the earliest average BB, had no significant correlation between recent temperatures and photoperiod.

ARTIFICIAL BUDBURST DATA

Many of the models gave low standard errors of prediction even when the BB dates were generated under the assumptions of one of the other models, although the smallest errors of prediction usually were given by the generating model. The spring warming, sequential chilling and parallel chilling models generally gave better predictions than the average date model. The photothermal method worked well on data generated by the photothermal model (Table 2), but in other artificial datasets it was not very useful and was often a worse predictor than the average date of BB.

Some limitations of the models became evident in the analysis of the artificial data. The sequential chill model, when applied to data generated by the parallel chill model, gave increasingly high error as the chilling requirement decreased (Table 2). If chilling requirements are so low that dormancy release occurs before temperatures rise above the 5 °C warming threshold, it is impossible to determine the chill requirement. Many different low chill values would give the same DD sum to BB. Similarly, when the sequential chill model was applied to BB dates generated by the spring warming model, the accuracy of predictions increased with later actual start dates, closer to the dates when the chilling requirements tried were surpassed (Table 2).

Good predictive ability of the photothermal model only occurred when temperatures just before BB had a strong effect, i.e. in datasets with high threshold temperatures or high chilling requirements (Table 2). The parallel chill model was not the best predictor for artificial data generated under its own assumptions (Table 2).

Discussion

To predict budburst dates of hardwood trees to within a few days, the best models were the spring warming model and the sequential chilling model. Both gave low standard errors of prediction for 26 species in an 18-year historical dataset. The parallel chilling model was not especially accurate at predicting BB in the historical dataset, especially for trees with low chilling requirements. This may be an artefact of the small range of chilling durations in Ohio: 116–149 days compared with 56–145 days in Murray, Cannell & Smith's (1989) British data. The historical dataset also showed that the photothermal model was only a slight improvement over simply the average BB day. The photothermal model was useless for species with the earliest BB dates (mostly species with diffuse-porous wood anatomy), but worked better for the later flushing, ring-porous hardwoods (Lechowicz 1984). It may be that the biological basis of BB control varies among physiological groups of trees.

Analysis of artificial datasets in which particular biological responses were simulated showed that there is little connection between predictive ability of a model and the biological basis of phenological responses. In artificial datasets, the model generating the BB dates usually, but not always, had the best predictive ability, and the differences between the models were small. Thus, in spite of the evident predictive abilities of the spring warming and sequential chilling models with the genuine data, it would be unwise to conclude that the trees were responding to the environmental cues in the ways assumed by the models.

Several limitations of the models were revealed through the use of artificial data. The sequential chill model is of limited utility if the chilling requirement is regularly satisfied before warming begins. In such a situation, it is impossible to determine the chilling requirement accurately from field data. This model was developed mostly with fruit trees with large chilling requirements that are not met in southern locales, where the concern has been to develop low-chilling cultivars. Similarly, the spring warming model will only identify the start date if temperatures above the warming threshold begin to accumulate before the start date.

A further feature illuminated by the artificial datasets is that there are inherent correlations among the variables. For example, there is a negative correlation between DDs to BB and the duration of chilling regardless of the model generating the BB dates (Fig. 2). This is because what is not a chilling day is usually a warming day, so the axes are correlated. Similarly, negative correlations between photoperiod and mean temperatures are not necessarily indicative of a photothermal response, but may arise from strong effects of temperatures just before BB (through high threshold temperature or large chill requirement).

Given that the relation between the DD sum to BB and the number of chilling days can arise from the inherent correlation of the axes, evidence supporting the parallel chilling model should be reassessed. In experimental manipulations where groups of trees are subjected to different chilling durations, the separation of heating and chilling is complete, because plants are forced at constant warm temperatures, unlike in natural conditions. Many such experiments have been carried out, so that the evidence for a parallel chilling response seems strong (Lamb 1948; Brierley 1948; Farmer 1968; Campbell & Sugano 1975; Amling & Amling 1980; Cannell & Smith 1983; Cannell, Murray & Sheppard 1985; Couvillon & Erez 1985; Murray, Cannell & Smith 1989). However, in natural conditions this effect may only be significant when chilling is of an unusually short duration, as in future scenarios (Cannell & Smith 1986; Murray, Cannell & Smith 1989), or when populations are grown beyond their natural range. Indeed, most experiments demonstrating such an effect have used non-native plants or cultivated plants of unknown provenance. Many of these studies also use photoperiods characteristic of summer instead of spring, which may also alter the response to chilling and warming (Campbell & Sugano 1975).

Chilling, photoperiod, and flushing temperatures may have very complex interactions in their effects on BB phenology. Campbell & Sugano (1975) found that chilling effects depended on the timing, duration and temperature of chilling. After chilling, the timing of BB depended further on photoperiod and the flushing temperature. However, they concluded that in the field BB date is primarily a function of spring warming. Chilling durations and photoperiods in the range that had large effects on BB dates rarely occurred before BB in natural conditions. The results of the current study reflect this: the spring warming and sequential chill models were the best predictors for most species in the Ohio dataset. To predict budburst dates in a single location, the simple spring warming or sequential chilling models are adequate. But to understand the controls on tree phenology or make predictions over large geographic ranges or under climatic change, we must come to grips with these complex interactions.

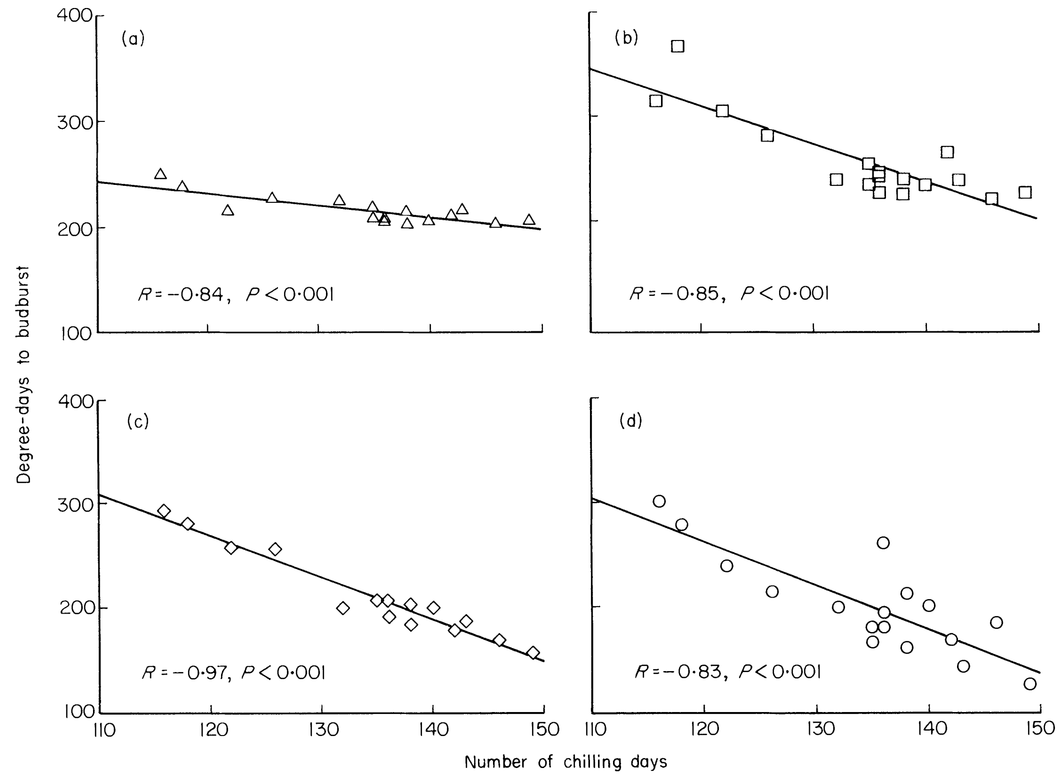

Fig. 2. Relation between degree-days to budburst above 5 °C from 1 January and number of chilling days below 5 °C from 1 November in selected artificial datasets in which budburst dates follow (a) the spring warming model, (b) the sequential chilling model, (c) the parallel chilling model, and (d) the photothermal model.

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