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THERMAL TIME, CHILL DAYS AND PREDICTION OF BUDBURST IN *PICEA SITCHENSIS*

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SUMMARY

(1) The dates of budhurst of lateral shoots on 2- to 10-year old trees of *Picea sitchensis* were recorded on fourteen occasions at sites near meteorological stations in lowland and upland Britain between 1960 and 1980.

(2) The following relationship accounted for 92% of the variation in thermal time from 1 February to the date of budburst among the fourteen observations:

$$\text{thermal time} = 67 \cdot 4 + 4401 \cdot 8 \exp\,(-0 \cdot 042 \times \text{chill days})$$

where thermal time was day degrees $> 5\,°C$ accumulated from 1 February, and chill days were the number of days $\leqslant 5\,°C$ counted from 1 November, both based on mean daily air temperature ((max. + min.)/2). This model may be used to estimate the date of budburst on young *P. sitchensis* of most provenances growing in upland Britain.

(3) The following features or assumptions of the model were examined with reference to the literature and/or by experimentation: the small effect of provenance; linearity in the relationship between bud growth rate and temperature; the large effect of chilling on thermal time to budhurst; the omission of daylength and soil temperature as variables; the choice of starting dates for effective chilling and thermal time; and the use of simple fixed base temperatures.

(4) The model was applied to mean daily temperatures at Eskdalemuir for the period 1912–82. The predicted dates of budburst ranged from 23 April in 1961 to 30 May in 1923, with a mean date of 12 May.

INTRODUCTION

The timing of vegetative budburst on north temperate conifers is of major importance in assessing the probability of spring frost damage (Day & Peace 1946; Cannell & Sheppard 1982), in modelling tree growth (Hari 1972) and in assessing the population dynamics of defoliating insects (Thomson 1979). Budburst is one stage of the bud elongation process, which is greatly dependent upon temperature. In many temperate tree species, budburst timing has been related to previously accumulated day degrees above a threshold temperature (thermal time), modified variously by winter chilling, photoperiod, soil temperature, and various plant characters (Campbell & Sugano 1975; Campbell 1978; Campbell & Sugano 1979; Lavender 1980; Thomson & Moncrieff 1982).

This paper presents an empirical model for the timing of budburst on *Picea sitchensis* (Bong.) Carr. based solely on thermal time and winter chilling. This model offers a useful predictive tool for budburst timing on 2- to 10-year-old trees of most of the provenances widely grown in Britain. The date of budburst is defined as the day when half of the lateral buds on half of the trees reach the stage when green needles first break free from the bud scales (Lines & Mitchell 1965, 'stage 3', see Fig. 3). This can usually be judged to within ± 2 days, although budburst within a population may occur over 2 weeks. Leader buds, and buds on large, mature trees, usually burst 1–2 weeks later than the laterals on young trees (Lavender 1980). After presenting the model, some of the assumptions underlying it are examined, and the dates of budburst at Eskdalemuir are predicted for the period 1912–82.

TABLE 1. Fourteen observations of the dates of budburst on young trees of *Picea sitchensis* growing near meteorological stations in Britain

Location	Lat.°N	Alt. (m)	Age*	Estimated mean date of budburst†	Source of data
(A) Bush, Midlothian	55°45'	184	3	24 April 1960	Lines & Mitchell (1965) and R. Lines (pers. comm.). Means of twelve provenances.
(B) Newton, Morayshire‡	57°35'	15	3	1 May 1960	
(C) Wykeham, Yorkshire§	54°15'	145	3	3 May 1960	
(D) Bush, Midlothian	55°45'	184	4	19 April 1961	
(E) Newton, Morayshire‡	57°35'	15	4	12 April 1961	
(F) Wykeham, Yorkshire§	54°15'	145	4	17 April 1961	
(G) Bush, Midlothian	55°45'	184	2	9 May 1972	Freezaillah (1974) Queen Charlotte Islands provenance
(H) Greskine Forest, Dumfriesshire¶	55°20'	229–480	3	21 May 1973	
(I) Bush, Midlothian	55°45'	184	4	12 May 1975	Kraus & Lines (1976)** and R. Lines (pers. comm.)
(J) Bush, Midlothian	55°45'	184	3–10	16 May 1979	Queen Charlotte Islands provenances
(K) Eskdalemuir, Dumfriesshire	55°19'	242	3–10	20 May 1979	
(L) Moorhouse, Cumberland	54°41'	556	10–20	5 June 1979	
(M) Bush, Midlothian	55°45'	184	3–10	10 May 1980	
(N) Eskdalemuir, Dumfriesshire	55°19'	242	3–10	12 May 1980	

* Beginning of *n*th growing season after germination.
† Stage 3 of budburst (see Fig. 3) of buds on lower lateral branches.
‡ Meteorological station at Kinloss, Morayshire, 57°39'N 5 m.
§ Meteorological station at Silpho Moor, Yorkshire, 54°20'N 203 m.
¶ Meteorological station at Eskdalemuir, Dumfriesshire, 55°19'N 242 m.
** Mean of sixty-four provenances.

AN EMPIRICAL MODEL

Fourteen accurate records were assembled of the mean date of 'stage 3' lateral branch budburst on healthy young trees of *P. sitchensis* growing close to meteorological stations. The locations included lowland sites, Eskdalemuir and Greskine as typical upland plantation sites, and Moorhouse (556 m) which is above the altitude limit of most *P sitchensis* plantings (Table 1).

For each record, thermal time was calculated from 1 February to the date of budburst as:

$$T_x = \sum_{m=1}^{n} (t_m - x) \tag{1}$$

where T_x was day degrees with a base temperature of x °C, n was the total number of spring days with a mean temperature greater than x °C, and t_m was the mean daily temperature on those days, taken as (max. + min.)/2. Chill days were counted as the number of days from 1 November to the date of budburst when the mean daily temperature was equal to or below the base temperature. All temperatures were recorded in standard Stevenson screens.

When thermal time to budburst was plotted against date of budburst, there was a clear, inverse relationship, but with considerable scatter (Fig. 1, inset). The relationship suggested that increased chilling during April–May decreased the thermal time requirement for budburst. Therefore, the method of least squares was used to find the best-fitting relationship between thermal time and accumulated chill days or units (Fig. 1). Decreasing exponential models fitted better than linear models when points K and L were included, and the seven methods listed in Table 2 were applied, with and without $\log_e$ transformation. Methods 1–3 varied the base temperature. Methods 4–6 were attempts to calculate actual degree hours of thermal and chilling time above and below 5 °C, respectively, assuming a square-wave, triangular or sine-wave diurnal fluctuation between the day maximum and night minimum temperatures. Method 7 used estimated degree

TABLE 2. Comparison of eight methods used to estimate heat sum and chill days prior to the fourteen records of budburst in Table 1, in terms of the accuracy with which a decreasing exponential relationship between them (as in Fig. 1) explained the variation in date of budburst. Thermal time was counted from 1 February, chill units from 1 November

Methods of calculating thermal time and chill units (see text)	Percentage of variation accounted for*		Means ($n = 14$) and extreme deviations from actual dates of budburst in days	
(1) Day degrees and chill days with 5 °C base temperature	92	90†	2·6	−6 to +7
(2) As (1) with 3 °C base temperature	78	85†	3·2	−5 to +8
(3) As (1) with 7 °C base temperature	76	62†	4·6	−13 to +10
(4) Degree hours above and below 5 °C with square wave diurnal pattern	83	84†	2·8	−6 to +5
(5) As above with 'triangular' diurnal pattern	85	87†	2·7	−7 to +7
(6) As above with sine wave diurnal pattern	77	81†	2·9	−7 to +8
(7) Degree hours above 5 °C derived from an empirical relationship (see text)	83	81†	2·5	−5 to +7

* Percentage reduction in residual mean squares.
† With $\log_e$ transformation.

hours >5 °C derived from an empirical relationship between (y) daily degree hours >5 °C recorded at Eskdalemuir (55°19′N, 242 m) and Turnhouse Airport, Edinburgh (55°57′N, 35 m) from 1 February to 31 May in 1970 to 1976, and (x) mean daily temperature. A relationship of the form: $y = a + bx^2$ explained 88% of the variation. Additionally, calculations of arbitrary chill units were tried, assuming an optimum chilling temperature of 3 °C decreasing to zero effect at both −3 °C and +10 °C, as suggested by Sarvas (1975, his Fig. 5 and Table 5). However, this produced no discernible relationship with day degrees >5 °C, apparently because it underestimated the effect of chill days at the colder sites when mean temperatures were below 3 °C.

Method 1, the simplest method, provided the best fitting model, namely:

$$\text{day degrees} > 5\ ^\circ\text{C} = 67 \cdot 4 + 4401 \cdot 8 \exp(-0 \cdot 042 \times \text{chill days} \leqslant 5\ ^\circ\text{C}) \qquad (2)$$

This accounted for 92% of the variation in date of budburst among the fourteen records, predicting all within 7 days, with an average deviation of ±2·6 days (Table 2).

After the model had been derived, the date of budburst on young trees was observed at Bush (55°45′N, 184 m) on 8 May 1981 and 11 May 1982. Both these dates were within 2 days of predictions using eqn (2). Also budburst was observed around 15 April 1980 on 3-year-old trees at Cascade Head, Oregon (45°02′N, 46 m; J. Booth, pers. comm.) which, again, was within 2 days of the prediction using local daily air temperatures. Equation (2) may, therefore, be a valuable predictive tool to estimate budburst timing in past years on young *P. sitchensis*, provided extrapolations are not made outside the range of values in Fig. 1.
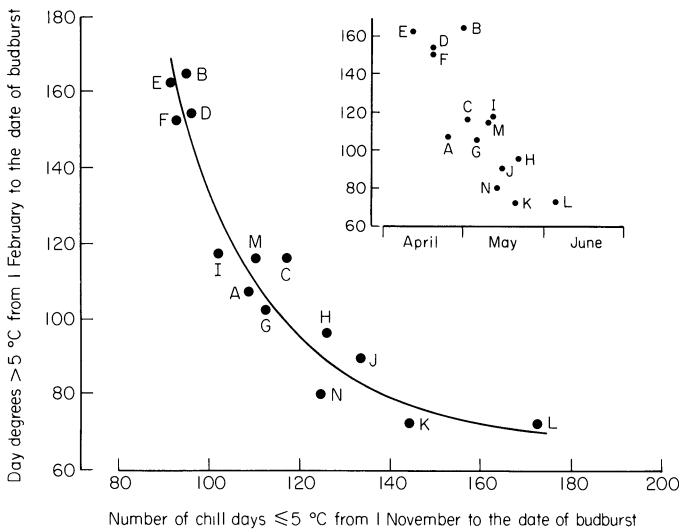

FIG. 1. Relationship, for fourteen records of the dates of budburst of *Picea sitchensis* in Britain (A to N, Table 1), between the number of chill days with mean temperatures ≤5 °C from 1 November to the time of budburst (stage 3, Fig. 3) and day degrees >5 °C received from 1 February to the time of budburst (see text eqn (1)). Temperatures are based on daily maxima and minima recorded at meteorological stations as detailed in Table 1. The fitted line is described by eqn (2) in the text and the goodness-of-fit is given in Table 2, method (1). The inset graph shows the poorer inverse relationship when thermal time was plotted against the actual date of budburst rather than chill days.

ASSUMPTIONS OF THE MODEL

Some of the explicit and implicit assumptions underlying the model were examined with reference to the literature on conifer budburst timing and/or by experimentation.

Effect of provenance

Unlike many other conifers (e.g. *Pseudotsuga menziesii*, Campbell 1974) there is rarely more than 5 days difference in the *mean* date of budburst between most of the widely-planted provenances of *Picea sitchensis* growing in British climatic conditions (Aldhous 1962; Lines & Mitchell 1965; Lines 1963; Kraus & Lines 1976). Burley (1966) and Falkenhagen (1977) also failed to find any appreciable or systematic differences in date of budburst among low altitude provenances of *P. sitchensis* growing in Connecticut and Vancouver, respectively. The model in Fig. 1 (eqn (2)), based on observation of mostly Queen Charlotte Islands provenances, may therefore be applied to most *P. sitchensis* provenances growing in Britain. However, the parameters would need to be modified to account for genetic variation among families and clones *within* provenances (e.g. Cahalan 1981).

Linear relationship between thermal time and bud growth

The use of thermal time implies that a thermal unit is equivalent to a growth unit, so that accumulated day degrees become equivalent to accumulated growth units. Strictly speaking, the model in Fig. 1 assumed a linear relationship between bud elongation rate and temperature above a threshold (Arnold 1959; Wang 1960). Only then would accumulated growth be linearly related to thermal time.

Campbell (1974, 1978) and Campbell & Sugano (1979) showed that, on well chilled *Pseudotsuga menziesii* seedlings, bud growth rates increased logarithmically with temperature over the range 10–20 °C, and Hari (1972) assumed that, because metabolic rates often increase logarithmically with temperature, growth rates do so as well. However, others have shown that plant growth rates, including shoot elongation rates of trees, can be linearly related to temperature within the range 5–20 °C (Monteith 1977; Bloomberg 1978; Squire 1981; E. D. Ford, pers. comm.). Also, small deviations from linearity over the relevant range of 5–10 °C would not invalidate the use of thermal time if there were fluctuating temperatures without any marked tendency to increasing temperatures, because the relationship between day degrees and bud lengths would then be
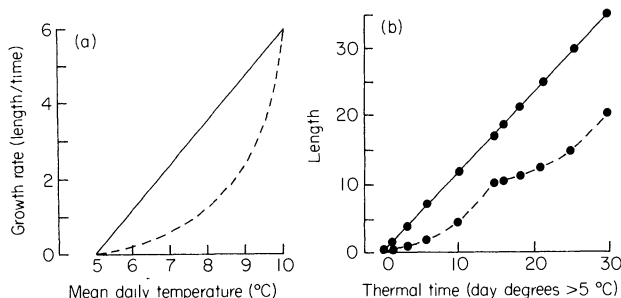

FIG. 2. (*a*) Hypothetical linear and non-linear relationships between temperature and rate of growth in length. (*b*) Equivalent relationships between thermal time and length for a succession of days with mean temperatures of 5, 6, 7, 8, 9, 10, 6, 7, 8, 9 and 10 °C.
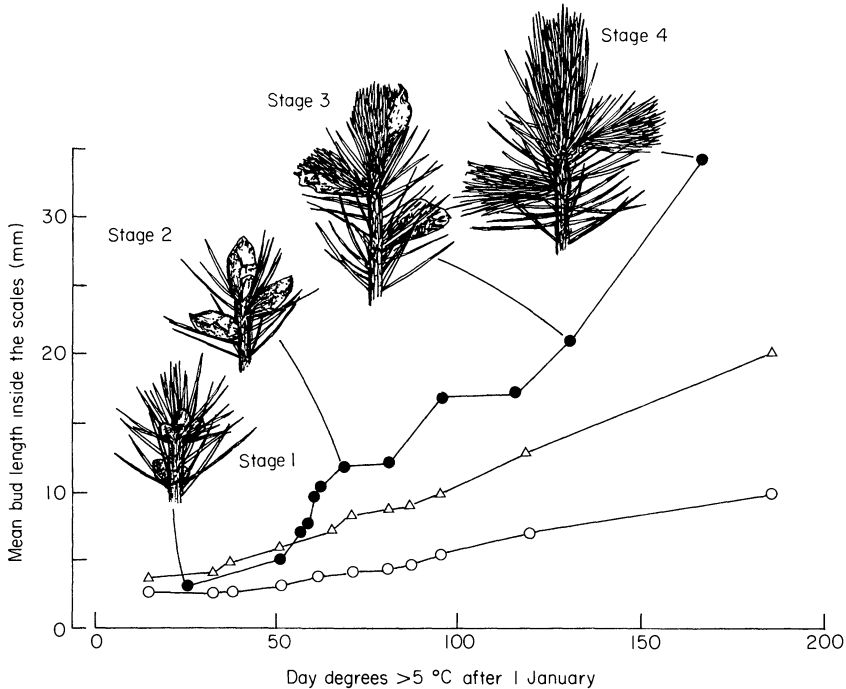
FIG. 3. Relationship between thermal time and the lengths of buds of *Picea sitchensis*, measured inside the scales, prior to budburst. The drawings depict budburst stages 1–4 as defined by Lines & Mitchell (1965). ●, Leader buds detached from different 12-year-old trees at Greskine Forest (55°20′N, 351 m) at 3–4 days intervals, from Cannell & Bowler (1978, their Fig. 4); temperature data from Eskdalemuir (55°19′N, 242 m). ○, Vegetative and △, male buds on branches measured non-destructively on the lower parts of crowns of 41-year-old trees at Roseisle Forest (57°41′N, 10 m) from Moir & Fox (1975, their Fig. 14); temperature data from Elgin (57°39′N, 15 m).

approximately linear, even if the relationship between bud growth rate and temperature was not (Fig. 2). Published data on bud lengths of *Picea sitchensis* prior to budburst suggested that this was often the case (Fig. 3).

Effects of chilling

On most temperate tree species the winter buds enter a state of 'dormancy' in October–November which is 'broken', or progressively decreased, by exposure to chill temperatures (see Vegis 1973; Landsberg 1974). According to Campbell's (1978) model for *Pseudotsuga menziesii*, within limits the longer the buds are exposed to chill temperatures, the greater is the rate at which they will grow when subsequently exposed to warm temperatures, i.e., chilling increases the slope of the bud growth rate/temperature relationship, thereby decreasing the thermal time to budburst.

This was the logic of the model in Fig. 1 (Eqn (2)) which was supported by published data for many comparable tree species, where the relationship between chill days and thermal time to budburst often also tended towards a decreasing exponential (Fig. 4).

A seedling experiment was done to further substantiate the existence of this relationship in *P. sitchensis*. Seedlings of Masset (Queen Charlotte Islands) and Hoquiam (Washington) provenances were sown in March 1979, potted and hardened off in June, and
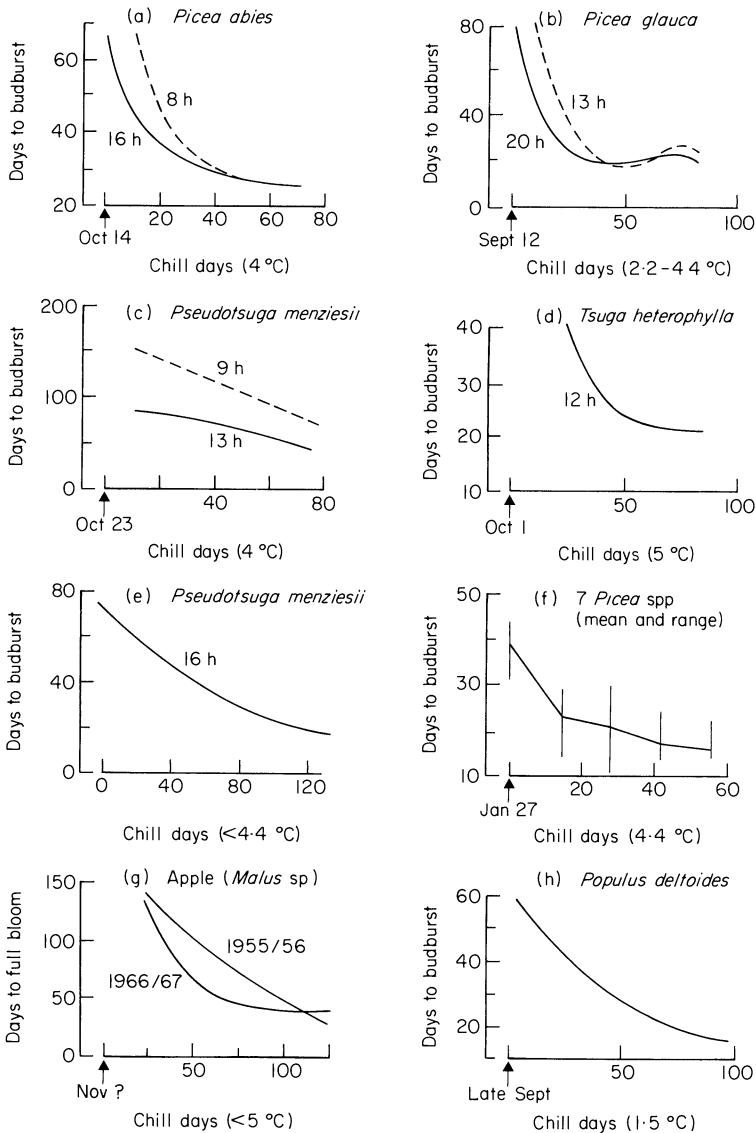
FIG. 4. Relationships for different tree species between days to budburst in warm temperatures and the duration of previous exposure to chill temperatures. (a) From Worrall & Mergen (1967), 2-year-old clones, days to budburst at 23°/14 °C day/night temperatures, continuous chill days at 4 °C. (b) From Nienstaedt (1966), 2-year-old seedlings, days to budburst in a 'warm' glasshouse, continuous chill days at 2·2–4·4 °C. (c) From Campbell (1978), 1-year-old seedlings, days to budburst at 15·5 °C, continuous chill days at 4 °C. (d) From Nelson & Lavender (1979), 1-year-old seedlings, days to budburst at 22/18 °C day/night temperatures, continuous chill days at 5 °C. (e) From van den Driessche (1975), 2-year-old seedlings of Pemberton provenance (50°28′N, 457 m), days to lateral budburst in a glasshouse at about 24 °C with 16 h photoperiods following continuous chilling. Similar curves, but with lower chilling requirements, were presented by Campbell & Sugano (1975) for 1-year-old seedlings. (f) From Nienstaedt (1967), 1-year-old seedlings, days to budburst at 22/14 °C day/night temperatures, continuous chill days at 4·4 °C. (g) From Landsberg (1974), c. 3–4-year-old potted trees, days to bloom in natural daylengths at 51 °N in a 'warm' glasshouse in 1955/56 and in 4 weeks of 11 °C followed by 15 °C in 1966/67, natural intermittent chill days in 1955/56 and continuous 5 °C in 1966/67. (h) From Thielges & Beck (1976), unrooted cuttings, days to budburst at 24/15 °C day/night temperatures, mean of 16 h and natural photoperiods, continuous chill days at 1·5 °C.
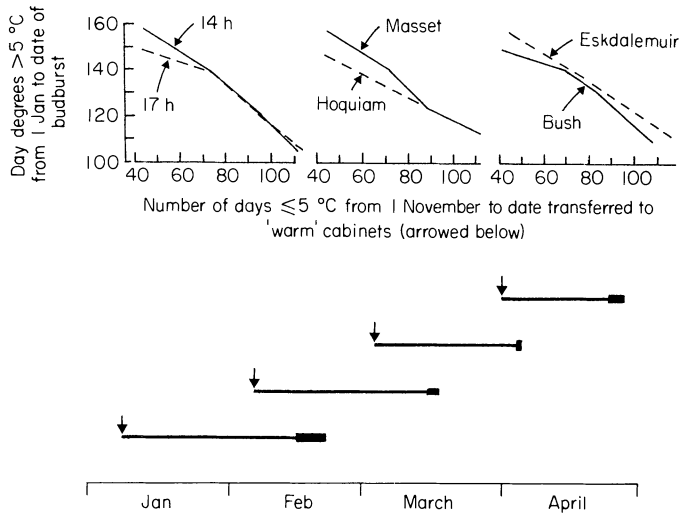
FIG. 5. Lower part: dates when seedlings of *Picea sitchensis* were transferred from outside at Bush and Eskdalemuir to 'warm' cabinets (arrowed), the subsequent periods of bud development (thin lines) and dates of budburst (thick lines spanning all treatments). Upper part: relationship between the number of chill days received outside, and thermal time before budburst (accumulated before and after transfer to 'warm' cabinets). Left: effects of two photoperiods in the cabinets. Centre: differences between two provenances (Masset, Q.C.I., and Hoquiam, Washington). Right: differences between seedlings kept outside at Bush and Eskdalemuir.

transferred in November 1979 to sites near meteorological stations at either Bush or Eskdalemuir. On 7 January, 5 February, 3 and 31 March 1980 twenty seedlings of each provenance at each site were transferred to each of two controlled environment cabinets. These provided either 14 h or 17 h photoperiods, with about 150 W m^{-2} of photosynthetically active radiation at plant level, and 12°/5 °C day/night temperatures on a 12 h cycle. Treatments were randomized, and the seedlings and regimes were switched between cabinets every 2 weeks to avoid bias resulting from any differences between cabinets. Observations were made of the dates of budburst on lateral branches.

An inverse relationship was found between (a) number of chill days ≤5 °C recorded at the meteorological sites between 1 November and the date the seedlings were transferred to the cabinets, and (b) the day degrees >5 °C outside and inside the cabinets between 1 January and budburst (Fig. 5). The relationship was approximately linear up to about 110 chill days, which agrees with the model in Fig. 1, where non-linearity was dependent upon the inclusion of points with well over 110 chill days. The relationship was not quantitatively the same as in Fig. 1, because the temperature regime in the cabinets did not simulate normal diurnal fluctuations. Chilling at Bush was apparently more effective than at Eskdalemuir (possibly because the seedlings suffered less winter desiccation at Bush) and the southerly Hoquiam provenance had a smaller thermal time to budburst than Masset, but only when poorly chilled.

Effects of daylength

In some tree species the promotive effects of chilling can be partly replaced by long photoperiods; the longer the photoperiods the less the influence of further chilling, and the longer the period of chilling the less the effect of long photoperiods (*Pinus sylvestris*,

Jensen & Gatherum 1965; Aronsson 1980; *Picea glauca*, Nienstaedt 1966; Pollard & Ying 1979; *Picea abies*, Worrall & Mergen 1967; *Pseudotsuga menziesii*, Campbell & Sugano 1975, 1979; Campbell 1978; Figs 4 and 5). The studies on *P. sylvestris*, *P. abies* and *P. glauca* suggest that the promotive effect of long photoperiods of 16–20 h decreases to zero after relatively short periods of chilling (*c.* 40 days at 4 °C) and so might have no effect after February–March in many north temperate regions. But the studies on *P. menziesii* (loc. cit., Fig. 4) show a substantial promotive effect of long photoperiods following well over 80 days continuous chilling at 4 °C.

The seedling study suggested that *Picea sitchensis* behaves like *P. abies* and *P. glauca* Photoperiods of 17 h (corresponding to about 28 May at 56 °N) decreased the thermal time to budburst compared with 14 h photoperiods (12 April at 56 °N) only when the seedlings were poorly chilled (Fig. 5). After 1 March, lengthening the photoperiod over the range 14–17 h had no effect on the date of budburst (Fig. 5).

This finding was checked by observing the effect of 17-h photoperiods, beginning 29 February 1980, on the date of budburst of 8-year-old potted trees of *P. sitchensis*, of Queen Charlotte Islands provenance, growing outside at Bush. Nine trees in natural daylengths were compared with nine trees under floodlamps giving about 200 W m^{-1} at mid-tree level from 6.00 to 9.00 h and 18.00 to 23.00 h. There was no difference between the treatments in the dates of budburst on lateral or terminal shoots (10 and 17 May, respectively).

It was concluded that in British upland conditions, with over 60 winter days with mean temperatures $\leqslant 5$ °C, photoperiod plays a minor role in regulating budburst timing compared with temperature. Indeed, it was not possible to account for any additional variation in the fit of the model to the data in Fig. 1 by including daylength as a modifying variable.

Soil temperature

There is some evidence that budbreak in temperature trees is *initiated* by substances originating in the roots, but less evidence that soil temperatures in spring regulate bud growth (Lavender *et al.* 1973; Bachelard & Wightman 1974; Sorensen & Campbell 1978;
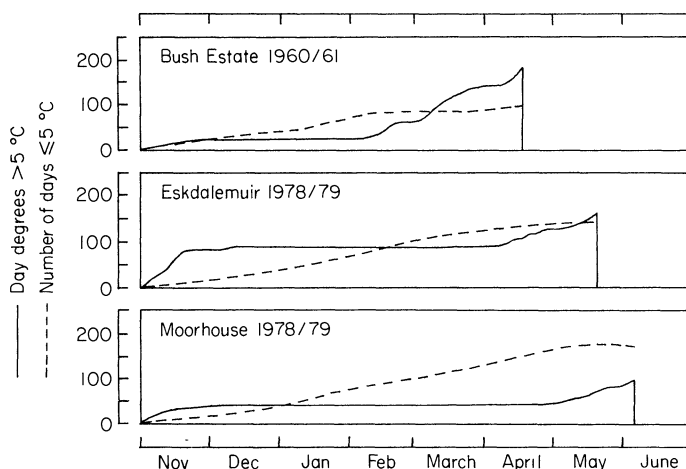

FIG. 6. Thermal time and chill days accumulated from 1 November to the date of lateral shoot budburst on young *Picea sitchensis* at three contrasting sites in upland Britain.

Paton, Slattery & Willing 1979). In any case, in Britain, soil temperatures in the range 6–10 °C in April–May at 30 cm (where, in clay soils, the diurnal amplitude is damped to about 5% of that at the surface) are approximately linearly related to day degrees >5 °C. At Bush and Eskdalemuir an increase of 1 °C in soil temperature in April–May is equivalent to about 25 day degrees >5 °C. Thus, little would be gained by incorporating soil temperature into the model, even if soil temperature data were available.

Starting dates of effective chilling and thermal time

The starting date for chilling was chosen as 1 November (a) on the assumption that before this date the buds might be 'non-dormant' and (b) because, in most years, relatively few chill days occur before 1 November in upland Britain. Most workers agree that chilling becomes effective only after bud activity ceases (Fig. 4). Nienstaedt (1966, 1967) determined that effective chilling of *Picea* spp. buds in Wisconsin began between 20 October and 20 November, and Campbell & Sugano (1975, 1979) found that chilling was relatively ineffective when begun while the buds were 'immature'. In this model (Fig. 1) bud 'maturity' was ignored as a variable because, in most years, the meristems within lateral buds on 2–10-year-old *P. sitchensis* in Britain are inactive by mid-October (Cannell & Willett 1975).

The starting date for thermal time was chosen as 1 February (a) because warm days in November–December have a negligible effect on bud growth (Cannell & Willett 1975) and (b) because relatively few days with mean temperatures >5 °C occur during January in upland Britain (Fig. 6).

Base temperature and the calculation of thermal time and chill units

The predictive value of the model (Fig. 1) could not be improved by attempts to account for diurnal temperature fluctuations (Table 2) or to use optimum chill temperatures. The choice of base temperature for shoot elongation agrees with that of others working on north temperate conifers (*Picea abies*, Sarvas 1975; *Picea glauca*, Owen, Molder & Langer 1977; *Pinus sylvestris*, M. Kanninen, pers. comm.) but the simplicity of the model in Fig. 1 probably reflects the robustness of thermal time as a predictive tool rather than the simplicity of environmental cues for vegetative budburst. There is evidence from other studies that (a) all chill temperatures below a base are *not* equally effective (Richardson, Seeley & Walker 1974; Campbell & Sugano 1975), (b) the base temperature for growth may be lowered following chilling (Vegis 1973; Campbell & Sugano 1975), and (c) chill days alternating with warm days can be less effective than the same number of continuous chill days (Timmis & Worrall 1974; Campbell 1978; and compare Fig. 4(g) 1955/56 and 1966/67). However, these second-order effects seem to be unimportant as long as one keeps within the bounds of British upland temperature and daylength conditions.

APPLICATION OF THE MODEL

Using daily maximum and minimum air temperatures Eqn (2) was used to estimate the date of budburst at Eskdalemuir for the years 1912–82 (Fig. 7). Predictions ranged from 23 April in 1961 to 30 May in 1923, with a mean date of 12 May. The frequency distribution did not differ significantly from normal, although it appears to be positively kurtotic (i.e. peaked). A full account of model predictions, for a range of sites, will be reported separately.
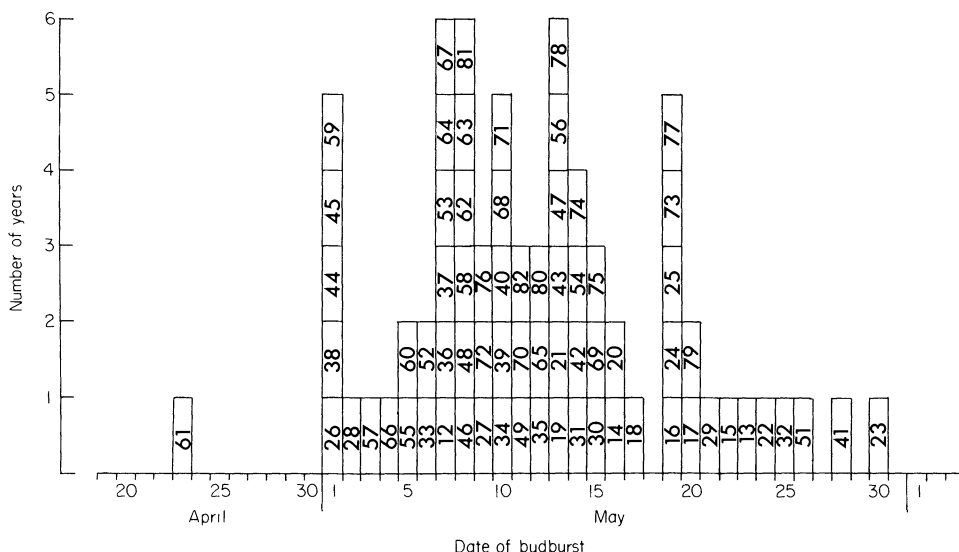
FIG. 7. Frequency distribution of the predicted dates of budburst at Eskdalemuir 1912–82. The numbers in each rectangle denote the years, e. g. 61 = 1961. Predictions were made using eqn (2) in the text (Fig. 1; Table 2, method (1)). 1950 is omitted because of a break in the winter temperature records.

GENERAL DISCUSSION

This study has demonstrated that a simple decreasing exponential relationship between day degrees > 5 °C and chill days ⩽ 5 °C (Eqn (2)) may be used to estimate the date of budburst of lateral branches on young trees of *Picea sitchensis* of the main provenances grown in upland Britain (mostly Queen Charlotte Islands and Washington). The error of a single estimate may be ± 7 days, but the error of means over 10–20 years will be less than ± 3 days (Table 2), which is adequate for most practical purposes, bearing in mind that budburst on different shoots and trees is usually spread over several days. It should be stressed that the parameters in the model would need to be modified to predict budburst on leaders and on mature trees, and to account for differences in mean date of budburst that occur among families and clones.

P. sitchensis appears to have a high chilling requirement, equivalent under British winter conditions to over 140 days with mean temperatures ⩽ 5 °C (Fig. 1). Chill saturation is reached before budburst only during cold winters or at high altitude sites. Such prolonged chilling, often followed in Britain by a rapid return to warm weather in April or May would, according to Campbell & Sugano (1975), tend to lessen any variation in date of budburst between provenances. A high chilling requirement would also serve to protect a maritime coastal species such as *P. sitchensis* from untimely budburst during warm weather in winter, although *Tsuga heterophylla*, which has a similar natural range, has been found to have a relatively low chilling requirement (Nelson & Lavender 1979; Fig. 4d).

Despite an extensive literature on the effect of photoperiod on budburst timing in tress, the studies presented here suggest that, in upland Britain, photoperiod has a negligible effect on the date of budburst in *P. sitchensis*; daylengths are too short in winter to replace chilling and they have little effect after about 1 March over the range 14–17 h.

This study also suggests that little precision has been lost by ignoring other environmental variables, such as diurnal temperature range and soil temperature, bearing in mind that this paper offers a predictive tool, not a dynamic model. Thermal time alone is widely used to forecast field crop development (Arnold 1959; Wang 1960). Clearly the exponential model presented here should not be extrapolated beyond the bounds of day degrees and chill days in Fig. 1, and the true environmental cues for budburst may be very complex. Strictly speaking, the decrease in thermal time to budburst in spring could be due to a seasonal internal rhythm, such as postulated by Schwarz (1968) to explain seasonal changes in the freezing tolerance of *Pinus cembra* kept in constant temperatures and daylengths. Under natural conditions time-dependent rhythms and chilling are confounded because there can be no temperature-less time: non-warm days must always be chill days.

ACKNOWLEDGMENTS

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