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CLIMATIC WARMING, SPRING BUDBURST AND FROST DAMAGE ON TREES

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SUMMARY

(1) If future CO_2-induced warming of 2 °C increased the incidence of warm springs, of the type that have occurred in Britain during this century, then warming would induce earlier blossoming and budburst in many temperate trees, with an increase in the risk of subsequent damaging frosts. There would, for example, be an increase in the already high incidence of frost damage to apple blossom (*Malus pumila* Mill.) cv. Cox's Orange Pippin, in Kent and to new vegetative shoots of *Picea sitchensis* (Bong.) Carr. in the Scottish uplands.

(2) If budburst occurred after a constant thermal time (e.g. 100 day °C > 5 °C after mid-January), then budburst would occur so much earlier in the spring that, on average, the temperature on the date of budburst would be lower than at present. Consequently, the risk of damaging frosts occurring after budburst would be much increased.

(3) However, in many trees there is an increase in the thermal time to budburst with decreased chilling. This increase prevents very early budburst in warm springs, and lessens the risk of frost damage.

(4) Theoretically, warming could delay or advance budburst, depending upon the extent to which a tree's chilling requirements are currently met.

(5) Empirical thermal time-chilling models suggested that, on average, Cox's apple in Kent would blossom 18–24 days earlier than at present following 2 °C warming, but that *P. sitchensis* in the Scottish uplands would burst its buds only 5 days earlier than at present.

INTRODUCTION

The timing of leaf emergence and blossoming on temperate forest and fruit trees is critical in determining the lengths of the periods of foliation and fruiting and the probability of spring frost damage to the newly emerging leaves and flowers. In Kent, spring frosts at the time of blossoming of apple (*Malus pumila* Mill.) cv. Cox's Orange Pippin, cause major reductions in yields about once every 5 years (Hamer & Jackson 1975), while in the Scottish uplands, spring frosts damage the new vegetative shoots on young *Picea sitchensis* (Bong.) Carr. about once every 3–5 years (Cannell & Smith 1984).

If the current mean atmospheric CO_2 level of 340 $\mu l\ l^{-1}$ continues to rise at $1{\cdot}5\ \mu l\ l^{-1}\ yr^{-1}$ there is a high probability of an increase in global mean temperatures (NRC 1983).

It might be supposed that climatic warming would bring about earlier dates of blossoming and budburst, but to what extent might such a trend be offset or reversed by a failure to break bud 'dormancy' owing to a decrease in the duration of winter chilling? And would any trends toward earlier budburst be associated with a decreased or increased risk of frost damage? These questions are examined in this paper, with special reference to Cox's apple in Kent and *P. sitchensis* in the Scottish uplands.

SOME ASSUMPTIONS

Nature of future climatic warming

In the first part of this paper, it is assumed that fluctuations in spring temperatures during the 20th century provide a satisfactory analogue of future temperature fluctuations, and that future warming will be equivalent to an increase in the incidence of past warm years. In the second part of the paper, it is assumed that future warming will be equivalent to a uniform increase in past long-term daily mean temperatures. This is an unreal assumption, but it is helpful to reveal the way in which trees regulate the timing of budburst and to show the different effects of climatic warming on trees with different chilling requirements. In most instances, this study is restricted to the effects of up to a 2 °C increase in temperature, which is within the range predicted by general circulation models for the temperate zone following a doubling of current atmospheric CO_2 levels (NRC 1983).

Environmental cues for blossoming and budburst

The vegetative and floral buds on temperate tree species normally enter a state of 'dormancy' in the autumn, which is progressively decreased during the winter by exposure to 'chilling' temperatures. This loss of dormancy can be described as a decrease in thermal time (temperature summation above a base temperature) to blossoming or budburst with increased chilling. The thermal time to budburst decreases to some minimal value, when the buds are said to be fully chilled.

In the first part of this paper, it is assumed that buds are always fully chilled, so that blossoming or budburst occurs after a fixed thermal time. There are several reports on trees where year-to-year variation in the timing of budburst has been satisfactorily accounted for by yearly differences in thermal time alone (budburst on trees: Lindsay & Newman 1956; Valentine 1983; blossoming on fruit trees: Anstey 1966; Eisensmith, Jones & Flore 1980).

Later, it is recognized that the thermal time to blossoming or budburst may increase as a result of climatic warming because of a decrease in the duration of chilling. Thermal time-chilling models described by Landsberg (1974) and Cannell & Smith (1983) are used to estimate the dates of budburst on Cox's apple and *P. sitchensis*, respectively. Factors other than chilling are ignored, or are assumed to have second-order effects on the thermal time to blossoming or budburst: these factors include soil temperature (Harding, Cochrane & Smith 1976), solar radiation (e.g. Caprio 1974), day length (Campbell & Sugano 1975; Campbell 1979; Cannell & Smith 1983), and bud 'maturity' in the autumn (Landsberg 1974; Kobayashi & Fuchigami 1983).

Risk of damaging frost after blossoming or budburst

The risk of damaging frosts occurring in the period between the date of budburst and 30 June (an arbitrary summer date), is assumed to be inversely proportional to the minimum screen air temperature (T_{min}) in that period, and proportional to the number of days with minimum screen air temperature $\leqslant 2$ °C (N) in that period. (The value 2 °C was chosen because tissue temperatures can be 1–3 °C lower than screen air temperatures on still, clear nights.) Taking long-term temperature means, Fig. 1 shows that the earlier the date in spring the lower the mean temperature and the value of T_{min} and the greater the value of N. Thus, any decrease in mean temperature on the date of budburst is likely to increase the risk of subsequent frosts. Clearly, if climatic warming increased the variance in

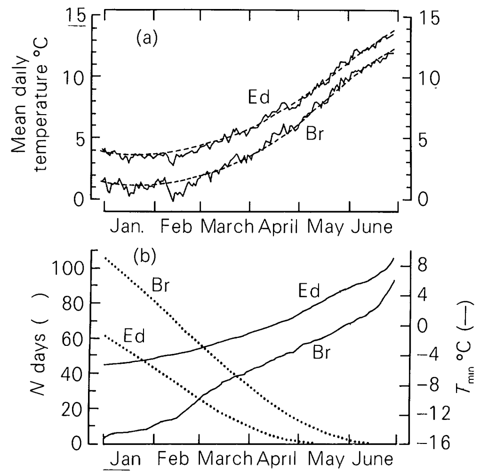

FIG. 1. Spring temperature trends at Edinburgh (Ed) and Braemar (Br). (a) Mean daily air temperatures (T). (——), averages for 1897–1978 at Edinburgh and 1912–78 at Braemar; (---) values calculated using Craddock's two-term harmonic functions (Table 1). (b) (——), minimum daily temperature subsequent to each day up to 30 June (T_{min}); (····) numbers of days with minimum daily temperatures ⩽2 °C subsequent to each day up to 30 June (N). These are means for the periods in Table 1a.

spring temperatures, the risks of frosts occurring after budburst would increase even if there were no change in temperature on that date.

SOURCES OF TEMPERATURE DATA

Mean daily temperatures for sites in Britain are well fitted by two-term harmonic functions of temperature on time (Smith 1984). The functions fitted by Craddock (1956), based on the period 1921–50, were used to describe the seasonal change in mean daily temperatures and to calculate temperature summations, at seven contrasting sites in Britian (Table 1b). The fit of Craddock's functions is illustrated in Fig. 1. However, when counting the number of chill days, and when running the phenological models of Landsberg (1974) and Cannell & Smith (1983), it was necessary to use actual daily temperature records. (Smoothed temperature curves give underestimates of the actual mean numbers of chill days.) The sites and spans of years used are given in Table 1a.

DEFINITIONS

The following symbols are used in the text and figures:

- C_x Number of 'chill' days in winter on which T is less than or equal to a base temperature of x °C (usually 5 °C), counted to day D.
- D Julian day (i.e day after 1 January) on which a given thermal time (temperature summation) (P_x) has been reached, being the thermal time required to reach 50% vegetative or floral budburst.
- G Arbitrary units of bud growth of Landsberg (1974), reaching a value of about 100 on day D (see text).

TABLE 1. Sources of daily mean air temperatures (T) for locations in Britain. (a) Meteorological records of T were obtained for each year in the period shown. (b) Two-term harmonic equations for T (in °F), calculated by Craddock (1956) for the period 1921–50, where θ is day number counted from zero at midnight on 31 December

(a)

Location	Latitude (°N)	Altitude (m)	Period
Braemar	57°00′	339	1912–1978
Durham	54°47′	102	1881–1978
Oxford	51°46′	63	1890–1978
East Malling	51°17′	30	1935–1982
Edinburgh	55°47′	26	1897–1978

(b)

Braemar	$T = 43{\cdot}57 - 10{\cdot}05 \cos\theta - 4{\cdot}00 \sin\theta + 0{\cdot}72 \cos 2\theta + 1{\cdot}08 \sin 2\theta$
Cambridge*	$T = 49{\cdot}73 - 11{\cdot}40 \cos\theta - 4{\cdot}41 \sin\theta + 0{\cdot}22 \cos 2\theta + 1{\cdot}29 \sin 2\theta$
Durham	$T = 47{\cdot}56 - 10{\cdot}01 \cos\theta - 4{\cdot}40 \sin\theta + 0{\cdot}39 \cos 2\theta + 1{\cdot}21 \sin 2\theta$
Edinburgh	$T = 47{\cdot}44 - 9{\cdot}09 \cos\theta - 4{\cdot}30 \sin\theta + 0{\cdot}61 \cos 2\theta + 1{\cdot}16 \sin 2\theta$
Kew†	$T = 50{\cdot}76 - 11{\cdot}44 \cos\theta - 4{\cdot}36 \sin\theta + 0{\cdot}50 \cos 2\theta + 1{\cdot}21 \sin 2\theta$
Oxford	$T = 50{\cdot}20 - 11{\cdot}18 \cos\theta - 4{\cdot}32 \sin\theta + 0{\cdot}22 \cos 2\theta + 1{\cdot}26 \sin 2\theta$
Plymouth‡	$T = 51{\cdot}51 - 8{\cdot}07 \cos\theta - 4{\cdot}51 \sin\theta + 0{\cdot}32 \cos 2\theta + 0{\cdot}90 \sin 2\theta$

* 52°12′N 13 m; † 51°28′N 6 m; ‡ 50°21′N 27 m.

I Arbitrary units of chilling used by Landsberg (1974); the sum of $1/T$ from 1 October to day D where, if $T < 5$ °C then $T = 5$ °C.
N Number of days with minimum air temperature $\leqslant 2$ °C between day D and 30 June.
P_x (day °C), thermal time above a base temperature of x °C (usually 5 °C).
T (°C), mean daily screen air temperature, (max + min)/2.
T_D (°C), screen air temperature on day D.
T_{min} (°C), minimum screen air temperature between day D and 30 June.

ANALOGY WITH PAST YEARLY VARIATION IN SPRING TEMPERATURES

Year-to-year variation in the risk of spring frost damage during the 20th century was examined with reference to variation in the date when a fixed thermal time was reached, and in the recorded dates of full bloom of Cox's apple in Kent and the estimated dates of budburst on young *P. sitchensis* at Braemar.

Risks of frosts after given thermal times

Screen air temperature records were examined for Braemar, Durham, Edinburgh and Oxford within the period 1890–1978 (Table 1a). For each year, determinations were made of the Julian day, D, on which a given thermal time was reached, beginning summations on the date of the minimum mean daily temperature (defined using Craddock's harmonic functions), using thermal times in the range 50–250 day °C > 5 °C. Values of D were then correlated with T_{min}, N and C_5 (the number of chill days $\leqslant 5$ °C).

In all instances, correlations between D and T_{min}, and between D and C_5, were significantly positive, while those between D and N were significantly negative ($P < 0{\cdot}05$). That is, the earlier in spring a given thermal time was reached, the shorter the previous

TABLE 2. Correlation coefficients (r) for four meteorological stations in Britain between year-to-year variation in the Julian day, D, in spring on which accumulated day degrees > 5 °C first exceeded 100, and (a) T_{min}, the lowest air minimum temperature between day D and 30 June, (b) N, the number of days between day D and 30 June on which air minimum temperatures were $\leqslant$2 °C, and (c) C_5, the number of chill days $\leqslant$5 °C throughout the winter. Correlations are based on the spans of years given in Table 1

	Correlations with D		
Location	T_{min}	N	C_5
Braemar	0·57	−0·72	0·77
Durham	0·54	−0·77	0·81
Oxford	0·57	−0·71	0·83
Edinburgh	0·73	−0·71	0·80

duration of chilling, and the lower and more numerous were the subsequent cold air temperatures, and hence the greater was the risk of subsequent damaging frosts. Table 2 gives the correlation coefficients corresponding to dates when thermal times reached 100 day °C > 5 °C (P_5).

Early 20th-century warming was reflected in progressively earlier values of D between about 1910 and 1950 at all sites except Oxford (Fig. 2 illustrates Edinburgh). This warming trend was paralleled by changes in C_5, but it was not paralleled by a decrease in T_{min} or an increase in N (Fig. 2). The long-term trends in D, T_{min} and N were not related, as revealed by (i) visual examination of 5-, 11-, 21-, 31- and 41-year moving means, (ii) visual examination of 11-year moving means expressed as deviations from average values, and (iii) cross-correlations between 5- to 41-year moving means of D, T_{min} and N. However, the moving mean residuals (i.e. differences between the moving means and the actual values) were all significantly cross-correlated in the same way as were the actual values. Thus, the correlations between D, T_{min} and N in Table 2 were attributable mainly to large year-to-year fluctuations rather than to long-term trends.

Risk of frosts after blossoming and budburst

Figure 3 presents the recorded dates of full bloom of Cox's apple at East Malling, Kent since 1936 (Luton & Hamer 1983; G. Browning, personal communication), and the dates of vegetative budburst on young *P. sitchensis* at Braemar since 1913, predicted by Cannell & Smith (1984) as functions of chilling as well as of thermal time. In both instances, early spring warming has tended to induce early blossoming or budburst with an increase in the risk of frost damage. Thus, the dates of budburst were (i) positively correlated with the

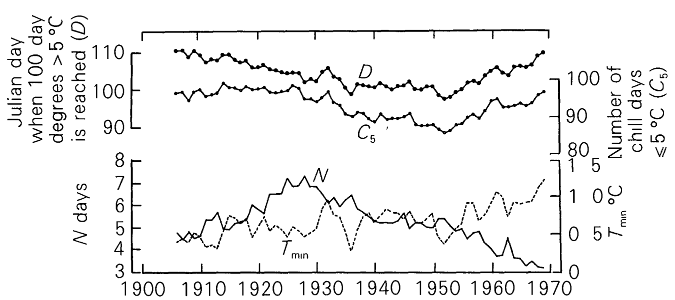

FIG. 2. Trends during the 20th century in D (after 100 day degrees > 5 °C), C_5, N and T_{min} at Edinburgh. Definitions are given in the text. These are 21-year moving means.

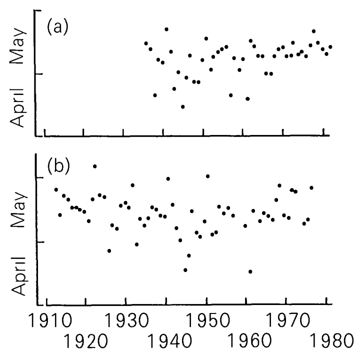

FIG. 3. (a) Recorded dates of full bloom of Cox's Orange Pippin apple at East Malling, Kent. (The date for 1953 was estimated relative to the date of full bloom of Conference pear.) (b) Dates of vegetative budburst on young *Picea sitchensis* at Braemar predicted by Cannell & Smith (1984).

date on which 100 day °C > 5 °C was reached (Cox's, $r = 0{\cdot}51$; *P. sitchensis*, $r = 0{\cdot}88$), (ii) positively correlated with T_{min} (Cox's, 0·53; *P. sitchensis*, 0·39), and (iii) negatively correlated with N (Cox's, −0·67; *P. sitchensis*, −0·46).

HYPOTHETICAL EFFECTS OF UNIFORM WARMING

In this section it is assumed that warming is equivalent to a uniform increase in past long-term daily mean temperatures (T) as defined by Craddock's harmonic functions (Table 1b). If the temperature requirements for budburst can be largely defined in terms of thermal time (P_x) and the duration of chilling (C_x or I) then four scenarios may be envisaged, giving different effects of climatic warming on the timing of budburst (on day D), on the temperature on day D, (T_D), and hence on the risk of frosts occurring after day D. Having defined these scenarios, the models of Landsberg (1974) for Cox's apple, and Cannell & Smith (1983) for *P. sitchensis* are used to determine which scenarios might be followed by those species.

Scenario I: climatic warming decreases both D *and* T_D

Consider a tree whose chilling requirement is currently far exceeded, so that decreased chilling as a result of climatic warming would have no effect on the thermal time preceding budburst or blossoming. This might be the case, for instance, for species transferred from areas with mild, short winters to areas with colder, more prolonged winters.

Let it be assumed that budburst (on day D) occurs after 100 day °C > 5 °C (P_5) accumulated from the day of the minimum mean daily temperature, where T is calculated using Craddock's functions (Table 1b). At Edinburgh and Braemar, D occurs on 11 May and 30 May with T_D values 9·2 and 9·6 °C, respectively (Fig. 4). If temperatures (T) were increased uniformly by 1, 2 . . . 5 °C, then P_5 would be achieved at earlier dates (arrowed in Fig. 4) and at lower temperatures (i.e. lower T_D) with warming by 3 °C at Edinburgh and by 5 °C at Braemar. These trends are the inevitable consequence of the convex shape of the curve of T with time during spring, as will be appreciated by comparing the two shaded areas in Fig. 4 for Braemar. Each shaded area is equal to 100 day °C > 5 °C, but the area corresponding to 4 °C warming has a longer base and hence a smaller height, T_D.

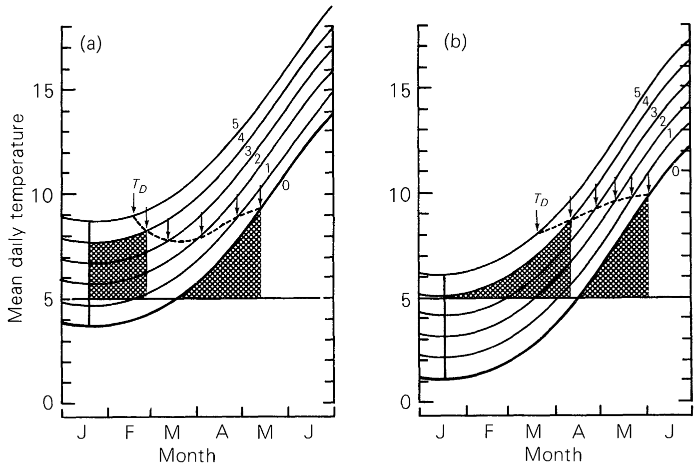

FIG. 4. Mean daily air temperatures at (a) Edinburgh and (b) Braemar with 0, 1, 2, 3, 4 and 5 °C uniform warming, calculated using Craddock's two-term harmonic functions (Table 1). The shaded areas mark the temperature integrals equivalent to 100 day °C > 5 °C (P_5) with 0 and 4 °C warming. The arrows mark the days (D) and temperatures (T_D) on which P_5 is achieved on each curve. The vertical lines in January mark the starting dates for accumulating P_5, and are the dates of the lowest mean daily temperatures.

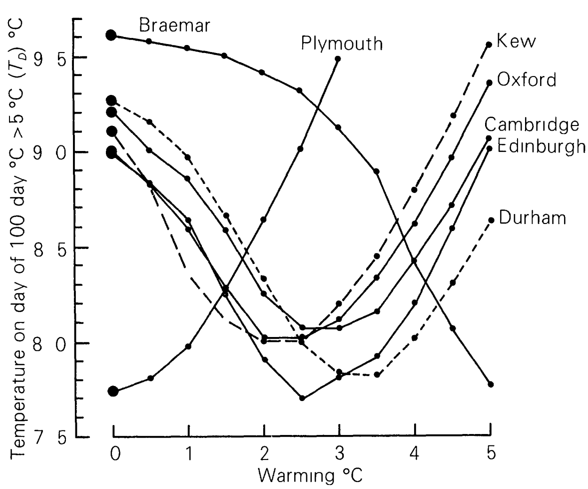

FIG. 5. Mean temperature (T_D) on the days on which 100 day °C > 5 °C (P_5) is achieved at seven sites in Britain with 0–5 °C uniform warming. P_5 was calculated as in Fig. 4.

This smaller value of T_D implies an increase in the risk of frost damage with climatic warming—i.e. an increase in N and a decrease in T_{min} (Fig. 1).

Figure 5 shows the change in T_D following 1, 2 ... 5 °C warming at seven contrasting locations in Britain, using the same criteria for P_5 as used above, and Craddock's functions to calculate T. At five of the sites, T_D decreased by 1·0–1·5 °C with 2–3 °C warming. This trend was reversed with 4–5 °C warming, when the minimal value of T (on the starting date for P_5) exceeded the base temperature (5 °C) by more than 1 °C (see Fig. 4

for Edinburgh). This reversal did not occur at the cold, upland site, Braemar, whereas at the warm, coastal site, Plymouth, any warming caused an increase in T_D.

Scenario II: climatic warming decreases D *without decreasing* T_D

Consider a tree that is only just fully chilled at present, so that any decrease in the number of chill days below 5 °C (C_5) following climatic warming of 2 °C would cause an increase in thermal time (P_5) to day D. Now consider the special case where the increase in P_5 with decreased C_5 is exactly that needed to keep T_D constant, and hence to prevent an increase in the risk of frost damage at or following day D. The required increase in P_5 is defined in Fig. 6a by relationship II between P_5 and C_5, based on temperature data for Edinburgh. At Edinburgh, the effect of such an increase in P_5 with decreased chilling would be to limit the decrease in D (to earlier dates) to 21 days, rather than 39 days in scenario I (Fig. 6b).

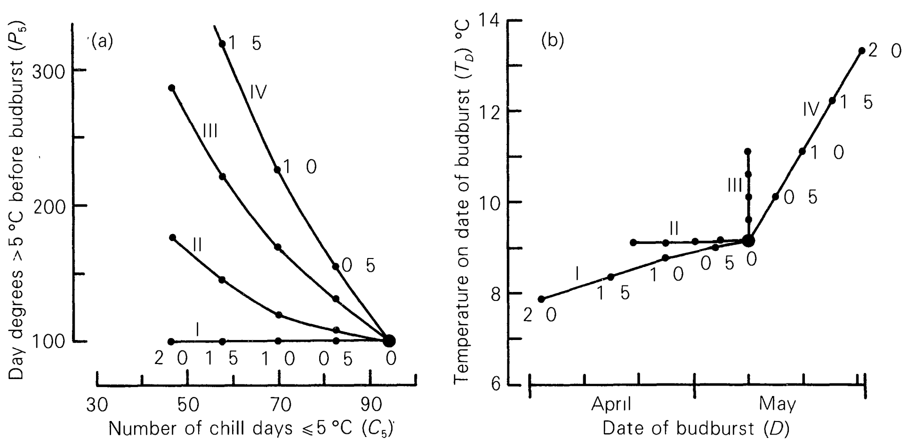

FIG. 6. (a) Four theoretical scenarios (I–IV) of the change in thermal time (P_5 of 100 day °C) to budburst or blossoming, with decrease in chilling following 0, 0·5, 1·0, 1·5 and 2·0 °C uniform warming. (b) Consequent effects on the date (D) and temperature on the date (T_D) of budburst or blossoming. These calculations were based on temperatures for Edinburgh: P_5 values were calculated using Craddock's two-term harmonic function (Table 1b); C values are the means derived from temperature records for each year from 1897 to 1978.

Figure 7a shows the relationship between P_5 and C_5 required to keep T_D constant at Oxford, Durham, Braemar and Edinburgh. The curves in Fig. 7a tend to converge, and they bear a striking resemblance to empirically derived thermal time-chilling relationships for budburst and blossoming on trees (Landsberg 1974; Cannell & Smith 1983; see Figs 8 and 10 below). The shapes of the curves result directly from the shapes of the curves describing the change is temperature with time in spring.

Scenario III: climatic warming increases T_D *without changing* D

Scenario III in Figs 6 and 7b describes the relationship between P_5 and C_5 needed to maintain budburst or blossoming on the same mean day despite climatic warming. In this instance T_D rises by the same amount as the degree of warming. For this scenario to occur at Edinburgh, there needs to be about a 3-fold increase in P_5 following 2 °C warming, using the same criteria to calculate P_5 and C_5 as above. The thermal time-chilling curves

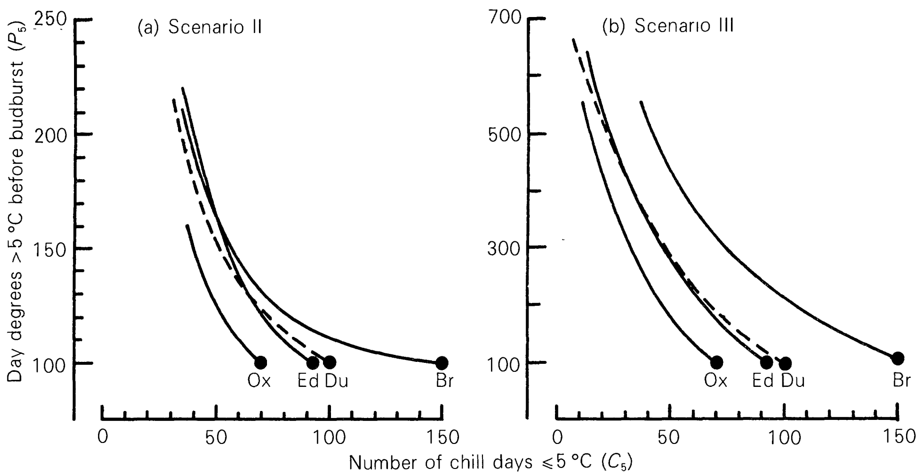

FIG. 7. The increase in thermal time (above P_5 of 100 day °C) with decreased chilling (following climatic warming) required (a) to prevent a decrease in T_D (scenario II, see text) and (b) to prevent a change in D (scenario III, see text). Ox = Oxford, Ed = Edinburgh, Du = Durham, Br = Braemar.

for different sites (Fig. 7b) converge less than those for scenario II, although they are still similar in shape to observed thermal time-chilling relationships.

Scenario IV: climatic warming increases both D *and* T_D

Some cultivars of fruit trees may be grown in warm climates, such as southern California or Florida, where they are often inadequately chilled (Chandler *et al.* 1937; Weinberger 1956; Overcash 1963; Weinberger 1967; Aron 1983). In such circumstances, the flower buds can remain 'dormant' throughout warm winters and require very large thermal times to open in spring. Blossoming is then delayed and the flowers are often misshapen.

This general situation forms a fourth scenario, which may be defined, arbitrarily, as the thermal time-chilling relationship giving the same shift in date of budburst with climatic warming as in scenario II, but with later rather than earlier dates (Fig. 6). In this scenario there is an immediate large increase in P_5 following even a small decrease in chilling, and an increase in T_D which is about double the degree of warming (Fig. 6).

PREDICTIONS USING EMPIRICAL MODELS, ASSUMING UNIFORM WARMING

Blossoming of Cox's apple in Kent

Landsberg's (1974) model, and a simple thermal time-chilling model, were used to examine the possible effects of 2 °C warming at East Malling, Kent, on the date of full bloom (D) and T_D, averaged over the period 1936–82, of Cox's Orange Pippin apple. The accuracy of the models were examined with reference to the actual records of full bloom of Cox's at East Malling for the years 1936–82.

Landsberg's model

Landsberg proposed that the date of full bloom of Cox's apple in southern England could be estimated from mean daily temperatures using the equation:

$$G = A/(1 + b \exp -k(I) \cdot P_5), \quad (1)$$

where G and A were arbitrary bud growth units, and $b = 100$. Experiments on trees given different durations of chilling suggested that:

$$k(I) = 0{\cdot}02\ (1 - \exp I/6{\cdot}7), \quad (2)$$

which was the case when buds were fully chilled (with little further decrease in P_5) when $I \simeq 20$ (I_{opt}, Landsberg 1974). The variable A was included to account for the effect of warm autumn temperatures, where:

$$A = 102 - 0{\cdot}2\ t_D, \quad (3)$$

and t_D was the number of days from 1 August to the starting date for accumulating P_5. The optimum starting date for accumulating P_5 was estimated (by us) to be the first day after 1 October on which $T \leqslant 4$ °C. This value gave the closet fit between predicted and observed dates of full bloom at East Malling for 1936–82. The inputs for the model were daily mean temperatures starting 1 October, and G was calculated daily. Full bloom was reached when $G = 0{\cdot}95A$.

Although Landsberg's model is one of the better attempts to describe the mechanisms involved in budburst (see, however, Kobayashi & Fuchigami 1983), it accounted for only half of the variation in observed dates of full bloom at East Malling between 1936 and 1982 ($r = 0{\cdot}71$). The calculated mean date of full bloom was 15 May (6 days later than the observed mean), the mean starting date for P_5 was 9 November, with $I = 20$ on 4 March, and, on the day of full bloom, mean $P_5 = 385$ day °C, $I = 29{\cdot}5$ and $T_D = 12{\cdot}3$ °C.

Figure 8a illustrates the form of Landsberg's thermal time-chilling ($P_5 - I$) model, and the change in I and P_5 predicted for 0, 0·5 ... 2·0 °C uniform warming at East Malling. (The points do not all fall on the line owing to changes in t_D and hence A.) From this figure we might expect Cox's apple to fall within the first scenario, but it behaves more like a member of scenario II. There is little evidence for any change in T_D with warming by 2 °C, and the predicted date of full bloom is only 24 days earlier than at present (rather than 39 days in scenario I above) (Fig. 8b). This effect is partly attributable to autumn warming (which decreased A and hence the G value for full bloom), and partly to the year-to-year variation in temperatures. With 2 °C warming the mean starting date for P_5 was 28 November, with $I = 20$ on 5 April, and, on the day of full bloom, mean $P_5 = 400$ day °C, $I = 20{\cdot}8$ and $T_D = 12{\cdot}1$ °C.

A thermal time-chilling model

Attempts were made to derive, empirically, a relationship between P_x and C_x which best fitted the year-to-year variation in P_x and C_x occurring on observed dates of full bloom of Cox's at East Malling from 1936 to 1982. All combinations of values of P_x were examined with base temperatures of 0, 1 ... 7 °C, starting dates of 1 November, 1 December, 1 January and 1 February, and C_x with base temperatures of 1, 3, 5 and 7 °C. There were, in most instances, significant increases in P_x with decrease in C_x. The best fitting relationship was given by.

$$P_2 = 852 - 5{\cdot}6C_3 + (0{\cdot}016C_3)^2, \quad (4)$$

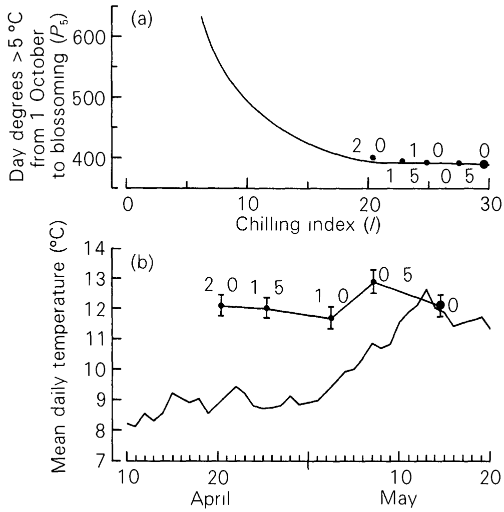

FIG. 8. (a) Landsberg's (1974) model of decreasing thermal time (P_5) to full bloom in Cox's apple with increase in chilling (I, see text). The points mark the mean values of P_5 and I for 1936–82 at East Malling corresponding to uniform warming of 0, 0·5 ... 2·0 °C. (b) Mean predicted dates of full bloom (D), and mean daily temperatures at full bloom ($T_D \pm$ S.E.), of Cox's apple at East Malling following 0, 0·5 ... 2·0 °C warming. Predictions were made using Landsberg's model for the period 1936–82. Values are shown in relation to mean daily temperatures at East Malling for the period 1936–82.

where P_2 was day degrees >2 °C from 1 December, and C_3 was days $\leqslant 3$ °C counted from 1 October. Days with temperatures between 2 and 3 °C contributed to both thermal time and chill days.

Equation 4 accounted for 72% of the variation in observed dates of full bloom ($r = 0{\cdot}85$). The model gave a mean date of full bloom for 1936–82 of 10 May—only 2 days later than the observed mean—with mean $P_2 = 645$ day °C and $C_3 = 45$ days.

Figure 9a illustrates Equation 4 and the mean change in C_3 and P_2 corresponding to warming of 0, 0·5 ... 2·0 °C at East Malling, averaged over the period 1936–82. This is a scenario-II type of relationship, as shown in Fig. 9b in which a 2 °C warming induces little change in T_D, and the date of full bloom is brought forward by only 18 days.

Overall, from this analysis, it may be concluded that 2 °C climatic warming would bring about appreciably earlier blossoming on Cox's apple in Kent, but with little change, on average, in the temperature on the date of blossoming. However, from the previous analysis of past yearly variation in temperatures, it may be concluded that there would be an increase in the risk of frost damage.

Vegetative budburst on Picea sitchensis *in Scotland*

The thermal time-chilling model derived empirically by Cannell & Smith (1983) to predict the dates of vegetative budburst on young *Picea sitchensis* in the British uplands was:

$$P_5 = 67{\cdot}4 + 4401{\cdot}8 \exp(-0{\cdot}042C_5), \tag{5}$$

where P_5 was accumulated from 1 February and C_5 was counted from 1 November.

Figure 10a illustrates Equation 5 and the mean change in C_5 and P_5 corresponding to warming of 0, 0·5 ... 2·0 °C at Braemar, averaged over the period 1913–78. Figure 10b

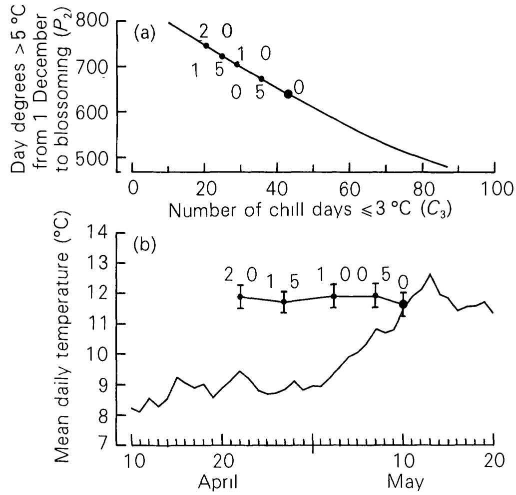

FIG. 9. (a) An empirical thermal time-chilling ($P_2 - C_3$) model for full bloom of Cox's apple at East Malling (see equation 4). The points mark the mean values of P_2 and C_3 for 1936–82 corresponding to uniform warming of 0, 0·5 . . . 2·0 °C. (b) Mean predicted dates of full bloom (D) and temperatures at full bloom ($T_D \pm$ S.E.), using the above model, as in Fig. 8b.

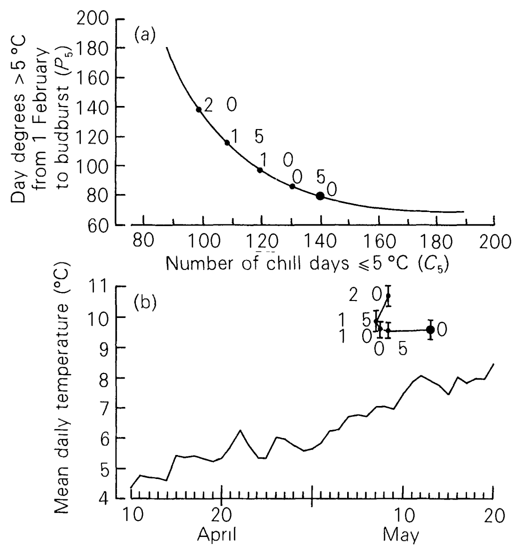

FIG. 10. (a) Cannell & Smith's (1983) model of decreasing thermal time (P_5) to vegetative budburst on young *Picea sitchensis* with increase in chilling (C_5) (see equation 5). The points mark the mean values of P_5 and C_5 for 1912–78 at Braemar corresponding to uniform warming of 0, 0·5 . . . 2·0 °C. (b) Mean predicted dates of budburst (D), and mean daily temperatures at budburst ($T_D \pm$ S.E.) on young *Picea sitchensis* at Braemar following 0, 0·5 . . . 2·0 °C warming. Predictions were made using Cannell & Smith's model for the period 1912–78. Values are shown in relation to mean daily temperatures at Braemar for the period 1936–82.

shows that warming by temperatures greater than about 0·5 °C produced such a large increase in P_5 (owing to decreased chilling) that the date of budburst changed very little, and with further warming to 2 °C, D was delayed as in scenario IV, with an increase in T_D. (Interestingly, the mean value of T_D with 0 °C warming was greater than mean T on the same day, because a high proportion of D values occurred on warm days.)

Thus, on this evidence, climatic warming of between 0·5 and 2·0 °C would not greatly change the date of budburst on young *P. sitchensis* growing in the Scottish uplands, and the current risk of frost damage would not be greatly increased unless there was a large increase in the variance of spring and summer temperatures.

DISCUSSION

The most important finding of this study was that future climatic warming could increase the incidence of front damage at or following the date of blossoming or budburst on trees in Britain.

If it is assumed that future warming will be equivalent to an increase in the incidence of warm springs of the type that have occurred during this century, then early spring warming will induce early budburst without a corresponding decrease in the incidence of subsequent frosts. During this century, year-to-year variations in temperature before budburst have occurred independently of those after budburst (e.g. a warm March has not necessarily been followed by a warm April), and trends in the timing of budburst have not been paralleled by trends in the incidence of subsequent frosts. Consequently, early blossoming of Cox's apple and early budburst on *P. sitchensis* have been associated with an increased risk of encountering subsequent frosts.

If budburst occurred after a fixed thermal time (i.e. if the buds were always fully chilled) uniform 2 °C warming would advance budburst by up to about 40 days at many sites in Britain, and the mean temperature on the date of budburst would actually decrease. For instance, with a fixed thermal time of 100 day °C > 5 °C the temperature on the date of budburst at many sites would decrease by 1·0–1·5 °C. This decrease is due to the nonlinear increase in mean daily temperatures with time during the spring (Figs 4 and 5).

In most temperate trees, the thermal time to budburst can increase with decrease in the duration of winter chilling. The four scenarios illustrated in Fig. 6 show how the effects of uniform climatic warming depend critically on the extent to which a tree's chilling requirements are currently met. If they are fully met in most years at present, then climatic warming will cause only a small increase in thermal time to budburst, and a marked shift towards earlier budburst, with little change in the temperature on the date of budburst. This seems to be the case for Cox's apple in Kent. If a tree's chilling requirements are less fully met at present, then climatic warming will cause a greater increase in the thermal time to budburst, which in turn will prevent any marked shift towards earlier budburst, and there will be an increase in the temperature on the date of budburst. This seems to be the case for *P. sitchensis* in Scotland. Theoretically, if a tree's chilling requirements are very poorly met at present, climatic warming could delay budburst, although this effect may be prevented by increased autumn temperatures, and increased soil temperatures and daylengths in spring.

The most desirable response to warm springs is to reach budburst as soon as possible—taking full advantage of the early warming—while minimizing the risk of encountering subsequent frosts. This response is described by scenario II in Fig. 6 in which there is no change in temperature on the date of budburst. Interestingly, this scenario implies a near exponential increase in thermal time with decreased chilling, similar to that actually found in trees, including Cox's apple and *P. sitchensis* (Figs 7, 8 and 10). If a unit decrease in thermal time to budburst is equivalent to a unit decrease in bud 'dormancy' then it could be argued that trees have involved patterns of decrease in 'dormancy' with increased chilling that optimize their dates of budburst. The reason for the exponential loss in 'dormancy' with increased chilling is that there is an accelerated increase in mean daily temperatures with time in spring.

Empirical thermal time-chilling models suggested that uniform 2 °C warming would advance the date of blossoming of Cox's apple in Kent by 18–24 days, with little change in temperature on the date of blossoming. Past records of blossoming would suggest that the already high incidence of frost damage would increase, even without increased variance in spring temperatures. A similar model for vegetative budburst on young *P. sitchensis* in Scotland suggested that 2 °C warming would advance budburst by only about 5 days, with an increase in temperature on the date of budburst. Consequently, for this species there may be little or no increase in the incidence of frost damage following climatic warming.

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