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DATE OF BUDBURST OF FIFTEEN TREE SPECIES IN BRITAIN FOLLOWING CLIMATIC WARMING

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SUMMARY

(1) The thermal times (T) (day °C > 5 °C since 1 January) to vegetative budburst were measured on fifteen woody perennials in Britain after different durations of chilling (C) (number of days ≤5 °C since 1 November).

(2) Late-flushing species, like *Fagus sylvatica*, had high values of T, even after 145 chill days, and T increased greatly with decreased chilling. Early-flushing species, like *Crataegus monogyna*, had small values of T, which did not increase much until there were fewer than 80–100 chill days.

(3) Relationships of the form $T = a + b \exp(r\,C)$ were fitted for each species, which were then classified into five groups. Past meteorological records were then used to estimate the mean dates of budburst of each group of species at Edinburgh (26 m altitude) and Braemar (339 m) with 0–3 °C uniform climatic warming.

(4) Climatic warming did not markedly shift the date of budburst of any group of species at Edinburgh, so they flushed in warmer conditions and failed to exploit the earlier springs. However, at Braemar, the species with small thermal time and chilling requirements, like *C. monogyna*, flushed much earlier following climatic warming.

INTRODUCTION

If the levels of atmospheric CO_2 and other greenhouse gases continue to rise, there is a high probability of an increase in mean global temperature, with the largest increase at high latitudes (Lough, Wigley & Palutikof 1983; MacCraken & Luther 1985). It might be supposed that this increase in temperature will bring about earlier dates of budburst and blossoming on trees, but Cannell & Smith (1986) showed that this was not necessarily the case. The buds of most temperate tree species require chilling to release winter dormancy. If climatic warming means that the buds are inadequately chilled, then the buds will remain partially dormant in spring and will require a large thermal time (temperature summation above a base temperature) to reach budburst. The date of budburst in a warmer climate could, therefore, be the same as now, or later.

There is considerable evidence that the thermal time to budburst decreases with increased duration of previous chilling, down to some minimal thermal time, when the buds may be said to be fully chilled (Lamb 1948; Landsberg 1974; Campbell & Sugano 1975; Cannell & Smith 1983; Cannell 1988). Cannell & Smith (1986) suggested that the effect of climatic warming depended upon where on this curve of decreasing thermal time with increased chilling the buds normally occurred after a British winter. If the chilling requirement of the species is normally far exceeded, then climatic warming, and a decrease in winter chilling, will not alter the thermal time needed to reach budburst, and budburst will occur much earlier than at present. This might be the case for *Malus pumila* Mill. cv. Cox's Orange Pippin growing in Kent (Cannell & Smith 1986). However, if the chilling requirement of the species is poorly met at present, then climatic warming, and a decrease

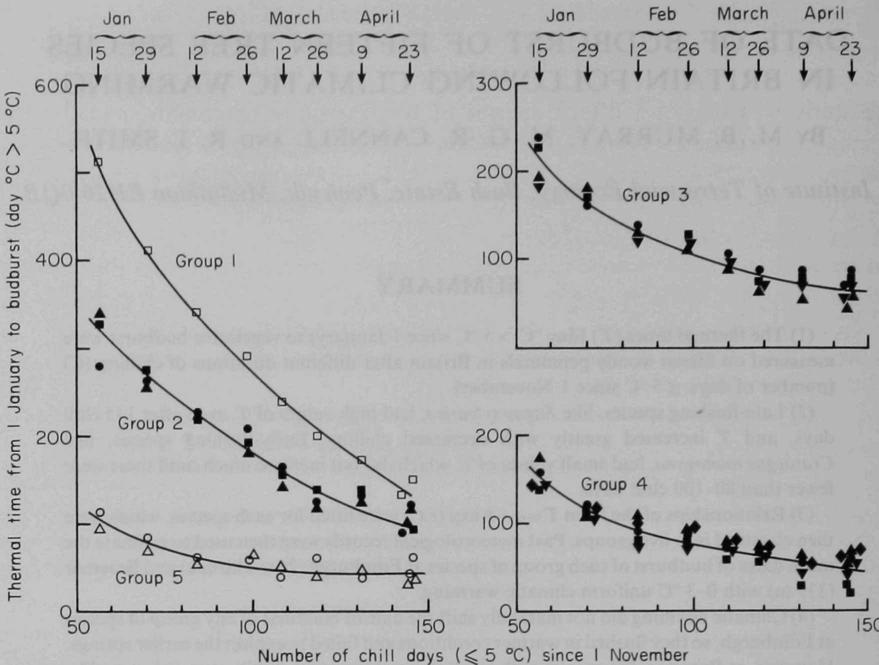

FIG. 1. Relationships between the thermal times —$T+(N\times 7{\cdot}5)$ in eqn (1).— to budburst and the accumulated number of chill days for fifteen woody perennial species, arranged into five groups. The dates given are when the plants were brought from outside into a warm glasshouse.
Group 1. *Fagus sylvatica* (beech) (□).
Group 2. *Robina pseudoacacia* (locust tree) (▲), *Tsuga heterophylla* (western hemlock) (■), *Picea sitchensis* (Sitka spruce) (●).
Group 3. *Rubus idaeus* (raspberry) (▲), *Sorbus aucuparia* (rowan) (▼), *Betula pendula (birch)* (■), *Corylus avellana* (hazel) (●).
Group 4. *Sambucus nigra* (elderberry) (▲), *Rosa rugosa* (rose) (▼), *Salix viminalis* (willow) (◆), *Larix decidua* (larch) (■), *Prunus avium* (cherry) (●).
Group 5. *Populus trichocarpa* (Balsam poplar) (△), *Crataegus monogyna* (hawthorn) (○).

in winter chilling, will greatly increase the thermal time needed to reach budburst, and budburst will occur at about the same time as now, or later. This might be the case for *Picea sitchensis* (Bong.) Carr. growing in the British uplands (Cannell & Smith 1986).

In this study, the thermal time to budburst was measured, with different durations of chilling, for fifteen contrasting woody species. The inverse relationship between thermal time to budburst and duration of chilling was then used to estimate the effect on the date of budburst of a uniform increase in mean daily temperatures at Edinburgh (26 m altitude) and Braemar (339 m).

Differences between species are examined on the assumption that all species detect days cooler than 5 °C as chill days and those warmer than 5 °C as promoting growth. This simple assumption is probably wrong, but it does not invalidate a species comparison. Similar results would be obtained using different base temperatures.

MATERIALS AND METHODS

Plant material, treatments and observations

The study was done on fifteen species of hardy woody perennials, namely, three conifers (*Picea sitchensis* (Bong.) Carr. (Queen Charlotte Islands provenance), *Tsuga heterophylla* (Raf.) Sarg. and *Larix decidua* Mill.), four broadleaved trees (*Betula pendula* Roth., *Fagus sylvatica* L., *Populus trichocarpa* Hook. clone from Washington State, and *Salix viminalis* L.), four perennials grown as ornamentals or 'amenity trees' (*Sorbus aucuparia* L., *Crateagus monogyna* Jacq., *Robinia pseudoacacia* L. and *Rosa rugosa*), and five perennials that yield fruits or nuts (*Corylus avellana* L., *Prunus avium* L., *Rubus idaeus* L. and *Sambucus nigra* L.). The common names are listed in the legend to Fig. 1.

Bare-rooted nursery stock, 1–2 years old from seed or cuttings, was potted into 125-mm pots in March 1985. During 1985, and the winter 1985/86, they were grown outside at the Bush Estate near Edinburgh (55°51′N, 198 m).

During 1986, batches of ten plants per species (but see below) were transferred from the nursery into a warm glasshouse (15–20 °C, 17-h photoperiods) on 15 and 29 January, 12 and 26 February, 12 and 26 March, and 9 and 23 April. These eight treatments (dates) gave the different batches 56, 70, 84, 98, 109, 118, 131 and 144 chill days, respectively, calculated as days since 1 November* 1985 when the mean screen air temperature ([max + min]/2) was $\leqslant 5$ °C. A further batch of 10 plants per species was left outside to receive full natural chilling of 145 chill days. Only healthy plants were used, and the following species were omitted on the following intake dates: *B. pendula* on 15 January, 12 February, 12 March and 9 April; *R. pseudoacacia* on 15 January and 12 February; *P. avium* on 15 January and 23 April; and *F. sylvatica* and *T. heterophylla* on 15 January. Inside the glasshouse, two plants of each species were placed in each of five randomized blocks.

The mean date of budburst was determined on each plant. Both the terminal (leader) buds and the most advanced lateral branch buds were scored three times per week on the scale 1 = slightly swollen, 2 = swollen, 3 = green foliage showing and 4 = elongating. The date of budburst of each species was the day on which the average of the two scores reached 3 on 50% of the plants.

Calculation of thermal time–chilling relationships

A model was required that could be used to estimate the dates of budburst using daily maximum and minimum temperatures recorded in Stevenson screens at meteorological stations.

The thermal time (accumulated day degrees > 5 °C) received by the plants from 1 January to the date of budburst was experienced partly on warm days outside and partly in the warm glasshouse. In both places, daily thermal times were recorded at plant level using a screened temperature sensor and integrator (Δ-*T* Devices, Cambridge, England).

Thermal times recorded outside using the sensor (x) (over the range 100–250 day °C) were linearly related to thermal times calculated using mean daily temperatures (T) ([max + min]/2) recorded at a meteorological station at the Bush Estate, where $T = -90{\cdot}3 + 1{\cdot}06x$ ($r^2 = 0{\cdot}99$). This relationship was used to convert all values of x to values of T (i.e. to thermal times estimated from maximum and minimum daily

* 1 November was chosen because few chill days occur before this date in Britain and during October the buds can be 'non-dormant'.

TABLE 1. Values of a, b and r ($\pm$S.E.) in eqn (1) in the text (with $g=7{\cdot}5$ °C) for the five groups of woody perennials shown in Fig. 1; group 1 has the largest chilling requirement, and group 5 has the smallest

Species group (see Fig. 1)	Parameter values ± S.E.		
	a	b	(exp r)
Group 1	-147 ± 155	1084 ± 48	$0{\cdot}991\pm0{\cdot}004$
Group 2	-56 ± 78	602 ± 30	$0{\cdot}991\pm0{\cdot}003$
Group 3	36 ± 17	514 ± 96	$0{\cdot}981\pm0{\cdot}004$
Group 4	39 ± 9	468 ± 126	$0{\cdot}974\pm0{\cdot}005$
Group 5	46 ± 3	961 ± 613	$0{\cdot}952\pm0{\cdot}011$

temperatures). Thermal times recorded in the glasshouse until budburst were linearly and closely related to the number of days in the glasshouse (N).

For each species, a non-linear regression was fitted (using 'Optimize' in GENSTAT), assuming normally distributed errors, relating the thermal times received outside (T) and in the glasshouse until budburst (N) to previous days of chilling (C), of the form:

$$T+(Ng)=a+b\,\exp\,(rC) \tag{1}$$

where C is the number of chill days $\leqslant 5$ °C from 1 November to the date of budburst, a, b and r are constants, and g is the 'effective' number of degrees Celsius accumulated each day in the glasshouse. The mean value of g was $7{\cdot}5$ °C ($\pm 0{\cdot}6$ °C) and this value was then used to estimate the parameters a, b, and r in eqn (1) for each species.

An 'effective' temperature of $7{\cdot}5$ °C, above an assumed base temperature of 5 °C, meant that the continuous 15–20 °C in the glasshouse was equivalent to a mean daily temperature outside of $12{\cdot}5$ °C ($7{\cdot}5+5{\cdot}0$ °C). Previous work had shown that thermal times received as continuous warm temperatures were not as effective as the same thermal times received with a diurnal temperature fluctuation (Cannell, Murray & Sheppard 1985).

The species fell into five groups, and eqn (1) was fitted after pooling the data for species within each group.

Predicting effects of climatic warming on the date of budburst

Equation (1) was used to estimate the dates of budburst of each of the five groups of species, for the years 1890–1978, at Edinburgh (55°48′N, 26 m) and Braemar (57°00′N, 339 m), where $T=([\max+\min]/2)$, $N=0$, and a, b and r are given in Table 1. An iterative computer programme was used in which C was counted from 1 November, T was calculated daily after 1 January, and the estimated date of budburst was the day on which T first equalled or exceeded the calculated T requirement. Dates of budburst were estimated assuming 0, 1, 2 and 3 °C uniform warming.

THERMAL TIMES TO BUDBURST

For all species, eqn (1), with $g=7{\cdot}5$ °C, well fitted the expected decrease in thermal time to budburst with increase in number of chill days, accounting for 83–98% of the variation. For all species, eqn (1) accounted for a larger proportion of the variation than a straight line. The data and parameter values for the five groups of species are presented in Fig. 1 and Table 1.

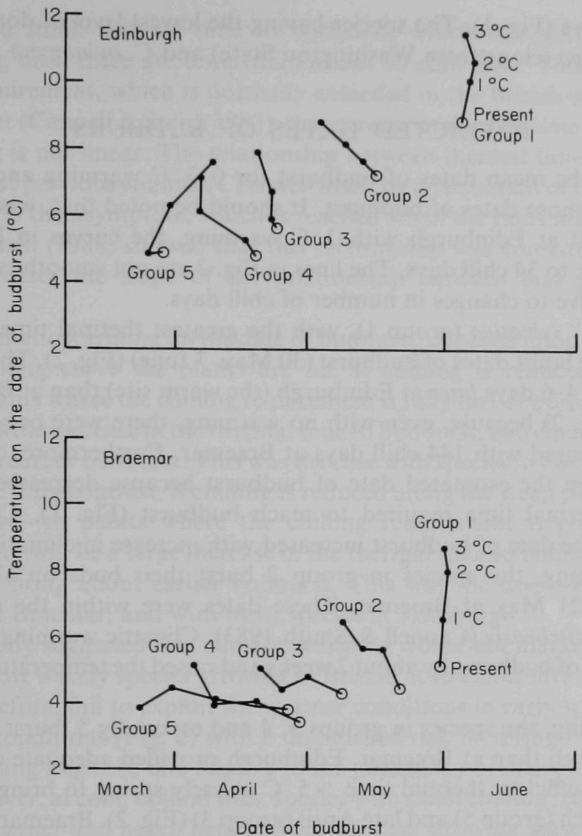

FIG. 2. Predicted mean dates of budburst (and the mean daily temperature on the date of budburst), of species in the five groups (see Fig. 1) at Edinburgh and Braemar (1890–1978) at present (○) and after 1, 2 and 3 °C uniform climatic warming. Predictions were made using eqn (1) with the parameter values given in Table 1.

F. sylvatica (sole member of group 1) burst its buds very late, and so had a much larger thermal time to budburst than all the other species. This thermal time decreased greatly with increased chilling (Fig. 1), but even after 145 chill days, the thermal time to budburst had not reached an asymptote*, and was greater than the thermal time required for budburst by other species (Fig. 1). Thus, the buds of *F. sylvatica* seemed to have a high level of dormancy, which was not fully released after 145 chill days.

R. pseudoacacia, and two of the conifers, *T. heterophylla* and *P. sitchensis*, (group 2) had a smaller thermal time to budburst (a lower level of dormancy) than *F. sylvatica*, but an asymptote was not reached after 145 chill days (Fig. 1). Previous work on *P. sitchensis* (Cannell & Smith 1983) suggested that an asymptote of 67 day °C was reached after about 200 chill days (which was within the 95% confidence limits of *a* for group 2 in Table 1).

All the other species (groups 3, 4 and 5) burst their buds after receiving less than half as much thermal time as *F. sylvatica*, and the thermal time to budburst decreased very little

* The asymptote is given by *a* in Table 1 (-147 ± 155 day °C), but, clearly, it could not be accurately determined.

after 100 chill days (Fig. 1). The species having the lowest level of dormancy (group 5) were *P. trichocarpa* (clone from Washington State) and *C. monogyna*.

PREDICTED DATES OF BUDBURST

Figure 2 shows the mean dates of budburst for 0–3 °C warming and the mean daily temperatures on those dates of budburst. It should be noted that, when estimating the dates of budburst at Edinburgh with 3 °C warming, the curves in Fig. 1 had to be extrapolated back to 34 chill days. The lines in Fig. 2 are not smooth curves because the model was sensitive to changes in number of chill days.

As expected, *F. sylvatica* (group 1), with the greatest thermal time requirement for budburst, had the latest dates of budburst (30 May–7 June) (Fig. 2). The estimated dates of budburst were 4–6 days *later* at Edinburgh (the warm site) than at Braemar (the high altitude site) (Fig. 2) because, even with no warming, there were only 97 chill days at Edinburgh, compared with 144 chill days at Braemar. Furthermore, climatic warming had little effect on the estimated date of budburst because decreased chilling greatly increased the thermal time required to reach budburst (Fig. 1). Consequently, the temperature on the date of budburst increased with increase in climatic warming.

With no warming, the species in group 2 burst their buds on about 17 May at Edinburgh, and 21 May at Braemar. These dates were within the range previously estimated for *P. sitchensis* (Cannell & Smith 1983). Climatic warming of 3 °C brought forward the dates of budburst by about 2 weeks and raised the temperature on those dates by about 2 °C.

With no warming, the species in groups 3, 4 and especially 5, burst their buds much earlier at Edinburgh than at Braemar. Edinburgh provided adequate chilling for those species and had sufficient thermal time >5 °C in early spring to bring about budburst between late March (group 5) and late April (group 3) (Fig. 2). Braemar, by contrast, did not provide sufficient thermal time >5 °C for budburst until late April (group 5) or mid-May (group 3).

Climatic warming had markedly different effects on the dates of budburst at Edinburgh and Braemar for the species in groups 3–5. At Edinburgh, decreased chilling, from about 94 to 34 chill days, considerably increased the thermal time required for budburst, as will be appreciated by extrapolating the steep parts of the curves in Fig. 1. Consequently, warmer weather in March–April did not cause markedly earlier budburst at Edinburgh. By contrast, at Braemar, climatic warming decreased the number of chill days from about 145 to 78, and, over that range, there was little change in the thermal time to budburst (Fig. 1). Consequently, warmer weather in March–April at Braemar caused markedly earlier budburst: species in group 5 burst their buds almost 5 weeks earlier following 3 °C warming, with little change in temperature on the date of budburst.

DISCUSSION

It is well known from phenological records that there are large differences among woody perennials in the date of budburst in spring. This study showed that species with a late date of budburst, like *F. sylvatica*, have a large thermal time to budburst which increases greatly with a decrease in winter chilling of less than about 150 chill days ($\leqslant 5$ °C). In other words, those species have a large chilling requirement which may only just be fully met in the current British climate. By contrast, species which burst their buds early, like *C.*

monogyna, have a small thermal time to budburst, which increases very little with decreased chilling, until there are fewer than about 50 chill days. Those species have a small chilling requirement, which is normally exceeded in the British climate.

As shown earlier (Cannell & Smith 1983), the increase in thermal time to budburst with decreased chilling is not linear. The relationship between thermal time to budburst (T) and the duration of previous chilling (C) is well fitted by an equation of the form $T=a+b$ exp (rC), where a is the asymptote, which is reached when the buds may be regarded as fully chilled. Cannell (1988) showed that this relationship was consistent with the view that chilling increases the slope of the relationship between bud growth rate and temperature.

The effect of climatic warming on the date of budburst, depends upon which part of the thermal time–chilling curve the plants are on. If chilling is reduced just below the asymptote—in plants where the chilling requirement is fully met or exceeded at present—then there will be little increase in the thermal time to budburst, and climatic warming will bring about much earlier budburst. This was the case with species in our groups 3, 4 and 5 at Braemar (Fig. 2). By contrast, if chilling is reduced along the steep part of the thermal time-chilling curve—in plants where the chilling requirement is poorly satisfied at present—then there will be a large increase in the thermal time to budburst, and climatic warming will *not* bring about earlier budburst. This was the case with species in our groups 1 and 2 at Braemar, and with most species at Edinburgh.

Overall, this study suggested that climatic warming would not markedly shift the date of budburst of most woody species growing in Britain at lowland sites (e.g. Edinburgh). They would, therefore, fail to exploit the warmer conditions in early spring, they would flush in warmer conditions (Fig. 2) with a diminished risk of spring frost damage, and their time of flushing might be late relative to the phenology of many herbaceous plants and insects. However, at cool, upland sites, species with small chilling requirements would burst their buds earlier and hence benefit from a longer growing season (groups 1–3 at Braemar, Fig. 2). These species might be at greater risk from early frost damage, although there was little evidence in this study for a decrease in temperature on the date of budburst.

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