ONSET OF FLOWERING IN BIENNIAL AND PERENNIAL GARDEN PLANTS: ASSOCIATION WITH VARIABLE WEATHER AND CHANGING CLIMATE BETWEEN 1978 AND 2007

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ABSTRACT

Observations were made weekly over a period of 30 years of 208 species (trees, shrubs, herbaceous plants and geophytes) from more than 1,000 growing in a garden located 18km east of the Royal Botanic Garden Edinburgh (RBGE), Scotland (lat. 55º 56′N: long. 3º 09′W). Of these species, 27 were British native or naturalised.

The First Flowering Dates (FFD) of 67 species were without significant temperature associations with variable weather; the FFDs of the other 141 species reflected, in contrast, the net outcome of ‘major’ associations with late winter/spring temperatures and smaller impacts of autumn/early winter temperatures. Increases in late winter and spring temperatures advanced the onset of flowering in the current year; in contrast, increases in autumn and early winter temperatures tended to be associated with delayed flowering in the following year.

With stepwise regression, penalised signal regression and thermal-time models, it was possible to identify species with ‘strong’ associations with both air and soil temperatures and species with ‘weak’ associations with either air or soil temperatures.

Thermal-time models for each of 120 species, whose FFDs were associated with temperature, enabled the characterisation of (1) base temperatures, *Tb*(°C), at, and above which, development towards open flowers is possible; and (2) thermal constants (degree days accumulated between the start of development and the onset of flowering). Together these attributes suggested that each base temperature cohort has species with widely different degree-day requirements.

Between 1978 and 2007 mean air temperatures significantly increased by 0.080°C, 0.044°C and 0.026°C yr^{-1} in the first, second and third quarters; soil temperatures increased by 0.060ºCyr^{-1} in the first quarter. Over the 30-year period, the trends in flowering showed the early (February/March) flowering species flowering c. 24 days sooner; the later flowering species (April/May) advanced by only c. 12 days.

INTRODUCTION

Phenology, the study of organisms as affected by climate, especially dates of seasonal phenomena such as opening of flowers and arrival of migrants (MacDonald, 1972) gained adherents, both ‘amateur’ and professional, during the 20th century, although records of phenological phenomena associated with 24 species of plants and animals, taken in the Jingha District of China, can be traced back to the 12th century (Yoshino

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and Park Ono, 1996). The mid-1700s was a period of active interest with Gilbert White of Selborne fame starting to record many events of the horticultural year in his *Garden Kalendar* (1751–1771), which was superseded by his *The Naturalist's Journal* (1768–1793) (Commander, 1982). White's records owe much to a diary specially designed by Daines Barrington for recording natural events. It brought together (1) the occurrence of plants, vertebrates and invertebrates; and (2) associated physical aspects of the environment. In the diaries there were columns for air temperature, rainfall, "plants first in flower", "frogs first appear", occurrences of migratory birds, etc. (Mabey, 1982). At about the same time one of White's correspondents, Robert Marsham (Marsham and Bell, 1876), of central Norfolk (lat. 52°40′N: 0°54′W), initiated in 1736 a distinctive study that has proved to be invaluable (Margary, 1926). With some breaks, it was continued by members of the Marsham family until 1947. They recorded annually the first dates of (1) flowering; and (2) leafing of four and thirteen plant species respectively and also the first croaking, in the spring, of frogs and toads. These observations have attracted considerable interest in recent years: they suggest that first flowering dates (FFDs) of *Anemone nemorosa* (wood anemone), *Brassica campestris* (turnip), *Crataegus monogyna* (hawthorn) and *Galanthus nivalis* (snowdrop) are associated with early-season air temperatures but not with annual rainfall. Further, recent analyses of the *A. nemorosa* data, but not those of the other species, found a statistically significant trend to earliness of 0.064 day yr^{-1}, equivalent to an advance of 13.5 days between 1736 and 1947 – a span of 211 years (Sparks and Carey, 1995).

The above observations, although pioneering, were restricted to very few plant species and, as Usher (2007) warned in a paper concerned with the conservation of European diversity, "there is no norm … individual species behave differently". While Jeffree (1960) would have supported this warning it did not stop him using FFDs of only 14 'key' species when effectively characterising the Meteorological Districts of the British Isles. More recently the data from individual species have been included in the Geographic Information System (GIS) assisted bioclimate characterisation of Bavaria, Germany, where the phenology of *Forsythia suspensa* is proving to be of value (Jochner *et al.*, 2011); in East Asia *Prunus yedoensis* (Yoshino cherry) is the species of choice in a similar exercise (Omasa, 1998). With these developing interests combined with that of changing climate, Fitter *et al.* (1995) published a timely and detailed analysis of FFDs taken between 1954 and 1988 of 243 plant species growing, largely unmanaged, near Chinnor, Oxfordshire, in south central England (lat. 51°41′N: long. 0°56′E). Their results highlight the ways in which flowering, notably the onset of flowering, responds to variable weather with a very large part of the variation being associated with spring temperatures and, to a lesser degree, autumn temperatures.

In effect the current paper builds upon the observations made by Fitter and his colleagues, and also Last *et al.* (2003), while at the same time introducing a number of different procedures:

1 Fitter *et al.* made observations on unmanaged vegetation while the present study

focused on managed garden plants but not to the exclusion of British native and naturalised species. Inevitably, therefore, there was a major difference in species composition.

2 Fitter *et al.* concentrated on associations with air temperature while this study gave more or less equal attention to air and soil temperatures.

3 The current study included Penalised Signal Regression, and, to elucidate mechanisms, spring-warming (thermal-time) models in addition to Stepwise Regression.

Before proceeding, however, it is desirable to be mindful of the influences of 'temperature' as well as the roles of other factors, most notably 'photoperiod' that control, to differing extents in different species, the formation of winter buds, leaf abscission and so on, the release from dormancy and the onset of reproduction (flowering events) (Korner & Basler, 2010).

MATERIALS AND METHODS

Site

Observations were taken of biennial and perennial plants flowering in a garden in a semi-rural location (lat. 55°56′N: long. 2°54′W) near Longniddry in East Lothian, Scotland, close to the south shore of the Firth of Forth and about 18km east of RBGE. The garden is about 25m above sea level. It was converted from agricultural cropping in 1968 and extended to 0.5ha in 1973.

Soil type

The soil profile is typical of the Dreghorn Association: it has freely draining brown forest soil overlying freely draining raised beach sand mainly derived from carboniferous sediments (Furley & Smith, 2002). The land is assigned to Class 1: it is capable of carrying a wide range of plants, including those with exacting requirements, but for acid-loving plants soil was usually amended with peat.

Weather/climate

Records for 1977 to 2007 from RBGE were supplied by Dr Stephan Helfer. The values obtained are within the ranges expected of a northern temperate coastal location with conspicuous seasonal differences in daylength, sunshine hours and temperatures. In the coastal lowlands of East Lothian the growing period – defined as the times of year when the mean daytime air temperatures are 5°C or higher – usually stretches from mid/late March (spring) to mid-November (late autumn) (Furley and Smith, 2002); in reality the flowering and/or root growth of many species proceed at lower temperatures. The weather and climate values obtained are as follows:

- Daylength: data obtained from a public website of the US Naval Observatory (USNO, 2011). This varied from 7.1 hd^{-1} in December to 17.7 hd^{-1} in July.
- Sunshine: numbers of sunshine hours (hd^{-1}) were largest (4.3 hd^{-1}) in 1995 and 1998 and smallest (3.5 hd^{-1}) in 1980, 1983, 1985 and 1993.
- Precipitation: annual precipitation ($mmyr^{-1}$) was heaviest in 1985, 1990, 1995 and 2000, namely 760 $mmyr^{-1}$, and lightest (621 $mmyr^{-1}$) in 1996.
- Temperature: see Fig. 1
  - air (means of daily maximum and minimum measured c. 1.2m above ground (Stevenson screen)): warmest in 2006 (10.0ºC) and coolest in 1979 (8.2ºC). On average July (15.1ºC) was the warmest month and January (4.1ºC) was the coolest.
  - soil (means of recordings at 09.30 (GMT) at depths of 10cm and 30cm): warmest in 2007 (9.4ºC) and coolest in 1979 (8.0ºC). The coolest month was January (2.8ºC) and the warmest was July (15.7ºC).

The additional temperature data below Fig. 1 show that (1) the changes in soil and air temperatures followed very similar courses; and (2) the magnitude of some of the changes in February/March were conspicuously larger and sometimes in the opposite direction to those among the relevant annual means.

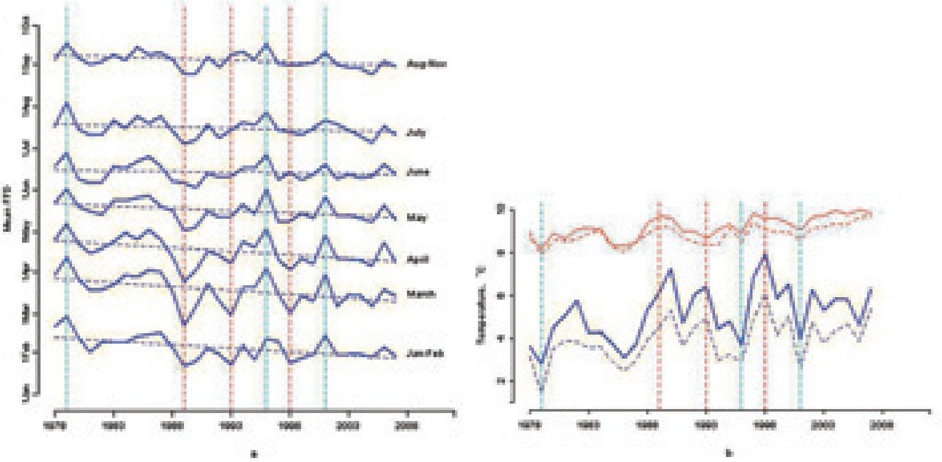


Fig. 1 Year-to-year variation between 1978 and 2007 in (top) First Flowering Dates of 208 plant species growing in East Lothian, Scotland. The monthly groupings were based on the FFDs of individual species. – – – indicates long-term trends between 1978 and 2007. For comparison, (b) shows the patterns of mean February/March temperatures (blue) and mean annual (red) temperatures (— air (mean of maximum and minimum) and – – – soil (mean of 10cm & 30cm below ground)). The vertical lines denote 'early' (red) and 'late' (blue) years.

Range of plants and their management

The garden in East Lothian was stocked with a range of species, mostly long-day plants and day-neutral plants (Halevy, 1985/1989) including:

- Trees (T) – tall woody plants usually distinguished from shrubs by having comparatively greater height and characteristically a single trunk with branches rather than several stems (buds project freely into the air).
- Shrubs (S) – woody plants of relatively low height distinguished from trees by having several stems rather than a single trunk (buds tend to be located nearer the ground than those on trees).
- Herbaceous plants (H) – plants with fleshy stems that generally die back at the end of each growing season (buds are at soil surface).
- Geophytes (G) – perennial plants that survive winters by having buds in the soil below ground, for example bulbs, corms, rhizomes, tubers and tuberous root buds usually concealed by soil and/or detritus.

These terms (trees, shrubs, herbaceous plants and geophytes) (Universal Dictionary, 1993) were adopted as being more in tune with the interests of horticulturists and gardeners (Owen, 2010) than Raunkiaer's system (Raunkiaer, 1934), which was derived from studies of natural ecosystems (T, Phanerophytes; S, Chamaephytes; H, Hemicryptophytes; and G, Geophytes).

Efforts were made to sustain the same levels of garden management from 1978 to 2007; after being planted geophytes remained undisturbed. A range of annuals were grown but it was decided to ignore them so as to avoid a consideration of germination and propagation. However, there were two exceptions – *Antirrhinum major* and *Limnanthes douglasii* – which, in the conditions prevailing in East Lothian, were grown as biennials/perennials.

Flower observations

After a trial run in 1977 a weekly series of observations was initiated in January 1978. It continued with few gaps until December 2007. This paper is primarily concerned with the first flushes of flowers produced in the 'current year'. Data for subsequent flushes, if any, have as yet only been examined cursorily; the minimum interval between the termination of one flush and the onset of the next was set at four weeks. The positions in the following analyses occupied by species with flushes spanning parts of two calendar years were determined by their mean FFDs.

Species/cultivars were considered to be flowering when stamens and/or stigmas could be seen in opened flowers without parting their associated bracts (sepals/petals/spathes). They were deemed to have stopped flowering when pristine stamens/stigmas could no longer be found – a decision subject to larger observer errors than when observing the onset of flowering.

When adopting this definition of flowering it was recognised that it encompassed two processes: (1) flower initiation and (2) subsequent flower development, both of which are controlled to a considerable extent by temperature (Rees, 1972).

Detailed analyses have been restricted to an eclectic selection of 208 out of c. 1,000 species; the choice was largely made on the basis of completeness of records and includes 27 British native or naturalised species. To minimise the risk of observer bias it was decided at the outset to collect data for at least 20 years before embarking upon the process of analysis. This decision was, however, revoked in 1989, after 12 years, when the UK Department of the Environment sought factual evidence of exceptional flowering associated in 1989 with unseasonably warm weather from mid-December 1988 to mid-February 1989 (Last, 1993).

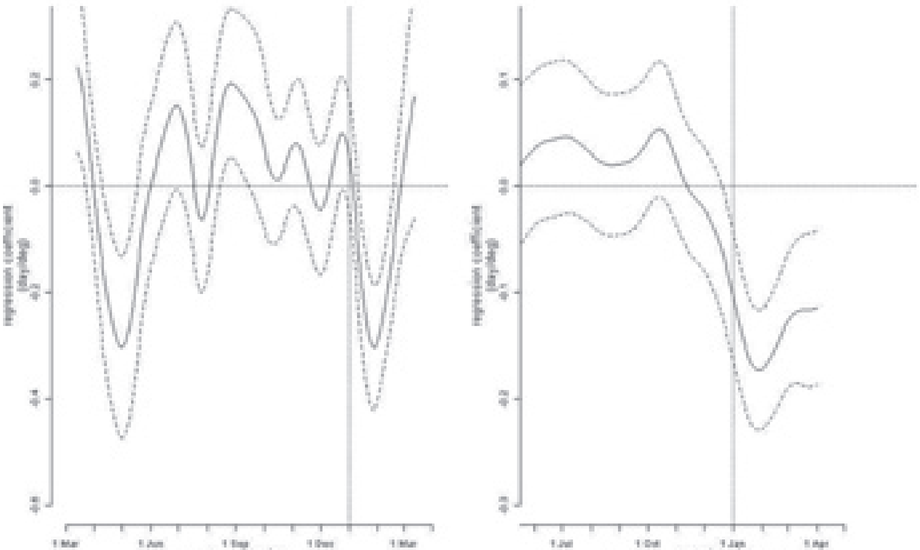
Statistical analyses

Four procedures were used to relate the FFDs of each species to environmental variables:

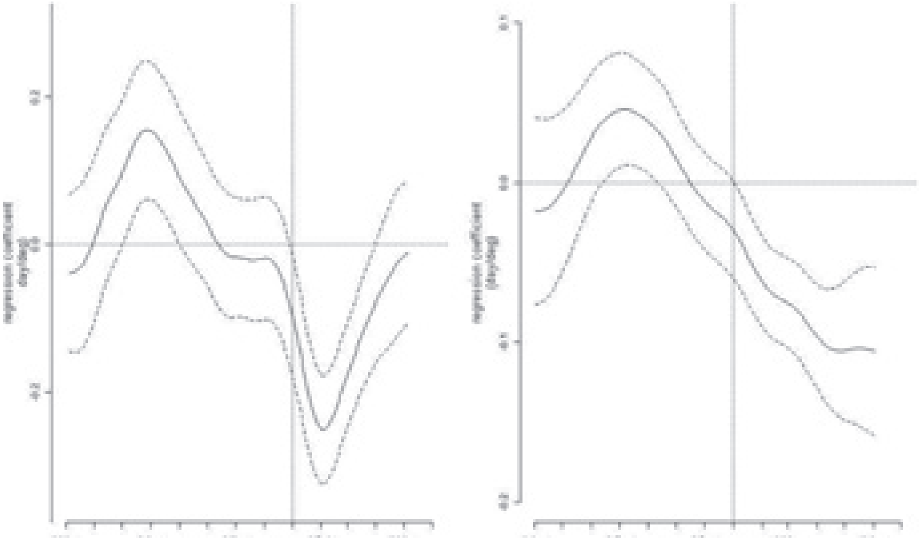
- Stepwise regression (Draper & Smith, 1981; Fitter *et al.*, 1995)
- Penalised signal regression (Marx & Eilers, 1999; Roberts, 2008, 2010, 2012)
- A two-dimensional extension of penalised signal regression (Eilers & Marx, 2003; Roberts, 2008, 2010) was used to examine the relationship between FFDs and temperature over sets of species.
- Spring-warming or thermal-time models (Chuine *et al.*, 1998; Chuine *et al.*, 2003; Trudgill *et al.*, 2005; Thompson & Clark, 2006; and Linkosalo *et al.*, 2008).

Stepwise regression

To reduce problems related to strong correlations between sequential covariates or predictors (for example daily temperatures) and to provide greater clarity, daily records of temperature were aggregated to form monthly means. Monthly mean temperatures for the 12 months preceding and including the month of the mean FFD of each species were treated as potential covariates. Following Efroymson (1960), a multiple regression model was built, step by step, from a model with no covariates. At each step, the covariate that most improved the fit of the model was added if the p-value associated with its partial F-statistic was less than 0.01. The least useful covariate already in the model could be deleted if its p-value was greater than 0.01. While stepwise regression yields results that are easily interpreted, there is an inevitable loss of information when daily temperature records are aggregated to monthly means. The method assumes that the effect of temperature is constant within calendar months and that some months have no effect.



(a) *Galanthus nivalis* (b) *Narcissus pseudonarcissus*



(c) *Rhododendron keiskei* (d) *Laburnum anagyroides*

Fig. 2 Interpretation of the relationships between the FFDs for four species and soil temperatures found by *P*-spline signal regression (PSR). —— corresponds to the line of regression coefficients while – – – corresponds to two standard errors above and below the regression coefficients. Each covariate-day is one of 365 (see text). All four species have significant relationships with spring temperatures but only two, *Rhododendron keikeis* and *Laburnum anagyroides*, appear to be influenced by autumn temperatures.

Penalised signal regression

This type of regression, unlike stepwise regression, facilitates the use of daily temperature records. It is based on the concept that temperatures on consecutive days are likely to have similar effects on FFD. This concept is turned into a constraint on differences between coefficients of consecutive days in the fitting process. The result is a multiple linear regression with a temperature covariate for each day. The regression coefficient for a covariate represents the change in FFD associated with a change of 1°C on that day. Negative coefficients indicate that an increase in temperature shortens the interval from 1 January to the onset of flowering: conversely a positive coefficient indicates that a 1° change will lengthen the interval to flowering. The regression coefficients, for each covariate plotted against the day-numbers for covariates, forms a smooth curve that is easy to interpret (Fig. 2). In practice penalised regression generally performs better than stepwise regression with the measure for 'fit' used for the latter – the coefficient of determination R^2 – being substantially over-optimistic (Roberts, 2012). A particular variant of penalised signal regression was used, known as *P*-spline signal regression (PSR), following the guidance in Roberts (2012). The temperatures for the 365 days up to the latest FFD of the species were used as covariates.

Two-dimensional P*-spline signal regression*

To investigate how the relationship with temperature varied according to the lateness of a species, an extension of PSR, two-dimensional *P*-spline signal regression (2-d PSR), was used. For a single species, PSR produces a curve showing how the effect of temperature on FFD changes over the days considered as covariates (Fig. 2). Using the mean FFD for each species as a further covariate, 2-d PSR produces a smooth two-dimensional surface of regression coefficients. This shows how the curve of (1) regression coefficients covering those days whose temperatures were used as covariates, changes with (2) mean FFD. For this analysis, the FFD values were standardised to ensure that species with highly variable FFDs did not dominate the less variable FFDs of other species. To clarify the plots of these surfaces, the regression coefficients were divided by their standard errors to give t-statistics. As for PSR, negative coefficients in response to higher temperatures indicate a shortening of the interval prior to flowering while positive coefficients signify delays.

Spring-warming model

Most poikilothermic biological entities (including plants and invertebrates) are adapted to particular temperature ranges. As environmental temperatures (t) cool, the rates of development of poikilothermic plants also decrease and, if the temperature drops low enough, development will cease altogether at T_b, their lower development (base) temperatures. Conversely when environmental temperatures increase, starting on day

θ, development progresses until the phase of development of interest is attained, in this paper FFD. From these relationships two constants of importance can be derived:

(i) the base temperature T_b and
(ii) the thermal constant or the number of degree days (DD) needed from day θ to complete a specified development on day 'd_f'.

The *DD* requirement in this model is based on the summation of the physiologically effective temperatures between θ and d_f, the day on which a species starts to flower:

$$\text{when} \sum_{d=\theta}^{d_f} F(t_d) = DD,$$
$$\text{where } F(t_d) = 0 \text{ when } t_d \leq T_b$$
$$\text{and } F(t_d) = t_d - T_b \text{ when } t_d > T_b$$

where t_d indicates the daily temperature (mean of maximum and minimum for air temperature and for soil temperatures, the daily means of temperatures at 10cm and 30cm below ground read at 09.00 GMT). This model was fitted using a grid search for θ in combination with the Nelder-Mead algorithm (Nelder and Mead, 1965) for the other two parameters, T_b and DD. The earliest date 'allowed' prior to the onset of flowering was nominated as 1 December in the year before flowering.

EVALUATION OF THE ASSOCIATIONS BETWEEN FIRST FLOWERING DATES AND TEMPERATURE

This section is in two parts: the first is concerned with short-term, annual changes associated with variable weather, and the second focuses on longer-term (thirty-year) trends associated with changing climate.

Short-term (annual) changes associated with variable weather

At an early stage in the project it became clear that seasonal patterns of flowering often differed greatly from year to year (Last, 2001). Thus in 1989 when January to mid-February temperatures, like those in the second half of the preceding December, were c. 3.5ºC warmer than the averages for 1978 to 1988, numbers of plant species in flower were, until the beginning of July, in excess of the mean numbers in 1978–1988 (Fig. 3a). During 1978–1988 they progressively increased from 8 at the end of January to 18 and 56 at the end of March and mid-May respectively – the comparable numbers in 1989 were 23, 42 and 76 respectively (Fig. 3a). Parallel analyses suggest that the number of species in flower strongly reflected their earliness (of flowering), together with less consistent influences of duration of flowering which remain to be fully elucidated in many. Many of the species that usually (1978–1988) started to flower in mid-April began at the end of January in 1989 (Fig. 3b). In many instances the period to the onset of flowering varied by ten weeks, as in *Choisya ternata*, *Eccremocarpus scaber*, *Euphorbia griffithii* and *Rhododendron keiskei* (see Appendix). In a simple analysis the FFDs between 1978 and 2007 of five ‘temperature sensitive species’ were plotted against the mean air temperatures for the months selected by stepwise regression (Fig. 4). This method identified a set of linear relationships in which the slopes differed markedly from one species to another (compare *Ribes sanguineum* and *Fritillaria meleagris*).

(a) *Galanthus nivalis* (mean FFD, 27 January);
(b) *Ribes sanguineum* (14 March);
(c) *Fritillaria meleagris* (7 April);
(d) *Doronicum plantagineum* (20 April) and
(e) *Malus domestica* (4 May).

For each species, the FFDs are plotted against the air temperature in a particular month, which was found by stepwise regression to most influence flowering.

In 2003 Hepper published observations of flowering made in his garden in Headingly (lat. 53°49′N: long. 1°34′W), Yorkshire, between 1947 and 1962 (Hepper, 2003). By rearranging his data – the FFDs of 18 perennial species (mostly ‘herbaceous’ plants and geophytes) – it was clear that the annual variation among species that usually started flowering in April (mean FFD, 108d) and June (mean FFD, 165d) very closely followed the pattern shown by plants that started to flower between February

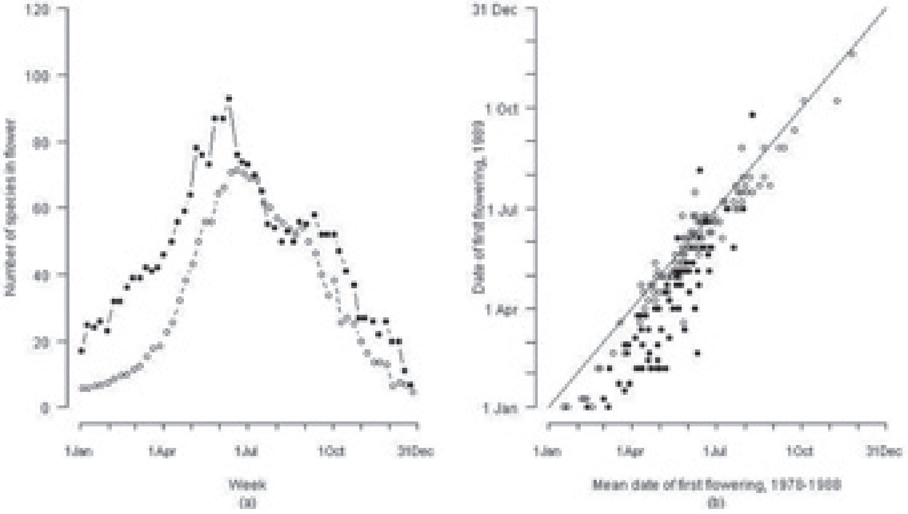
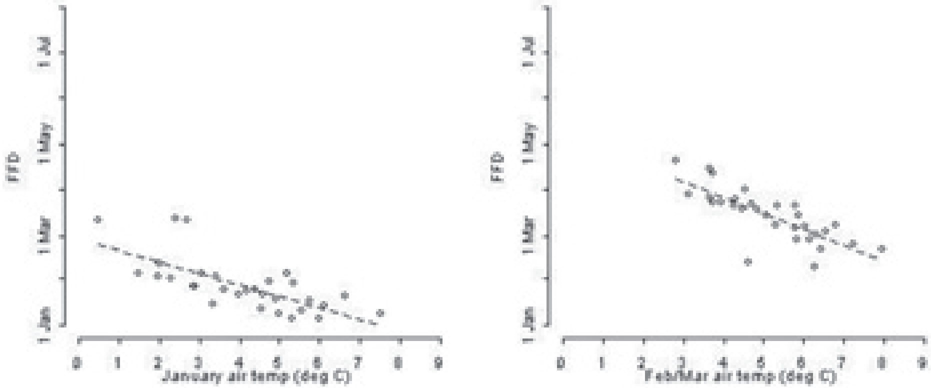
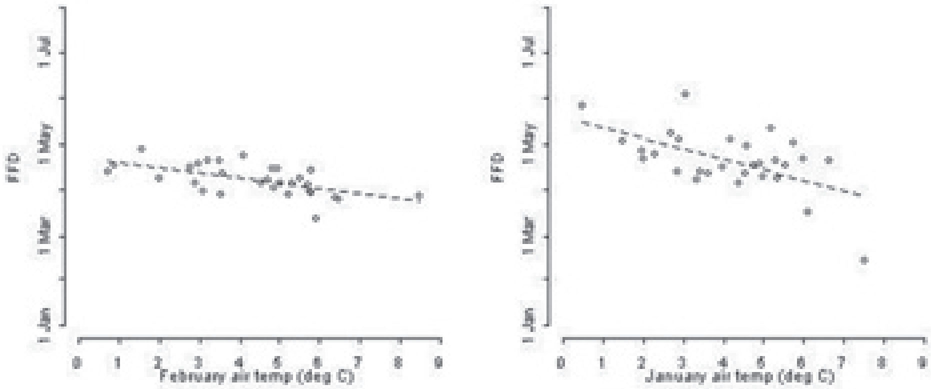


Fig. 3 Seasonal patterns of flowering in 1989, with exceptionally warm air temperatures between mid-December 1988 and mid-February 1989, compared with 1978–1988 means. (a) Weekly counts of numbers of species in flower: ●, 1989 and ○, means for 1978–1988. (b) FFDs in 1989 compared to mean FFD between 1978 and 1988 of the same species (○, 1989 FFD within 2 standard deviations of 1978–1988 FFDs; ●, 1989 FFD outside 2 standard deviations of 1978–1988 FFDs).



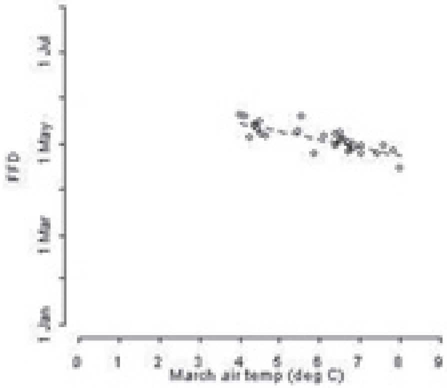
(a) Galanthus nivalis

(b) Ribes sanguineum



(c) Fritillaria meleagris

(d) Doronicum plantagineum



(e) Malus domestica

Fig. 4 Relationships, identified by a stepwise regression between air temperature, of the month found to most influence flowering between 1978 and 2007, and the FFDs of *Galanthus nivalis* (mean FFD, 27 January), *Ribes sanguineum* (14 March), *Fritillaria meleagris* (7 April), *Doronicum plantagineum* (20 April) and *Malus domestica* (4 May).

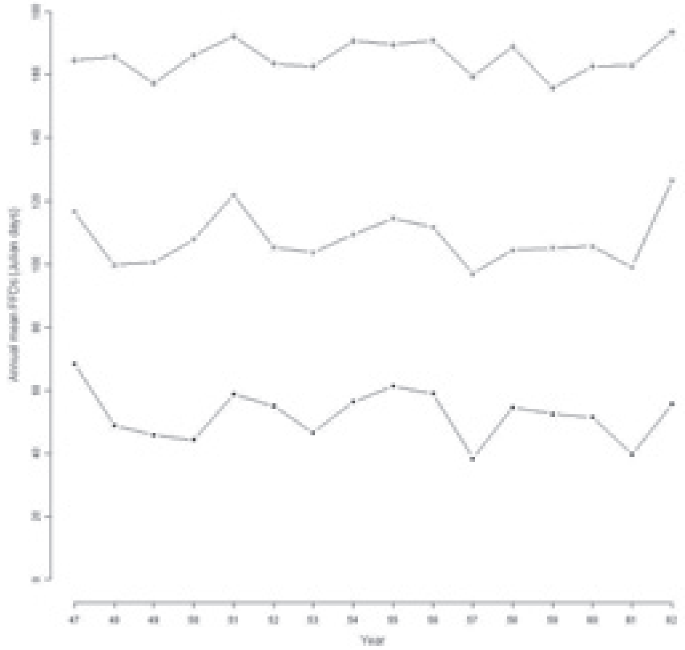


Fig. 5 Patterns of change (1947–1962) in mean FFDs of three groups, each of six plant species (mostly herbaceous) flowering in a garden located in Yorkshire, UK •-•, the earliest group (mean FFD, day 52.4), the intermediate group ∘-∘ (mean FFD, day 108.1) and the latest group +-+ (mean FFD, day 165.4) (Adapted from Hepper, 2003).

and mid-March (mean FFD, 52d) (Fig. 5). Thus in, and for some months following, a relatively cold spring, the onset of flowering in later flowering species was usually delayed (as in 1951, 1955 and 1962) whereas, if the spring was relatively warm the onset of flowering tended to be earlier (advanced) for much of the year (for example in 1957 and 1961): the amplitude of these changes, associated with delays/advances, was larger in February, March and April than later in the year.

The patterns seen in Fig. 5 compare well with those seen in the authors' data (Fig. 1). Mean FFDs over the species grouped according to the month of their mean FFD are shown in Fig. 1a. They show a clear similarity in profiles over the period between the groups, but with the earlier groups showing more pronounced variation. The general trend over the period was to earlier flowering. The peaks and troughs in mean FFDs were clearly linked to the peaks and troughs of the February/March temperatures but less so to the annual means (Fig. 1b).

Analyses with stepwise regression

Preliminary assessments, including evidence presented by Willis (see Smith, 1968; Fig. 6) and Fitter *et al.* (1995), suggest that the onset of flowering is, for at least five months of the year, strongly associated with the temperatures prevailing early in the year. Nevertheless, in a review of our data to 2001, it was decided to test relationships with rainfall (mmd^{-1}) in addition to eight measures of temperature including both soil and air (see Roberts *et al.*, 2004). In the event stepwise regression indicates that associations with rainfall were weak and lacked the consistency of those with air and soil temperatures whose 'goodness of fit' (mean R^2) averages more than 30 per cent (Table 1) – the mean R^2 for grass minimum temperature was only 23 per cent. These observations led to the use of means of (1) maximum and minimum air temperatures; and (2) of observations taken 10cm and 30cm below ground, at 09.00 GMT – a choice partly determined by the greater statistical 'security' gained from larger databases following the aggregation in each instance (air and soil) of two sets of data, and also influenced by the assessment made by Grace (1987) who opined, when discussing the effect of temperature on flowering, "at least we have to consider the plant as a whole and not get too concerned only with air temperature when soil temperature could be equally or more important".

	Dry bulb	**Air max**	**Grass min**	**Soil at 10cm**
Proportion of species for which the attribute was selected by stepwise regression	51%	55%	36%	54%
Proportion of species for which the attribute formed the 'best' model	10%	27%	7%	20%
Goodness of fit, average R^2	32%	34%	23%	33%

Table 1 Comparison of three attributes of air temperature and one of soil temperature when used in stepwise regressions to assess associations with 208 species (no associations were found for 28 per cent of these) over the period 1978 to 2001. Extracted from *Report No. 035* (Roberts *et al.*, 2004).

Stepwise regression indicates when the monthly temperature covariates in the year of flowering, and also in the preceding year (up to 12 months prior to flowering), had significant roles to play in determining the response of each species to a uniform 1ºC increase throughout the year. The red blocks in Fig. 7 indicate those months whose temperature covariates were associated with significant shortening of the periods to flowering thus leading to earliness (in the current year); blue blocks indicate when the different temperature covariates, mainly in the second half of the preceding year, were associated with longer intervals before the onset of flowering in the following year, the 'year of flowering' – they indicate trends to lateness. Thus, depending on the time of year, increased temperatures were associated with diametrically opposite effects and for this reason the eventual FFDs reflect the net effect of the two opposite influences. The number of monthly associations with air temperature maintained a February/March plateau (44–46), and then sharply declined: those for soil temperatures peaked in February (46) and thereafter steadily decreased.

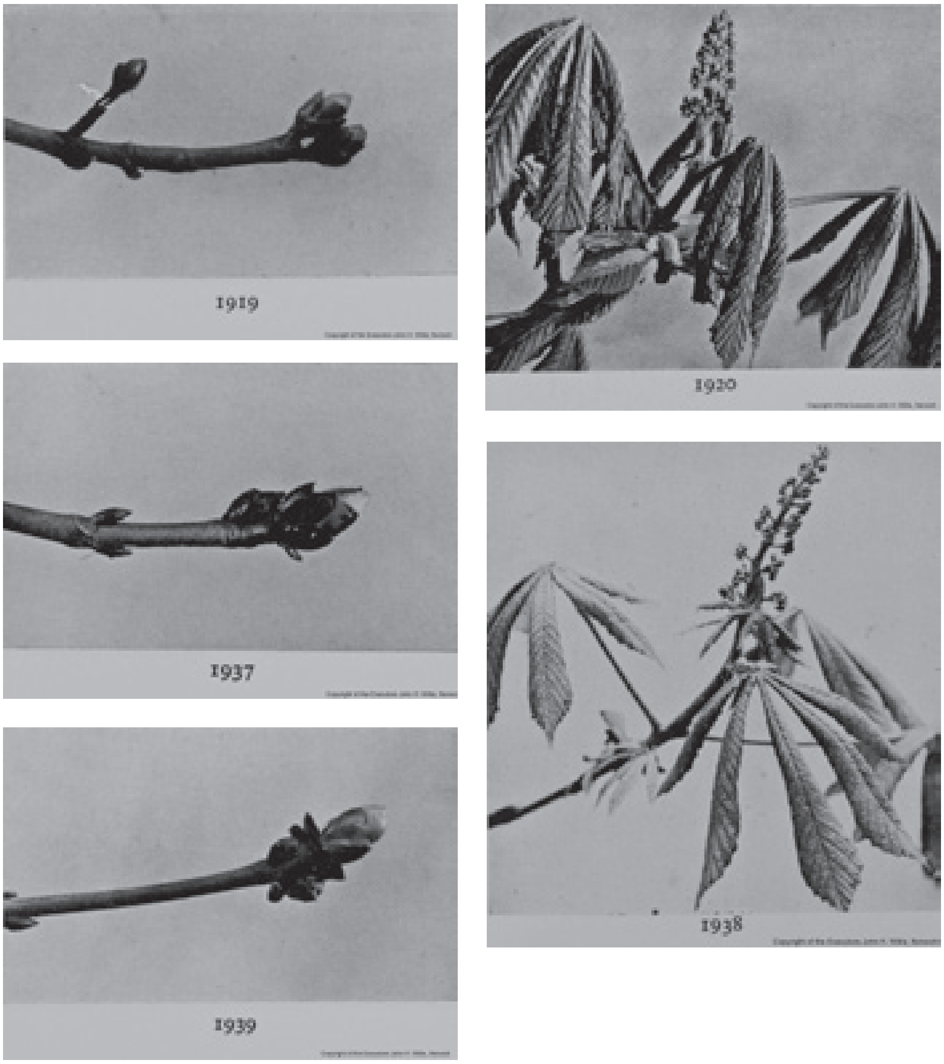


Fig. 6 *Aesculus hippocastanum* (horse chestnut). Selected pictures from an annual series (1913 to 1942) showing how the stage of inflorescence development reached by 1 April seems to be associated with the mean air temperature in the preceding month. Mean temperatures of the preceding month (March) are 1919: 3.8°C; 1920: 7.9°C; 1937: 3.8°C; 1938: 9.6°C and 1939: 5.5°C. Photographs of the same tree taken by J.H. Willis of central Norfolk, England (lat. 52°34′N; long. 0°51′E) (see Smith, 1968). Reproduced with permission of HarperCollins Publishers, Glasgow.

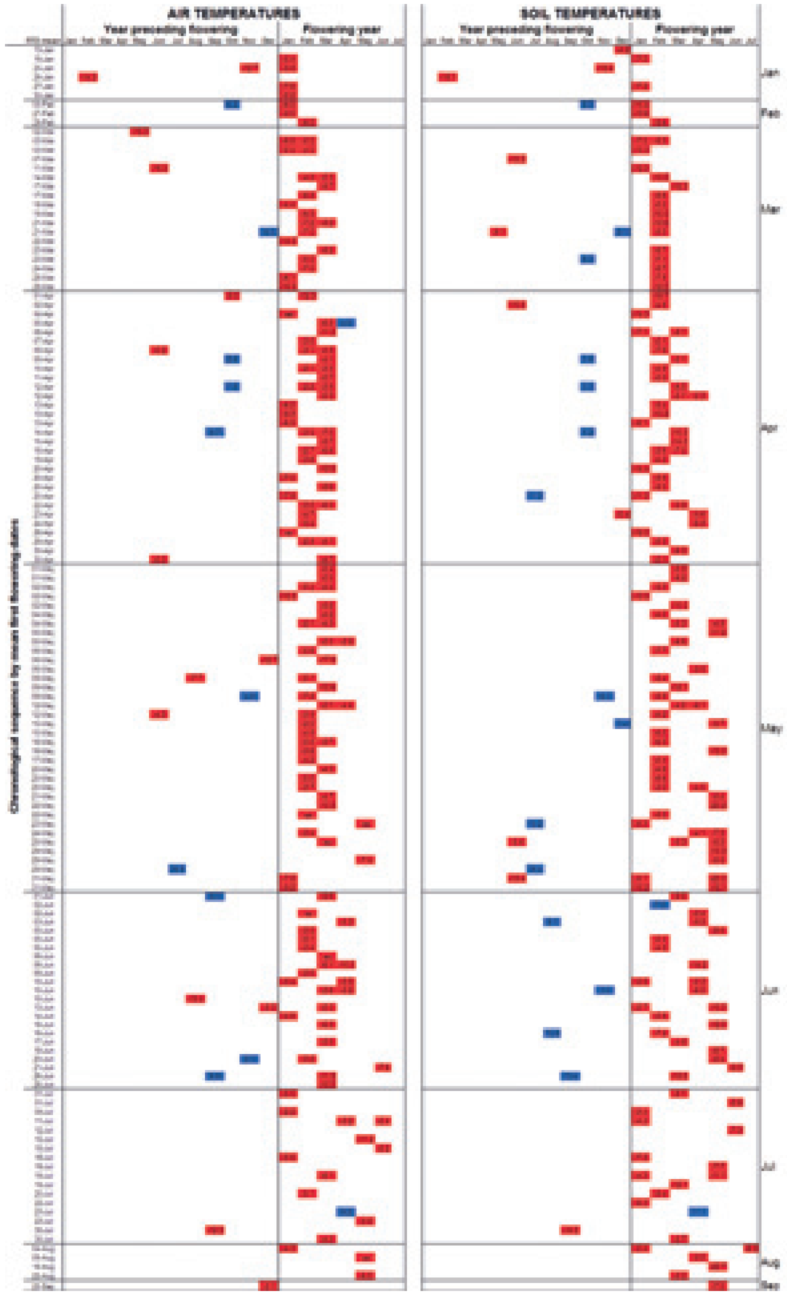


Fig. 7 Diagram showing when and how FFDs of 138 plant species, arranged chronologically on the ‘y’ axis, were found by stepwise regression to be significantly associated with mean air and/or soil temperatures in different months in East Lothian, Scotland (1978 to 2007). Seventy species were not found to be significantly related to air or soil temperature by stepwise regression.

🟥, a 1°C increase in temperature was associated with ‘earliness of flowering’ – the interval from 1 January to flowering was shortened; 🟦, a 1°C increase in temperature was associated with an increase in the interval from 1 January to flowering – ‘late flowering’.

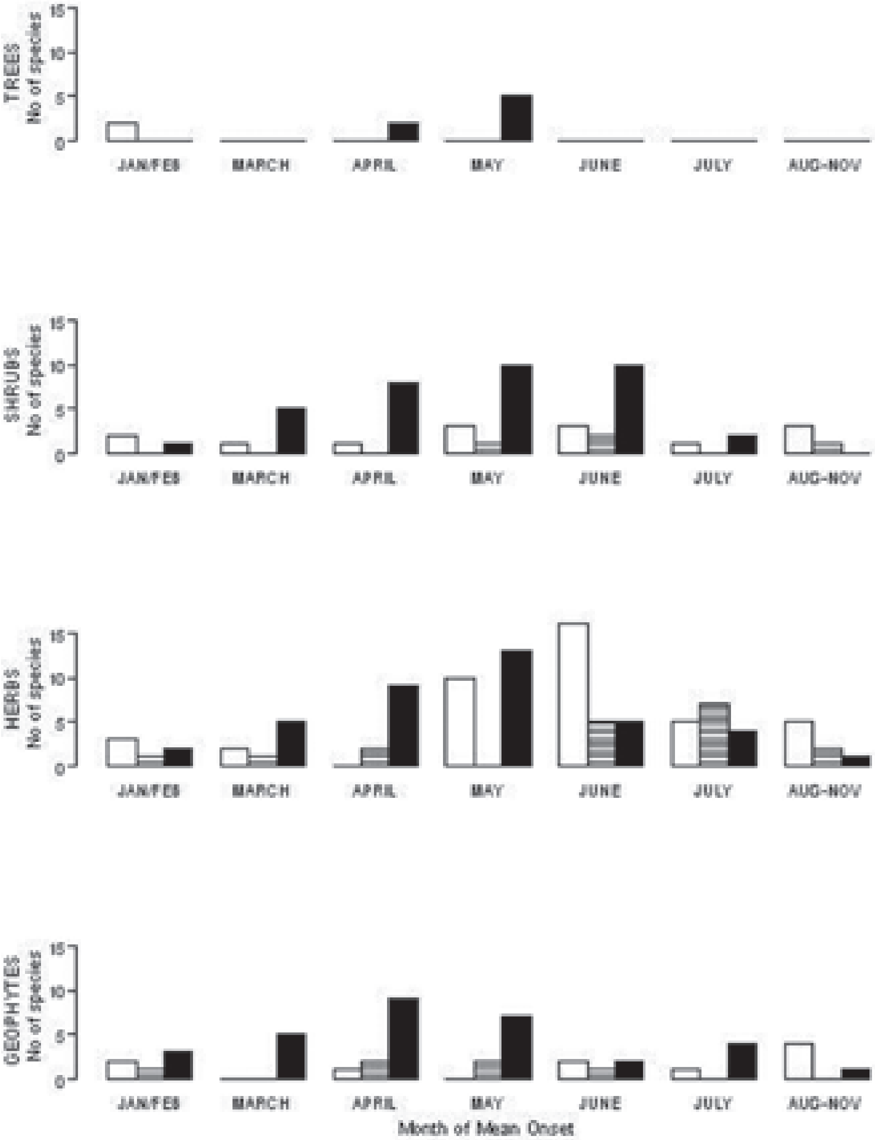


Fig. 8 The pattern (1978–2007) of flowering in East Lothian, Scotland of 208 plant species including trees, shrubs, herbaceous plants and geophytes. Each of these life forms was subdivided into (a) species whose FFDs were not significantly associated with temperature (□) and those that were either (b) weakly (≡) or strongly (■) associated with temperature. (See text for definitions of 'weak' and 'strong' associations with temperature.)

Penalised signal regression and spring-warming models were used alongside stepwise regression to exploit the advantages of each. To simplify the subsequent use of data from the three models each species was allocated to one of three categories (see Appendix 1):

- **None** FFDs had no statistically significant associations with either air or soil temperatures.
- **Weak** This classification implies a weak association of FFD with temperature. For either air or soil temperature, at least one of the following should apply:
  - p-value for spring flowering is less than equal to 0.05;
  - at least one covariate is selected by stepwise regression;
  - the (cross validated) R^2 for PSR is more than 30 per cent.
- **Strong** This classification implies a strong association with temperature. For either soil or air, at least one of the following should apply:
  - p-value for spring flowering is less than or equal to 0.01;
  - p-value for stepwise (with p-value for steps = 0.01) is less than or equal to 0.005;
  - R-squared for penalised regression is greater than 50 per cent.

At least one of the following should apply for a different temperature measure than above:

  - p-value for spring flowering is less than or equal to 0.05;
  - at least one covariate is selected by stepwise regression (so p-value for stepwise is less than or equal to 0.01);
  - R-squared for PSR is greater than 30 per cent.

While the flowering of trees was either strongly associated with temperature or not at all, the other life forms included some species that were weakly associated (Fig. 8).

Trees

The nine tree species started to flower before the end of May. The flowering of seven of them (including *Malus domestica*, *Prunus avium* and *Sorbus aucuparia*) was associated with temperature but that of two *Salix* spp. was not.

Shrubs (54 species)

The flowering of 36 (including *Choisya ternata*, *Ribes sanguineum* and *Rosa rugosa*) was strongly associated with temperature. Four were weakly associated while twelve (including *Garrya elliptica* and *Rhododendron keleticum*) were without temperature associations.

Herbs (98 species)

Thirty-nine species (including *Lamium galeobdolon* and *Pulmonaria angustifolia*) were strongly associated. Eighteen were weakly associated and forty-one (including *Calluna vulgaris* and *Dianthus barbatus*) were without temperature associations. The strongly associated species came into flower between March and June; those without temperature associations (including *Geum montanum*) spanned the period from May to November.

Geophytes (47 species)

Thirty-one species (including *Galanthus nivalis* and *Hyacinthoides non-scriptus*) were strongly associated; their numbers (nine) peaked in April. Six were weakly associated with temperature and ten (including *Colchicum autumnale* and *Crocus speciosus*) were without temperature associations.

Analyses with penalised signal regression

Regression coefficients produced by PSR are illustrated for four species in Fig. 2. In addition to the solid line showing the regression coefficients for each of the three hundred and sixty-five days up to flowering, the two dashed lines indicate two standard errors above and below the coefficients. These can be used to judge for which periods the temperature had clear associations with FFD; if all three lines are above or below the zero line, this demonstrates evidence of such a relationship. For example, in *Narcissus pseudonarcissus* (Fig. 2b), the plot shows that rising temperatures from mid-winter up to flowering were associated with earlier flowering. All four species showed this spring-warming effect. In addition, *Rhododendron keiskeis* and *Laburnum anagyroides* showed some evidence of an association between warmer autumnal temperatures and delayed flowering. The plot for *Galanthus nivalis* suggests that temperatures in the growing period in the previous year may affect the timing of flowering. Using the PSR results, an attempt has been made to classify whether species with strong spring associations also had relationships with autumnal temperature (Appendix). Of the 113 species with strong spring associations, 32 were thought to have autumnal relationships but this may be an under-representation because of the difficulty of ‘fitting’ these effects with data sets of inadequate size.

More generally the results for PSR were compared with the output from stepwise regression (Fig. 7). This confirmed that the delays associated with warm temperatures in the third quarter of the ‘preceding year’ tended to be markedly smaller than the advances (to earliness) associated with ‘warm’ temperatures from January onwards. In the ‘year of flowering’ the temperature changes from January to April were often dominant but later-flowering species often also had strong associations with temperature later in the year.

By summing, for each species, the monthly coefficients for stepwise regression and daily coefficients for PSR, the consequences of a uniform annual increase of 1°C can be estimated (Table 2). In species with significant responses – virtually all of which were negative – the net responses were minimal in *Pulsatilla vulgaris* and *Hypericum sp*. (namely 2.6 and +0.8 d/°C) and maximal in *Fuchsia* 'Riccartonii' (−18.3 d/°C), *Narcissus pseudonarcissus* (−15.6 d/°C) and *Rhododendron* 'Praecox' (−15.5 d/°C). Of the three species of *Rhododendron*, *R.* 'Praecox' and *R. keiskei* had significant responses to temperature but the onset of flowering of the third and latest species, *R. keleticum*, was not significantly associated with temperature. Table 3 shows the predicted effects on the flowering of *R. keiskei* of autumns and springs that are cooler and warmer by 2°C than the average over the study period. They indicated that the annual mean FFDs for this species might range from day 34 following a 'cold' autumn and 'warm' spring and day 141 following a 'warm' autumn and a 'cold' spring – a difference of 107 days.

Species	**Mean FFD, Julian days**	**Response to 1°C increase in air temperature, days/°C**	
		Stepwise	**PSR**
Galanthus nivalis	27.5	−7.6	−7.7
Rhododendron 'Praecox'	62.6	−11.9	−15.5
Narcissus pseudonarcissus	62.9	−9.4	−15.6
Ribes sanguineum	73.8	−10.8	−11.7
Ranunculus ficaria	83.2	−7.0	−5.4
Rhododendron keiskei	87.3	−10.0	−12.0
Hyacinthoides non-scriptus (blue)	98.3	−13.1	−11.7
Pulsatilla vulgaris	99.2	−1.5	−2.6
Prunus avium	108.5	−9.3	−9.8
Malus domestica	124.6	−6.4	−5.5
Ilex aquifolium	140.9	−3.7	−8.8
Rosa rugosa	141.5	−4.7	−6.6
Rhododendron keleticum	147.1	NR	NR
Fuchsia 'Riccartonii'	157.4	−16.1	−18.3
Rosa hybrids	167.2	−6.3	−5.6
Hypericum sp.	177.2	−2.4	+0.8
Lilium martagon	190.2	−2.2	−5.5
Buddleja davidii	200.1	−6.1	−8.7

Table 2 Net responses of FFDs for 17 species to a uniform annual 1°C increase in air temperature. (The net response balances the relatively small delaying effect of warmer autumns with generally larger trends to earliness associated with warmer springs.)

		Late winter to spring	
		Cold 2.8°C	Warm 6.8°C
Summer to early winter	Cold 8.9°C	day 103 (13 April)	day 34 (3 February)
	Warm 12.9°C	day 141 (21 May)	day 72 (13 March)

Table 3 Predictions of FFDs for *Rhododendron keiskei* using PSR and based on soil temperatures (see Fig. 2a). Predictions are based on temperatures during the periods summer to early winter (1 June to 31 December) in the year preceding flowering and late winter to spring (1 January to 4 May).

To investigate the relationship with temperature over all the species, they were grouped by the month of their average FFD: January and February, March, April, May, June, July and August to November. The mean FFD in each year was calculated for each of these groups, after first standardising the FFDs to ensure that more responsive species did not dominate. PSR was then applied to the means of these groups (Fig. 9). This procedure confirmed that the delays associated with warm temperatures in the third quarter of the 'preceding year' were markedly smaller than the advances (to earliness) associated with 'warm' temperatures from January onwards. In the 'year of flowering' the temperature changes from January to April were dominant, however all groups appeared to be affected by temperatures over the period up to flowering. Thus, in later groups, the advancing effect was spread over a longer period.

By moving from one-dimensional to two-dimensional *P*-spline signal regression, it is possible to further study how the net effect of autumn and spring temperature changes can be anticipated over sets of species. In Fig. 10, the oblique red broken lines indicate where the temperature days equate with mean FFDs; coefficients to the right of this line

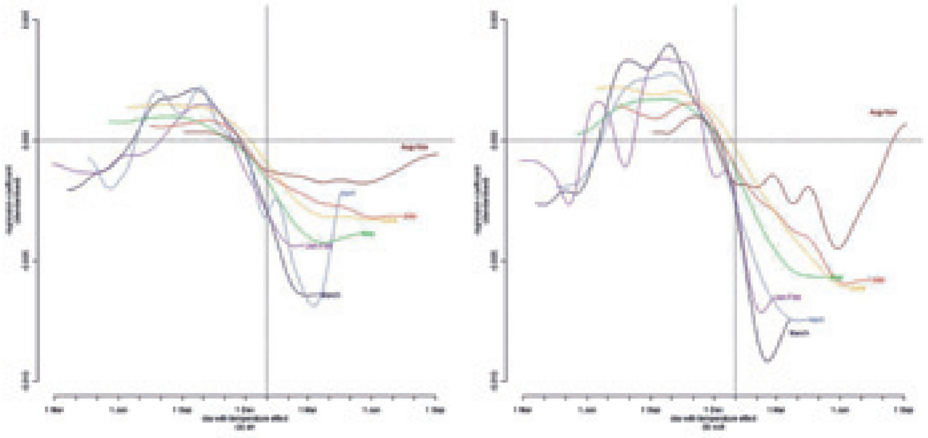
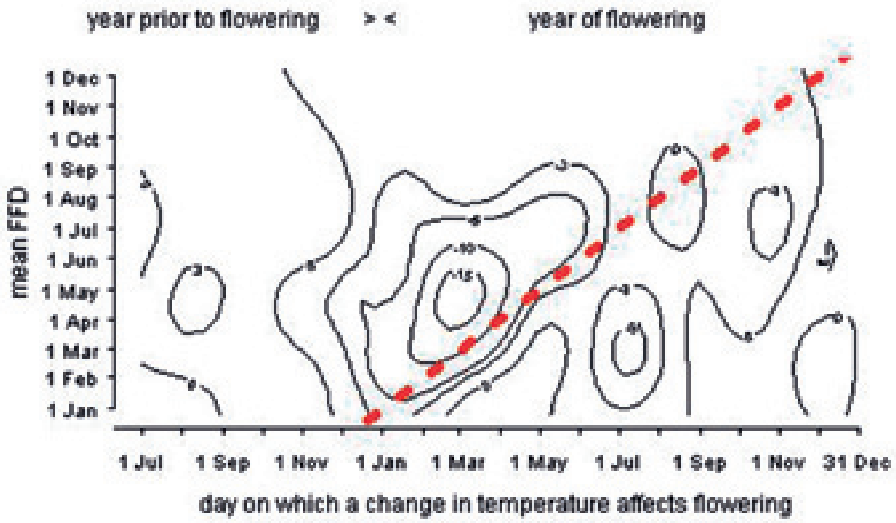
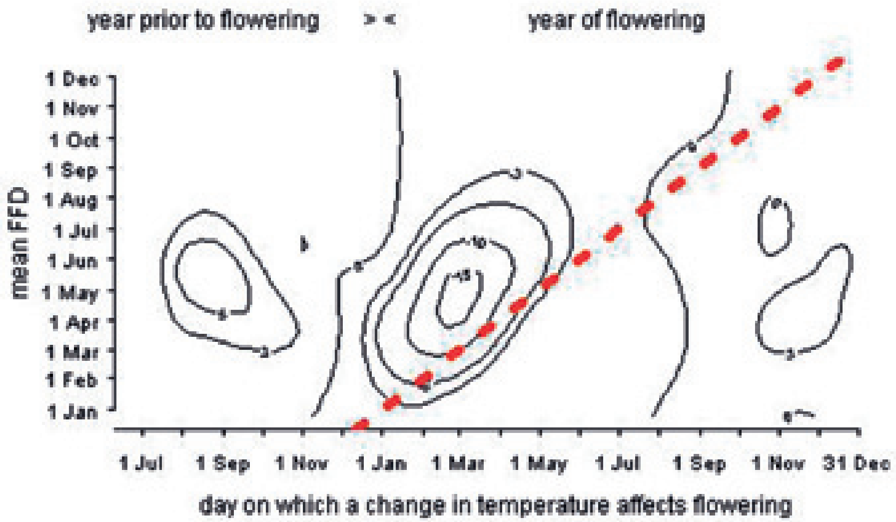


Fig. 9 Relationship found by *P*-spline signal regression between the mean standardised FFDs for species grouped by month of flowering and (a) air and (b) soil temperatures.



A. Response of species with associations with spring temperatures



B. Response of species with associations with spring and autumn temperatures

Fig. 10 Two-dimensional contour plots showing how an increase in temperature on any day in the period prior to flowering might influence the onset of flowering (FFD) as projected from observations made between 1977 and 2007 in East Lothian, Scotland. A: the data are restricted to species whose FFDs were significantly associated with spring temperatures. B: the data were related to species whose FFDs were found to have had some association with autumn temperatures as well as spring temperatures. Note that these plots are based on two-dimensional *P*-spline signal regression (Roberts, 2008) using flower dates standardised by species. The covariate values represented by the contours are standardised by their standard errors. Covariate values to the right of the red line should be discounted since they relate to dates after flowering.

Base temp °C	**Jan/Feb 1–59 d**	**Mar 60–90 d**	**Apr 91–120 d**	**May 121–151 d**	**June 152–181 d**	**July 182–212 d**	**Aug/Nov 213–334 d**
–0.5° t° +0.4°	(85) *Crocus vernus* (110) *Helleborus niger* (210) *Eranthis hyemalis* (290) *Petasites fragrans*	(240) *Arabis caucasia* (340) *Primula marginata* (420) *Narcissus pseudonarcissus* (520) *Mahonia aquifolium* (580) *Muscari botryoides*	(350) *Erythronium* 'White Beauty' (380) *Anemone ranunculoides* (410) *Erythronium* 'Pagoda' (550) *Prunus* 'Amanogawa' (620) *Doronicum plantagineum* (670) *Lamium galeobdolon* (780) *Hyacinthoides non-scriptus* (pink) (840) *Myosotis arvensis*	(450) *Galium odoratum* (600) *Allium ursinum* (660) *Syringa vulgaris* (670) *Laburnum anagyroides* (680) *Ourisia coccinea* (720) *Cotoneaster microphyllus* (750) *Sorbus aucuparia* (810) *Ilex aquifolium* (850) *Weigela florida* (900) *Potentilla fruticosa* (orange) (910) *Lonicera periclymenum*	(980) *Lupinus* garden hybrids (1000) *Astrantia major* (1000) *Hebe cupressoides* (1100) *Cephalaria gigantea* (1100) *Dactylorhiza majalis* (1100) *Photinia* (syn. *Stranvaesia*) *davidiana* (1100) *Rosa* hybrids (1400) *Aconitum napellus* (1400) *Iris pseudacorus* (1400) *Kniphofia caulescens*	(1600) *Spiraea* × *bumalda* (1600) *Leucanthemum* × *superbum* (1900) *Buddleja davidii*	
+0.5° t° +1.4°	(40) *Galanthus nivalis* (170) *Hamamelis mollis* (220) *Pulmonaria angustifolia* (230) *Pulmonaria saccharata*	(210) *Saxifraga oppositifolia* (210) *Ranunculus ficaria* (240) *Ribes sanguineum*	(180) *Fritillaria meleagris* (230) *Pulsatilla vulgaris* (270) *Tulipa tarda* (290) *Lunaria annua* (330) *Fritillaria pontica* (360) *Chaenomeles japonica* (390) *Dicentra formosa* (430) *Eccremocarpus scaber* (450) *Prunus avium*	(450) *Malus domestica* (500) *Centaurea cyanus* (540) *Rosa rugosa* (600) *Tellima grandiflora* (630) *Penstemon sp.* (630) *Deutzia pulchra* × *hybrida* (650) *Geranium phaeum* (650) *Paeonia mascula* (660) *Asarina procumbens* (700) *Cornus alba* (800) *Cistus* 'Sunset'	(740) *Olearia ilicifolia* (900) *Fuchsia* 'Riccartonii'	(1500) *Coreopsis verticillata*	

Base temp °C	Jan/Feb 1–59 d	Mar 60–90 d	Apr 91–120 d	May 121–151 d	June 152–181 d	July 182–212 d	Aug/Nov 213–334 d
+1.5° t° +2.4°		(60) *Chionodoxa forbesii* (150) *Rhododendron* 'Praecox' (160) *Forsythia* × *intermedia* (250) *Vinca minor* 'Burgundy'	(200) *Tulipa batalinii* (210) *Viola riviniana*	(340) *Meconopsis cambrica* (750) *Oxalis deppei* (syn. *O. tetraphylla*)	(580) *Viburnum opulus*		
+2.5° t° +3.4°		(100) *Tulipa turkestanica* (220) *Rhododendron keiskei*	(140) *Aurinia saxatilis* (270) *Skimmia japonica*	(650) *Iberis umbellata*		(980) *Triteleia laxa* (1100) *Stachys byzantina*	
+3.5° t° +4.4°							(1200) *Crocosmia* × *crocosmiiflora*
+4.5° t° +5.4°		(35) *Saxifraga* × *apiculata* (60) *Daphne mezereum*	(65) *Hyacinthoides non-scriptus* (blue) (80) *Aponogeton distachyos* (160) *Berberis thunbergii* f. *atropurpurea* * (170) *Cytisus scoparius* hybrid	(65) *Hyacinthoides non-scriptus* (blue) (80) *Aponogeton distachyos* (160) *Berberis thunbergii* f. *atropurpurea* * (170) *Cytisus scoparius* hybrid	(410) *Cotoneaster dammeri*		(1400) *Viburnum tinus*
+5.5° t° +6.4°			(55) *Rosmarinus officinalis* (140) *Tulipa aucheriana*	(160) *Caltha palustris* (200) *Osteospermum jucundum*	(270) *Hypericum olympicum* (320) *Rubus odoratus*	(630) *Catananche coerulea*	
+6.5° t° +7.4°			(85) *Trillium grandiflorum* * (95) *Choisya ternata*	(55) *Uvularia grandiflora*			
+7.5° t° +8.4°			(35) *Dicentra spectabilis*	(20) *Polygonatum multiflorum* (120) *Rosa sericea*		(340) *Alstroemeria sp.*	
+8.5° t° +9.4°				(25) *Convallaria majalis* * (35) *Oxalis* sp.	(130) *Calceolaria* sp.		(420) *Echinops bannaticus*
+9.5° +				(45) *Iris germanica hybrids*	(5) *Aster alpinus* (75) *Gladiolus illyricus*	(40) *Cortaderia selloana*	

Table 4 Spring-warming (thermal-time) model. Estimates of base temperatures for development, T_b, and thermal constants for development, in degree days (*DD*), in relation to mean date of first flowering. Data are provided for 120 species whose FFDs were weakly or strongly associated with temperature.

have no meaning but can be used to validate the importance of the other coefficients. Fig. 10a shows the coefficients for 2-d PSR for species with strong associations with spring temperatures but for which no autumnal effects were found. By drawing a horizontal line on the figure starting on the y-axis at a mean FFD of 1 March and running parallel to the x-axis up to the oblique red broken line it can be seen that this line traverses the ‘spring’ trough in the period from the turn of the year to flowering and that there was little effect of autumnal temperatures. Fig. 10b depicts the situation where species responded significantly to autumn and spring temperatures. Looking at the overall pattern in these two contour plots, the spring effect is evident in both, becoming later and perhaps more spread out for later flowering species. The evidence for the small autumnal delaying effect in Fig. 10b is not a surprise given the selection of species: the evidence for an autumnal effect in Fig. 10a is weaker.

Interpretation of contour plots in Fig. 10

In A, a line drawn parallel to the x-axis from mid-April on the y-axis to the oblique red line shows the mean effect of flowering for species flowering in mid-April, with large negative covariates in the period from about 1 February to 1 April, indicating a shortening in the period to flowering in response to increased temperature. In B, where there is additionally a period of positive covariates in the preceding late summer/autumn, flowering is subject to delay.

Spring-warming models

The results from stepwise regression and PSR indicated the importance of late winter and spring temperatures in relation to FFD. To gain an improved understanding, in the absence of controlled experiments of biological processes that determine the date of an event, for example FFDs, attention was turned to a modelling approach and in particular the exploitation of thermal-time models (see Trudgill *et al.*, 2005). The base-temperature, T_b, and thermal constant (degree days, *DD*), were estimated for each species (Table 4) based on the spring-warming model. After nominating −0.5°C as the lowest base temperature, the range had to be extended upwards to +9.5°C, as the estimated temperature needed to be reached before activating *Aster alpinus*, *Cortaderia selloana*, *Gladiolus illyricus* and *Iris germanica* hybrids – the last species/cultivars to flower (Table 4). Of the species with a T_b between –0.5°C and +0.4°C those that produced open flowers between January and the end of February needed to accumulate 55–290 degree days (e.g. *Crocus vernus* Dutch cultivars and *Eranthis hyemalis*); those flowering in March did so after accumulating 240–589 degree days (e.g. *Narcissus pseudonarcissus*): in April 350–840 degree days (e.g. *Erythronium* cultivars and *Prunus amanogawa*); in May 450–910 degree days (e.g. *Laburnum anagyroides* and *Sorbus aucuparia*); in June 980–1,400 degree days (*Dactylorrhiza majalis* and *Photinia davidiana*) and in July 1,600–1,900 degree days (e.g. *Buddleja davidii*) – in short, the T_b range of –0.5°C to +0.4°C serves species with very different degree-day requirements ranging from 65 to 1,900 degree days. Plants requiring base temperatures of +1.5°C to +5.4°C started flowering in March (e.g. *Daphne mezereum* and *Forsythia* × *intermedia*), of +5.5°C to +8.4°C started flowering in April (e.g. *Choisya ternata* and *Rosmarinus officinalis*) and of +8.5°C to +9.5°C in May (e.g. *Convallaria majalis* and *Iris germanica* hybrids). Taking into account all of the species the smallest degree-day requirement was 20 (*Polygonatum multiflorum*) and the largest 1,900 (*Buddleia davidii*), but with very different base temperatures T_b of –0.5°C to +0.4°C for the latter and +7.5°C to +8.4°C for the former. Caution is required when interpreting these estimates as the three parameters of the model, T_b, DD and θ, are strongly correlated.

Longer-term changes associated with warming temperatures between 1978 and 2007 – a period of 30 years

Between 1977 and 2007 inclusive, the annual mean air temperatures in the first, second and third quarters significantly increased by +0.080°C, +0.044°C and +0.026°Cyr^{-1}, equivalent, over 30 years, to 2.40°C, 1.32°C and 0.78°C respectively (Table 5); the first quarter mean soil temperature increased by +0.060°C yr^{-1}, equivalent to 1.80°C over 30 years. At the same time and despite the variations from year to year it was found that 39 per cent of species were flowering 15 days earlier in 2006 than 1978 (Table 6). Analysis has shown that this average conceals a systematic change: by 2006 the FFDs of 10 out of 12 species flowering between Julian days 1 and 50 had advanced, towards earliness, by 15 or more days, with 28 out of 69 and 5 of 21 species flowering between days 101 and 150, and 201 and 250 respectively. Further examination showed that the advances of 'strong' species identified in analyses of responses to variable weather were also those that responded consistently to long-term (30-year) changes of temperature. On average the interval between 1 January and the onset of flowering in this group decreased by 0.84 d/yr, 0.62 d/yr, 0.43 d/yr and 0.40 d/yr among species starting to flower on, or about, Julian days 50, 100, 150 and 200 respectively (Fig. 11).

	Air temperatures		**Soil temperatures**	
	Mean temp. °C	**Trend °Cyr^{-1}**	**Mean temp. °C**	**Trend °Cyr^{-1}**
Annual	9.2	**+0.045±0.008**	8.9	**+0.032±0.008**
First quarter (Jan/Mar)	4.8	**+0.080±0.023**	3.5	**+0.060±0.017**
Second quarter (Apr/Jun)	10.6	**+0.044±0.011**	11.1	+0.017±0.011
Third quarter (Jul/Sept)	14.4	**+0.026±0.012**	14.6	+0.014±0.012
Fourth quarter (Oct/Dec)	7.0	+0.029±0.021	6.3	**+0.037±0.015**

Table 5 Changes (linear trends) between 1978 and 2007 in annual and quarterly mean air and soil temperatures recorded at RBGE. The + sign is indicative of progressive warming; bold indicates that the trend is significant.

	Mean FFD, Julian days				
	1–50	51–100	101–150	151–200	201–250
Number of flowering species within each group	12	22	69	51	21
Number of species flowering at least 15 days earlier in 2006 than in 1978	10	16	28	9	5
% of species flowering at least 15 days earlier in 2006 than in 1978	83%	73%	41%	16%	24%

Table 6 Numbers and percentages of plant species, grouped by their mean FFDs, whose FFDs advanced by 15 days or more between 1978 and 2006.

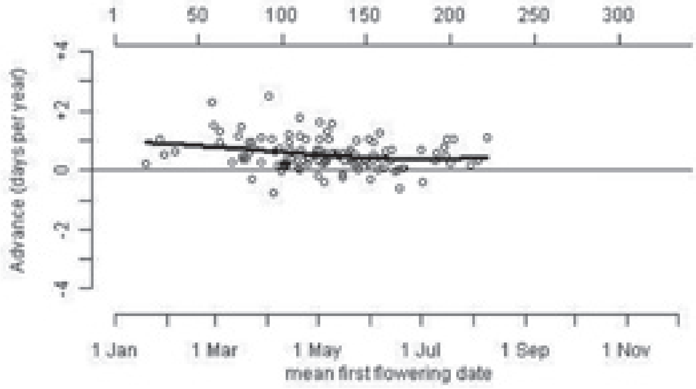


Fig. 11 Change (1978 to 2007) in the onset of flowering (dyr^{-1}) of species that had a 'strong' association with temperature (see Table 5 for related trends in annual and quarterly mean temperatures).

DISCUSSION

The studies of flowering, and principally of FFDs, made by Fitter *et al.* (1995) and Fitter & Fitter (2002) were focused on semi-natural and natural vegetation near Chinnor; their tools in the search for associations between FFD and air temperature were Principal Component Analysis and Stepwise Regression. Our observations, which for much of the time were made concurrently with those of the Fitters, targeted managed garden plants with the eventual analyses being widened to include (1) soil, in addition to air, temperatures; and (2) Penalised Signal Regression (PSR) and its variants, also spring-warming (thermal-time) models – the latter, being suitable for the analysis of poikilothermic entities (Trudgill *et al.*, 2005), were used to elucidate mechanisms of plant responses to temperature change.

With the range of analyses employed the following generalisations can be made about the flowering of perennial plants including trees, shrubs, herbaceous plants and geophytes:

(1) (i) FFDs of the majority of species (68 per cent) were significantly associated

with 'spring' temperature changes above and below the seasonal mean of variable weather in East Lothian: 32 per cent were without significant association. (ii) Of the species with significant associations with spring temperatures, most were related to both air and soil temperatures, referred to as 'strong' associations.

(2) Some species were significantly associated with temperatures in the autumn (fall) of the year preceding flowering; many more had indications of this type of association. (i) intervals from first January to the onset of flowering were shortened when there were significant associations with 'spring' temperature increases. In contrast, flowering was delayed by increases in autumnal temperatures the year before flowering. (ii) the responses per 1°C change in spring temperature were larger than those to a similar change in autumnal temperatures.

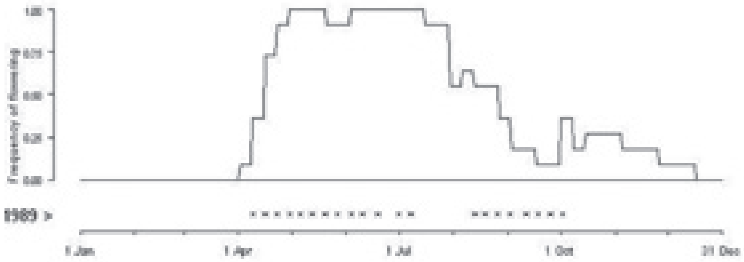
(3) Actual FFDs in the field are the integrals of the diametrically opposite effects of temperature changes in the autumn and spring plus a significant augmentation attributable to changing climate, in species with 'strong' temperature associations.

The implications of 2 (i) and (ii) help explain the unexpectedly large differences (to many horticulturists and gardeners) among the observed FFDs, particularly in the first quarter of the year. It is interesting to note that some species were associated with either air or soil temperatures while many species had significant associations with both. The latter is not unexpected, as we know that air and soil temperatures are closely correlated, but how should the former be explained? It is known that the effects of temperature on flowering may not be directly on shoot apices; the process may be induced in other plant structures (Lyndon, 1992), for example, leaves (Bernier *et al.*, 1981) and roots (Leakey *et al.*, 1981). Are these two sets of observations interlinked? Is it possible that the link of 'weak' species with either air or soil temperatures is a reflection of the ability or inability of leaves or roots to act as receptors/intermediaries for the conveyance of flowering stimuli? In his review of vernalisation, Schwabe (1986) referred to the action of 'high' temperature in causing de-vernalisation – a seemingly likely explanation of the delaying effects of warmer than average autumnal temperatures recorded by Fitter *et al.* (1995) and supported by the present study. Schwabe also opined that similar mechanisms may be involved in the flowering of fruit trees and flower stem elongation of bulbous plants such as *Crocus* spp. and *Hyacinthoides* spp.

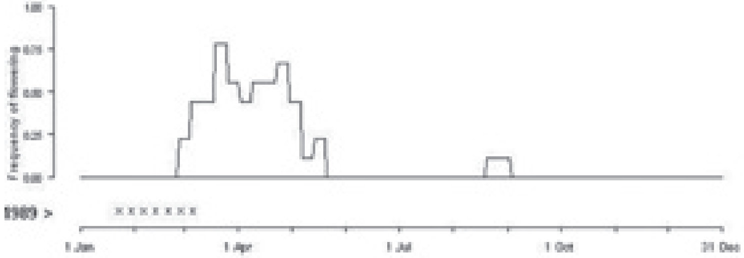
In extending our physiological understanding of flowering, the use of spring-warming (thermal-time) modelling shows considerable promise (Trudgill *et al.*, 2005). In our instance it has facilitated the identification of base temperature T_b and thermal constants (the number of degree days needed after the temperatures reached the relevant T_b to complete a specified development), for example the first day on which open flowers were observed. Many species started to develop when a base temperature of –0.5°C was reached (towards the end of winter) but thereafter it took more than five months before some of them (for example *Buddleja davidii* and *Chrysanthemum* × *superbum*) started to flower in July after the accumulation of 1,600–1,900 degree days. On the other hand *Crocus vernus* Dutch cultivars *Eranthis hyemalis* and *Helleborus niger* needed a maximum of 280 degree days to flower in January. Other species required T_b ranging from +0.5°C to +5.4°C, +5.5°C to +8.4°C and +8.5°C to +9.5°C to start the 'flowering process' before having open flowers in March, April and May respectively. As an illustration *Laburnum anagyroides*, *Cistus* 'Sunset' and *Osteospernum jacundum* started to flower in May but by different routes: *L. anagyroides* T_b −0.5°C to +0.4°C, 870 degree days; *Cistus* 'Sunset' T_b +0.5°C to +1.4°C, 800 degree days; and *O. jacundum* T_b +5.5°C to +6.4°C, 200 degree days. Elsewhere Abbott (1971) and Jackson and Hamer (1980) found that early flowering in apples could be associated with adverse effects on flower 'quality' and fruit set while Steckel (1960) recorded a negative correlation between February temperatures and yields of apple. Are the latter exceptional occurrences or are they widespread? If they are, they could have profound effects on the ability of plants to compete and change the composition of natural vegetation? Whatever the answer it is becoming clear that the study of FFDs is only part of the story. Preliminary assessments of our data concerned with duration of flowering have suggested three models (Fig. 12): (1) *Lunaria annua* model – its FFDs are strongly associated with temperature but duration remained unaffected primarily because its responses to temperature change were small compared with background 'noise'; (2) *Rhododendron* 'Praecox' model – its limited duration of flowering moved back and forth with changes in FFD in different years; and (3) *Choisya ternata* model – the duration of flowering was considerably augmented before the usual period of flowering (starting at the beginning of March).

The loss – or lack – of synchrony, particularly in relation to pollinating insects, also pests, has been mentioned by Usher (2007) but a change of flowering duration may, in some species, have an important role to play. Without doubt the loss of synchrony is likely to be a major concern with species following the *Rhododendron* 'Praecox' model (Fig. 12), in which flowering periods of unchanged duration are advanced, but less so with the *Lunaria annua* and *Choisya ternata* models in which warm spring temperatures are associated with considerably extended periods of flowering duration. In addition to FFDs the different durations of flowering should be of more than fleeting concern in relation to garden design. While the composition of mixed plantings may have evolved over many years of experience, a more structured approach based on a deeper understanding of the factors that control the onset and duration of flowering might be helpful.

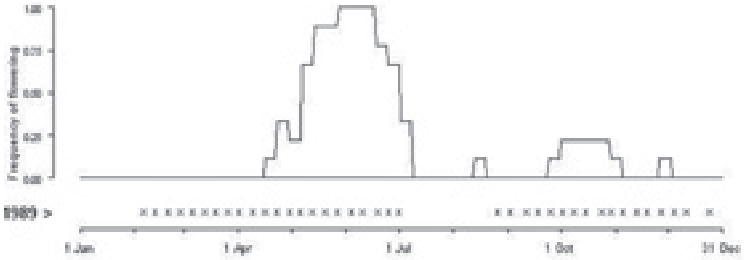
Much has been written about the holistic approach to ecosystem problems and aspects of biodiversity. It now seems appropriate to augment these by incorporating concurrent phenological approaches to studies of plants and their pollinators, pests, herbivores providing food for predators and pathogens. But how should this be done? Perhaps we should look back to the origin of regression analysis which was conceived as a tool to analyse the effects observed in controlled experiments (Yates, 1981). In reality 'plant temperature' in the field is a strong function of absorbed radiation and wind speed, and at the same time may be profoundly influenced by shape factors that provide shelter or stimulate turbulence – temperature may in reality be a surrogate, to differing extents, of many factors (Grace, 2006). For this reason some element of future



a *Lunaria annua*



b *Rhododendron* 'Praecox'



c *Choisya ternata*

Fig. 12 Distinctive flowering patterns in 1989 of three species: (a) *Lunaria annua*, (b) *Rhododendron* 'Praecox' and (c) *Choisya ternata*, following an exceptionally warm period (mid-December 1988 to early February 1989) when both the minimum and maximum air temperatures were c. 3.5°C warmer than the averages for the comparable periods in 1978 to 1988. × – weeks of flowering during 1989; histograms, frequency of flowering between 1978 and 1988.

work should take heed of Koch's postulates (Koch, 1891), namely the precise identification of the cause(s), in our case, of changing patterns of flowering and the eventual production of seed. To an extent this problem is being tackled by Wolkovich and her colleagues (Wolkovich *et al.*, 2012) in their warming experiments being conducted at a number of locations in the northern hemisphere. From the authors' standpoint it would seem worthwhile for Wolkovich *et al.* to ally their experimental conditions more closely to the different extent of temperature/climate changes in the different seasons (spring, summer, autumn and winter) of the year.

The value of observations made at one location, as is the case in this study, should not be overstated. They can, however, suggest the types of response that might occur elsewhere. In studies of flowering there are indications of recent and continuing temperature increases in East Asia (Omasa, 1998), the USA (Mones *et al.*, 2001) and the UK (Fitter & Fitter, 2002). At RBGE air and soil temperatures have risen, particularly in the first quarter of the year, the period that is widely acknowledged as being sensitive for the onset of flowering. Out of a total of 175 species flowering in 2006, 39 per cent flowered at least 15 days earlier than in 1978. In our analyses we, unlike Wolkovich *et al.* (2012), chose to relate FFDs to the relevant months of the year in which significant associations with temperature/climate were found using stepwise regression, penalised signal regression and thermal-time modelling; this contrasts to the exploitation of MAT (mean annual temperature) by Wolkovich *et al.* We found that the average period to the onset of flowering of early flowering species at our site in East Lothian was advanced by c. 0.8 days per year but among late flowering species by only 0.4 days per year, that is advances of 24 and 12 days over 30 years. Should these changes be associated with changes in the advance of annual mean air temperature of 1.35°C (= 0.045°C per year for 30 years) or with the advances in the first quarter mean temperature of 2.4°C (= 0.080°C per year for 30 years)? This is a significant difference remembering that the latter, but not the former, already exceeds the target (2°C) set by the UN in its attempts to thwart worldwide climate change by 2050 (Quarrie, 1992; Hulme *et al.*, 2002).

In thinking about the requirement for long-term sequences of data for phenological studies our attention periodically turned to the role of botanic gardens scattered throughout the world. They have two inestimable advantages: continuity and overlapping living collections of plants in a diverse array of environments. Those botanic gardens that already have an involvement with phenology should, in our opinion, be commended and encouraged to widen their involvement.

ACKNOWLEDGEMENTS

The authors wish to thank Scottish Natural Heritage for financing the computerisation of the flowering database as part of its Commissioned Report No. 035 (ROAME No. FOINAOL) (Roberts *et al.*, 2004), Dr Stephan Helfer of RBGE for making available meteorological records for 1997–2007 and members of the senior author's family who helped to ensure continuous records of flowering. They also acknowledge the encouragement and involvement of Dr Noranne Ellis (formerly of Scottish Natural Heritage), Miss Isabel Anderson (formerly of the Scottish Agricultural Science Agency), Emily Kempton and Mrs Diane Glancy (Biomathematics and Statistics Scotland) and Mr John Brand.

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APPENDIX 1

Species characteristics arranged by life form (tree, shrub, herbaceous plant and geophyte) and FFD.

Explanation of headings (British native and naturalised species in bold)

A Species/Cultivar.
B No. of years (of data available).
C Days per year (trend over 30 years; – and + indicate shortening or lengthening of the interval between 1 January and FFD as in 'early' and 'late' year respectively).
D Association with temperature (as judged from results of stepwise regression, penalised signal regression (PSR) and spring-warming model)
E Type of relationship (signifies, where applicable, significant relations with spring and, where applicable, autumn temperatures).

F to K are applicable to analyses of FFD with air temperature.
F Stepwise, days/°C (net effect estimated by stepwise regression of preceding autumn, and current year's spring, temperatures when uniformly increased by 1°C).
G PSR, days/°C (net effect estimated by PSR of preceding autumn and current year spring temperatures when uniformly increased by 1°C).
H T_b, base temperature for development towards flowering (ex spring-warming (thermal-time) models).
J DD (degree-days) accumulated after the start date, at or above the T_b threshold and before first observation of open flowers.
K θ (the start date for accumulating DD at or after T_b).

L–P are applicable to analyses of FFD with soil temperature**.**
L. as for F.
M. as for G.
N. as for H.
O. as for J.
P. as for K.

	A	B	C	D	E	F	G	H	J	K		L	M	N	O	P
						Air						Soil				
FFD mean	Species / Cultivar	No. of years	Days per year	Association with temperature	Type of relationship	Stepwise days/°C	PSR days/°C	*Tb*	DD	θ		Stepwise days/°C	PSR days/°C	T_b	DD	θ
						Trees										
12 Feb	*Salix caprea* 'Kilmarnock'	18	0.2	none												
19 Feb	***Salix daphnoides***	30	0.0	none												
18 Apr	***Prunus avium***	21	-0.3	strong	spring	-9.3	-9.8	0.6	450.5	26		-10.7	-7.6	1.6	258.5	29
29 Apr	*Prunus* 'Amanogawa'	30	-0.5	strong	spring + autumn	-6.9	-5.6	-0.2	551.4	31		-5.9	-5.8	0.3	413.1	33
04 May	*Malus domestica*	30	-0.3	strong	spring + autumn	-6.4	-5.5	0.9	447.4	49		-10.1	-5.4	-0.5	560.5	27
12 May	*Syringa vulgaris*	30	-0.6	strong	spring	-9.5	-9.3	-0.1	656.8	34		-10.6	-9.6	4.4	204.3	15
12 May	*Laburnum anagyroides*	28	-0.5	strong	spring + autumn	-8.1	-10.1	0.1	672.6	31		-6.2	-9.8	5.2	166.3	-25
16 May	***Sorbus aucuparia***	29	-0.6	strong	spring	-7.2	-6.6	-0.1	748.1	22		-6.3	-5.4	0.5	572.4	26
20 May	***Ilex aquifolium***	26	-0.4	strong	spring	-3.7	-8.8	-0.5	806.2	35		-8.0	-10.3	0.9	593.3	29
						Shrubs										
29 Dec	*Garrya elliptica*	15	-0.1	none												
19 Jan	*Hamamelis mollis*	26	-0.2	strong	spring	-5.4	-7.2	0.8	166.8	-26		-7.5	-8.2	-0.5	94.1	-9
25 Jan	*Mahonia japonica*	21	-3.5	none												
02 Mar	*Daphne mezereum*	15	-3.1	none												
03 Mar	*Rhododendron* 'Praecox'	28	-1.0	strong	spring + autumn	-11.9	-15.5	1.9	154.1	7		-15.2	-17.9	2.0	60.5	15
14 Mar	*Ribes sanguineum*	30	-1.2	strong	spring	-10.8	-11.7	0.8	235.1	12		-10.5	-10.0	1.1	124.3	18
19 Mar	*Mahonia aquifolium*	28	-0.4	strong	spring	-6.9	-5.0	-0.5	522.1	-25		-10.0	-5.3	1.8	87.1	25

	A	B	C	D	E	F	G	H	J	K		L	M	N	O	P
						Air						Soil				
FFD mean	**Species / Cultivar**	**No. of years**	**Days per year**	**Association with temperature**	**Type of relationship**	**Stepwise days/°C**	**PSR days/°C**	***Tb***	**DD**	**θ**		**Stepwise days/°C**	**PSR days/°C**	T_b	**DD**	**θ**
21 Mar	*Forsythia × intermedia*	23	-0.6	strong	spring + autumn	-1.0	-2.6	1.8	162.4	33		-8.4	-5.7	1.3	117.7	34
28 Mar	*Rhododendron keiskei*	29	-1.1	strong	spring + autumn	-10.0	-12.0	2.5	219.4	6		-12.5	-8.5	2.6	92.2	16
01 Apr	*Rosmarinus officinalis*	22	-2.5	strong	spring	-21.3	-39.0	6.2	54.4	8		-18.7	-32.4	1.5	281.2	-30
04 Apr	*Eccremocarpus scaber*	27	-1.1	strong	spring	-10.5	-20.0	1.4	427.8	-21		-14.3	-19.1	1.3	282.2	-15
06 Apr	*Skimmia japonica*	29	-0.7	strong	spring	-11.0	-14.3	2.5	273.2	-3		-15.2	-13.8	2.9	119.7	4
13 Apr	*Chaenomeles japonica*	30	-0.2	strong	spring	-6.5	-7.9	1.1	359.0	20		-8.4	-11.4	3.0	146.2	-4
20 Apr	***Cytisus scoparius* hybrid**	29	-1.8	strong	spring	-13.5	-24.8	4.9	174.3	-8		-14.4	-21.0	2.5	259.0	-30
22 Apr	*Berberis thunbergii* f. *atropurpurea*	28	-0.3	strong	spring + autumn	-9.5	-6.8	4.9	161.0	16		-9.8	-5.6	1.9	258.6	23
23 Apr	*Salix lanata*	16	-0.7	none												
24 Apr	*Aurinia saxatilis*	22	-0.2	strong	spring	-3.4	2.8	3.1	141.2	79		-6.8	2.7	6.9	22.2	51
26 Apr	*Choisya ternate*	27	-0.4	strong	spring	-9.1	-13.5	6.8	92.7	-23		-12.0	-14.5	1.3	387.2	-10
02 May	*Deutzia pulchra × hybrida*	30	-0.7	strong	spring	-9.8	-9.7	0.6	631.3	-1		-9.3	-9.1	1.7	365.1	2
06 May	*Lonicera periclymenum*	30	-0.3	strong	spring	-5.6	-5.3	-0.5	907.9	-24		-7.7	-5.9	4.1	197.7	-24
09 May	***Cotoneaster microphyllus***	30	-0.6	strong	spring + autumn	-3.0	-0.3	0.2	715.4	3		-2.5	0.8	1.3	452.9	14
16 May	*Dryas octopetala*	30	-0.1	none												
20 May	*Weigela florida*	30	-0.7	strong	spring + autumn	-5.5	-6.3	-0.5	854.6	22		-6.6	-4.2	4.1	290.1	-6

	A	B	C	D	E	F	G	H	J	K		L	M	N	O	P
						Air						Soil				
FFD mean	Species / Cultivar	No. of years	Days per year	Association with temperature	Type of relationship	Stepwise days/°C	PSR days/°C	*Tb*	DD	θ		Stepwise days/°C	PSR days/°C	T_b	DD	θ
21 May	*Rosa rugosa*	29	-0.3	strong	spring	-4.7	-6.6	1.3	535.4	58		-9.4	-7.6	4.1	281.3	58
22 May	*Cistus* 'Sunset'	25	-0.5	strong	spring	-10.9	-8.2	1.2	804.5	-14		-20.2	-7.4	11.8	2.3	119
22 May	*Potentilla fruticosa* (orange)	23	-0.2	strong	spring	-4.8	-8.6	0.0	899.2	0		-8.3	-10.8	1.3	582.1	11
23 May	*Halimium lasianthum*	29	-1.0	strong	spring + autumn	-9.6	-13.1	5.0	350.8	-30		2.0	-10.5	2.4	546.1	-30
23 May	*Rosa sericea*	27	-0.3	weak		-	-	7.8	118.7	35		-	-	10.9	11.1	122
27 May	*Rhododendron keleticum*	27	-0.1	none												
29 May	*Cornus alba*	27	-0.1	strong	spring	-	-7.6	0.8	697.5	47		-10.9	-11.7	5.0	279.3	49
29 May	*Daboecia cantabrica*	15	2.9	none												
31 May	*Iberis umbellata*	25	-0.2	strong	spring	-7.8	-19.1	2.8	653.0	-23		-42.5	-22.4	1.2	749.2	-22
01 Jun	*Weigela* 'Newport Red'	26	0.3	strong	spring + autumn	-0.4	-0.2	-0.3	930.9	28		-9.4	-1.7	3.7	420.1	-2
03 Jun	*Potentilla fruticosa* (cream)	26	-0.5	none												
03 Jun	***Viburnum opulus***	27	-0.5	strong	spring + autumn	-5.3	-7.8	2.3	575.9	64		-0.8	-8.8	4.8	344.3	64
06 Jun	*Cotoneaster dammeri*	18	0.0	strong	spring	-6.3	-	4.9	413.7	-28		-	-	13.8	1.0	121
06 Jun	*Fuchsia* 'Riccartonii'	30	-1.3	strong	spring	-16.1	-18.3	0.9	902.9	19		-14.2	-16.6	1.1	804.5	2
09 Jun	*Photinia* (syn. *Stranvevaesia*) *davidiana*	29	-0.1	strong	spring + autumn	-3.5	-3.0	-0.5	1094.7	23		0.0	-3.5	-0.5	1025.8	21
10 Jun	*Olearia ilicifolia*	27	-0.4	strong	spring + autumn	-6.8	-6.5	1.0	735.5	70		-3.5	-6.9	3.4	509.1	73

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FFD mean	Species / Cultivar	No. of years	Days per year	Association with temperature	Type of relationship	Stepwise days/°C	PSR days/°C	*Tb*	DD	θ		Stepwise days/°C	PSR days/°C	T_b	DD	θ
16 Jun	*Rosa* hybrids	30	0.0	strong	spring	-6.3	-5.6	-0.1	1116.0	26		-12.5	-8.2	3.6	590.5	-1
16 Jun	*Cistus ladanifer*	25	0.0	strong	spring + autumn	-	0.7	-	-	-		3.4	0.4	-	-	-
17 Jun	*Hebe cupressoides*	20	0.0	strong	spring + autumn	-3.9	-8.6	0.4	1011.0	50		-4.8	-10.3	3.7	583.6	63
20 Jun	*Hypericum olympicum*	29	0.1	weak		-	-	5.5	273.3	130		-	-	10.3	105.4	131
20 Jun	*Berberis verruculosa*	29	0.8	none												
21 Jun	*Rubus odoratus*	29	-0.1	strong	spring	-7.6	-3.5	6.2	319.6	105		-9.3	-6.9	9.6	142.7	126
24 Jun	*Erica tetralix*	9	-2.2	none												
26 Jun	*Hypericum* sp.	29	-0.3	weak		-2.4	0.8	-	-	-		-3.1	-5.2	0.2	1136.8	33
01 Jul	*Spiraea* × *bumalda*	28	-0.7	strong	spring	-5.0	-12.7	-0.5	1572.7	-13		-8.1	-15.6	-0.1	1353.4	-2
19 Jul	*Buddleja davidii*	30	-0.2	strong	spring	-6.1	-8.7	-0.5	1917.5	-27		-15.4	-15.9	0.4	1618.8	-23
19 Jul	*Olearia* × *haastii*	30	-0.4	none												
23 Aug	***Calluna vulgaris***	25	1.2	none												
29 Sep	*Viburnum tinus*	16	-3.0	weak		-	-	5.3	1378.3	57		-	-	5.2	1269.6	131
14 Oct	*Viburnum farreri*	29	-2.0	none												
23 Nov	*Jasminum nudiflorum*	29	-0.2	none												
Herbaceous																
17 Jan	*Helleborus niger*	30	-0.2	weak		-	-3.4	-0.5	110.3	-6		-	0.3	-	-	-
26 Jan	*Hepatica transsilvanica*	26	-2.1	none												
05 Feb	*Hepatica nobilis*	25	-0.7	none												

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13 Feb	*Omphalodes verna*	27	-0.2	none												
27 Feb	*Pulmonaria angustifolia*	26	-2.3	strong	spring	-9.5	-	1.3	223.2	-12		-13.6	-	3.9	16.3	13
28 Feb	*Pulmonaria saccharata*	26	-1.5	strong	spring	-6.5	-	0.5	226.3	1		-9.6	-	2.8	17.0	34
07 Mar	*Scilla sibirica*	25	0.4	none												
11 Mar	*Saxifraga oppositifolia*	13	-0.3	strong	spring	-16.0	-	1.1	210.6	12		-12.5	-	1.3	105.9	18
17 Mar	*Saxifraga* × *apiculata*	16	-1.5	strong	spring	-9.7	-	4.9	33.7	47		-12.3	-	2.2	60.8	35
17 Mar	***Arabis caucasia***	27	-0.5	strong	spring	-6.8	-1.5	-0.3	237.8	26		-8.6	-0.2	-0.1	156.2	30
21 Mar	*Vinca minor* 'Burgundy'	26	-0.9	strong	spring	-15.3	-13.0	1.6	249.3	4		-13.6	-9.2	4.2	20.0	34
22 Mar	*Brunnera macrophylla*	17	-1.9	weak		-14.5	-	-	-	-		-	-	-	-	-
23 Mar	*Primula marginata*	26	0.3	strong	spring + autumn	-5.0	1.6	-0.5	336.4	19		-1.1	6.0	1.5	107.1	34
30 Mar	***Primula veris***	23	0.2	none												
09 Apr	*Pulsatilla vulgaris*	30	0.1	strong	spring + autumn	-1.5	-2.6	0.7	229.5	57		-1.2	-1.8	0.5	177.0	60
10 Apr	*Viola riviniana*	29	-0.4	weak		-	-	1.7	211.1	49		-	-	4.0	41.7	78
12 Apr	*Lunaria annua*	30	-0.3	strong	spring + autumn	-4.3	-2.7	0.5	288.3	49		-3.1	-1.9	0.7	211.4	51
13 Apr	***Lamium galeobdolon***	28	-1.2	strong	spring	-8.3	-11.2	0.0	666.0	-25		-10.8	-6.7	0.5	353.9	4
14 Apr	*Dicentra formosa*	30	-0.7	strong	spring + autumn	-4.7	-3.5	0.5	389.5	30		-5.0	-1.5	0.5	292.5	33
15 Apr	*Aponogeton distachyos*	27	-0.4	strong	spring	-9.7	-11.9	5.4	80.0	45		-14.3	-15.7	4.9	49.5	36

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20 Apr	*Doronicum plantagineum*	29	0.0	strong	spring + autumn	-7.0	-3.2	0.4	621.1	-16		-8.8	-5.0	4.2	108.7	-21
20 Apr	*Dicentra spectabilis*	26	-1.2	strong	spring	-8.6	-13.9	7.7	36.8	54		-8.0	-10.7	5.9	41.8	18
20 Apr	*Trillium grandiflorum*	30	-0.7	strong	spring + autumn	-7.8	-7.9	6.7	85.7	-16		-0.5	-9.8	4.3	100.1	-21
23 Apr	*Myosotis arvensis*	28	-1.0	strong	spring	-4.7	-14.2	-0.5	838.5	-30		-14.9	-12.4	-0.5	670.1	-28
30 Apr	***Gentiana verna***	16	-0.3	weak		-	-	-	-	-		-6.9	-	-	-	-
01 May	***Galium odoratum***	30	0.2	strong	spring + autumn	-5.0	3.5	0.4	449.6	50		-6.2	2.9	3.2	186.1	62
02 May	*Asarina procumbens*	28	-1.6	strong	spring	-10.5	-18.8	1.1	660.0	-25		-13.9	-12.9	0.5	574.4	-23
02 May	*Geranium phaeum*	26	-1.1	strong	spring	-9.2	-10.8	0.6	645.4	1		-10.0	-9.6	0.6	494.3	7
05 May	*Phlox subulata*	24	0.4	strong	spring	-	-	-	-	-		-11.6	-3.8	10.1	0.5	118
05 May	*Meconopsis cambrica*	29	-0.6	strong	spring	-8.8	-8.8	2.2	339.2	55		-6.6	-6.4	2.3	309.8	25
06 May	*Osteospermum jucundum*	25	-1.3	strong	spring	-30.6	-26.7	5.7	199.1	-26		-	-20.6	1.3	504.1	-25
06 May	*Saxifraga* × *urbium*	26	-0.4	strong	spring	-	-9.1	4.8	153.2	74		-8.9	-8.2	7.8	24.6	76
07 May	*Dodecatheon* 'Red Wings'	24	0.3	none												
08 May	*Tellima grandiflora*	29	-1.1	strong	spring	-12.9	-22.9	1.2	604.7	5		-8.4	-19.6	0.6	538.7	5
08 May	*Saxifraga* sp.	28	0.6	none												
09 May	***Caltha palustris***	27	-1.6	strong	spring	-10.6	-19.4	6.3	160.1	-11		-12.1	-16.6	1.3	554.2	-29
15 May	*Penstemon* sp.	21	-0.6	strong	spring	-4.8	-4.4	0.8	628.6	19		-6.5	-6.0	1.6	458.1	18

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16 May	*Aquilegia vulgaris*	24	0.3	strong	spring	-3.6	-	-	-	-		-10.0	-	-	-	-
18 May	*Geranium endressii*	15	0.7	none												
18 May	***Ajuga reptans***	22	-0.4	none												
18 May	*Limnanthes douglasii*	28	-0.2	none												
20 May	*Centaurea cyanus*	30	-0.6	strong	spring	-4.3	-8.1	1.3	495.0	65		-4.6	-7.1	-0.5	778.0	15
22 May	*Aquilegia flabellata*	21	-0.4	none												
23 May	*Erinus alpinus*	21	-0.4	none												
25 May	*Myosotis scorpioides*	21	0.5	none												
25 May	*Ourisia coccinea*	27	0.0	strong	spring	-4.3	-3.2	-0.5	681.7	65		-18.0	-6.2	3.6	372.6	-18
28 May	*Geranium* sp.	28	0.5	none												
31 May	***Armeria maritima***	28	-0.4	none												
02 Jun	*Polemonium caeruleum*	23	1.6	none												
03 Jun	*Silene uniflora* 'Flore Pleno'	26	0.3	none												
05 Jun	*Papaver orientale*	25	0.2	weak		-3.0	-	-	-	-		-8.4	-	5.0	333.1	-12
05 Jun	*Dianthus barbatus*	30	0.4	none												
05 Jun	*Antirrhinum majus*	25	-0.2	none												
05 Jun	*Astrantia major*	26	-0.7	weak		-3.1	-4.4	-0.5	1011.2	34		-4.4	-3.6	-0.5	1015.4	13

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05 Jun	*Lupinus* garden hybrids	28	-0.2	strong	spring	-3.4	-4.8	-0.5	980.8	37		-4.9	-5.8	-0.4	922.3	38
07 Jun	*Ranunculus flammula*	29	0.3	none												
10 Jun	*Alchemilla mollis*	27	-0.3	none												
10 Jun	*Sisyrinchium graminoides*	28	0.4	none												
11 Jun	*Aster alpinus*	23	0.2	weak		0.0	-1.7	11.9	5.4	156		0.0	-2.6	10.3	74.6	120
12 Jun	*Borago officinalis*	18	1.4	none												
12 Jun	*Dianthus* × *allwoodii*	30	0.7	none												
13 Jun	*Kniphofia caulescens*	30	-0.3	strong	spring	-8.4	-7.2	-0.5	1396.1	-27		-13.7	-13.1	0.1	1133.3	-21
14 Jun	*Thymus serpyllum*	30	0.4	weak		-	-	-	-	-		-	-	10.1	79.1	137
14 Jun	*Aconitum napellus*	30	-0.7	strong	spring	-4.6	-8.0	-0.5	1380.4	-23		-5.6	-8.5	-0.5	1246.2	-21
15 Jun	*Oenothera acaulis*	16	0.5	none												
18 Jun	*Calceolaria* sp.	23	0.6	strong	spring	-	-	8.6	131.2	131		-8.7	-5.7	10.6	80.2	128
20 Jun	*Cephalaria gigantea*	26	-0.1	strong	spring + autumn	-0.9	-3.2	-0.5	1125.8	43		-8.4	-7.7	3.2	656.6	21
23 Jun	***Campanula glomerata***	30	0.3	none												
24 Jun	*Dianthus deltoides*	25	0.3	none												
24 Jun	*Eryngium alpinum*	23	0.1	none												

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26 Jun	*Achillea millefolium*	14	1.0	none												
26 Jun	*Campanula rotundifolia*	16	-0.5	weak		-10.5	-	-	-	-		-	-	-	-	-
27 Jun	*Leontopodium alpinum*	22	1.0	none												
30 Jun	*Scutellaria galericulata*	16	0.8	none												
01 Jul	*Thalictrum flavum*	26	0.1	none												
08 Jul	***Lychnis coronaria***	26	0.2	none												
12 Jul	*Lysimachia nummularia*	12	1.1	weak		-	-	-	-	-		-7.3	-	-	-	-
13 Jul	*Hosta* spp.	29	0.0	weak		-	-	-	-	-		-	-	5.5	644.9	55
14 Jul	*Sempervivum tectorum*	23	0.8	none												
15 Jul	*Stachys byzantina*	27	-0.8	strong	spring	-11.2	-14.7	3.0	1125.2	-17		-	-	-0.3	1650.3	-14
15 Jul	*Cortaderia selloana*	21	-1.3	weak		-	-	14.2	38.1	50		-	-	-	-	-
16 Jul	*Catananche coerulea*	16	-1.1	strong	spring	-5.6	-	6.2	629.0	-29		-7.8	-	-0.5	1815.7	-29
17 Jul	***Verbascum thapsus***	20	-1.2	none												
18 Jul	*Crepis incana*	28	-0.2	weak		-	-	-	-	-		-7.7	-	1.1	1252.7	68
20 Jul	*Leucanthemum × superbum*	30	-1.1	strong	spring	-5.1	-11.6	0.4	1636.0	2		-8.4	-9.6	-0.4	1716.0	5
22 Jul	*Veronica virginica*	26	0.3	weak		-	-	-	-	-		-6.3	-	2.2	1292.3	-21

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23 Jul	*Campanula trachelium*	25	0.9	weak		9.2	-	-	-	-		11.1	-	-	-	-
23 Jul	*Cicerbita alpina*	27	-0.7	weak		-8.8	-	-	-	-		-	-	-	-	-
27 Jul	*Persicaria vacciniifolia* (syn. *Polygonum vacciniifolium*)	29	4.0	none												
30 Jul	*Coreopsis verticillata*	30	-0.2	strong	spring	-4.5	-8.7	0.6	1536.7	57		-5.7	-13.0	2.6	1237.7	54
03 Aug	*Kniphofia galpinii*	29	0.4	none												
04 Aug	***Dipsacus fullonum***	23	-0.6	none												
04 Aug	*Echinops bannaticus*	29	-0.3	strong	spring	-4.3	-3.9	9.0	422.1	95		-12.3	-6.8	9.3	445.0	84
05 Aug	*Anaphalis margaritacea*	24	0.7	none												
16 Aug	*Carlina acaulis*	11	-1.0	weak		-	-	-	-	-		-25.7	-	-	-	-
20 Aug	*Cynara cardunculus*	21	0.3	none												
22 Aug	*Tricyrtis hirta*	22	-0.1	weak		-6.5	-	-	-	-		-5.0	-	-	-	-
26 Aug	*Sagittaria sagittifolia*	19	0.7	none												
						Feoprytes										
13 Jan	*Eranthis hyemalis*	27	-0.3	weak		-	-4.8	-0.5	213.4	-29		-4.2	-5.7	0.0	13.7	7
27 Jan	*Galanthus nivalis*	30	-1.1	strong	spring	-7.6	-7.7	1.0	39.5	14		-7.8	-2.2	1.3	12.8	14
30 Jan	*Crocus vernus* Dutch cultivars	30	-0.5	strong	spring	-5.2	-6.0	-0.5	85.2	9		-	-4.2	0.9	20.2	18

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05 Feb	*Petasites fragrans*	27	-0.7	strong	spring + autumn	-2.3	-3.9	-0.5	285.1	-25		-3.9	-1.8	-0.5	106.9	0
15 Feb	*Ipheion uniflorum*	25	-0.8	none												
16 Feb	*Anemone blanda*	29	0.7	none												
03 Mar	***Narcissus pseudonarcissus***	26	-1.3	strong	spring	-9.4	-15.6	-0.4	419.9	-25		-10.0	-9.3	-0.5	214.0	1
18 Mar	*Chionodoxa forbesii*	28	-0.4	strong	spring	-4.4	-3.4	1.9	57.8	63		-5.0	-2.2	-0.5	223.2	21
23 Mar	*Tulipa turkestanica*	21	-0.9	strong	spring	-8.2	-7.9	3.2	98.2	39		-8.7	-6.8	4.1	23.8	40
24 Mar	*Ranunculus ficaria*	25	-0.7	strong	spring + autumn	-7.0	-5.4	1.4	207.6	29		-8.7	1.0	5.5	1.0	80
28 Mar	*Muscari botryoides*	29	-0.3	strong	spring + autumn	-6.1	-6.8	-0.5	584.4	-25		-7.8	-10.8	5.9	6.7	29
02 Apr	*Tulipa* misc.	30	0.1	weak		-	-7.5	-0.5	339.3	33		-15.6	-14.0	-0.5	269.1	33
05 Apr	*Anemone ranunculoides*	20	0.7	strong	spring + autumn	-1.5	0.9	-0.5	377.8	35		-	5.6	-0.5	293.6	36
07 Apr	***Fritillaria meleagris***	30	-0.2	strong	spring + autumn	-3.5	-4.2	1.2	175.2	63		-5.1	-8.4	-0.5	328.5	26
08 Apr	***Hyacinthoides non-scriptus* (blue)**	30	-0.7	strong	spring	-13.1	-11.7	4.7	64.5	63		-7.8	-10.5	0.9	239.1	21
10 Apr	*Erythronium* 'White Beauty'	27	-0.2	strong	spring + autumn	-5.4	-2.6	-0.5	354.8	46		-4.8	-3.2	-0.5	360.9	25
11 Apr	*Erythronium* 'Pagoda'	27	-0.2	strong	spring + autumn	-5.7	-3.0	-0.5	413.1	33		-5.3	-1.6	-0.5	372.8	23
12 Apr	*Tulipa tarda*	28	-0.2	strong	spring	-5.3	-7.1	1.1	269.0	45		-10.3	-8.9	0.6	230.8	46

	A	B	C	D	E	F	G	H	J	K		L	M	N	O	P
						Air						Soil				
FFD mean	Species / Cultivar	No. of years	Days per year	Association with temperature	Type of relationship	Stepwise days/°C	PSR days/°C	*Tb*	DD	θ		Stepwise days/°C	PSR days/°C	T_b	DD	θ
13 Apr	*Hyacinthoides non-scriptus* (pink)	27	-1.0	strong	spring	-6.9	-13.0	-0.5	783.5	-30		-8.1	-12.6	-0.5	484.0	-1
19 Apr	*Tulipa batalinii*	20	-0.1	strong	spring	-3.6	-3.9	2.1	197.5	65		-4.9	-5.4	-0.5	391.7	34
26 Apr	*Tulipa aucheriana*	25	0.0	weak		-	-5.2	5.9	138.3	-22		-	-9.4	2.7	245.5	-23
30 Apr	*Geum montanum*	30	0.2	none												
30 Apr	***Fritillaria pontica***	29	-0.7	strong	spring	-9.7	-9.5	1.2	326.1	67		-5.1	-9.0	-0.5	548.2	20
01 May	*Allium ursinum*	19	-0.3	strong	spring	-5.4	-	-0.5	595.1	39		-5.9	-	5.3	99.5	41
04 May	*Polygonatum multiflorum*	30	-0.2	strong	spring	-4.2	-5.5	8.0	19.6	112		-4.0	-5.4	-0.5	582.8	21
13 May	*Uvularia grandiflora*	22	-0.5	weak		-	-6.1	7.4	52.6	112		-	-	-	-	-
15 May	*Convallaria majalis*	30	0.1	strong	spring + autumn	-2.5	-2.1	9.2	25.2	112		-6.3	-3.6	11.2	1.8	123
17 May	*Oxalis adenophylla*	26	0.2	weak		-	-	6.1	123.9	34		-	-	-	-	-
17 May	*Oxalis* sp.	28	-0.3	strong	spring	-4.2	-6.9	8.8	35.5	110		-5.4	-9.2	10.2	11.2	108
24 May	*Paeonia mascula*	30	-0.3	strong	spring	-3.4	-8.6	0.9	651.0	44		-12.0	-9.5	5.2	239.6	-19
29 May	*Iris germanica* hybrids	29	-0.4	strong	spring	-7.4	-9.9	10.0	45.6	77		-9.9	-11.2	3.2	470.4	-22
31 May	*Oxalis deppei* (syn. *Oxalis tetraphylla*)	22	-1.1	strong	spring	-9.2	-18.6	1.9	753.7	-11		-25.3	-26.4	0.8	777.7	-10
01 Jun	*Allium schoenoprasum*	22	0.7	none												
02 Jun	***Dactylorhiza majalis***	30	-0.9	strong	spring	-5.1	-9.8	-0.5	1082.7	9		-9.4	-13.7	0.7	782.7	11
10 Jun	***Iris pseudacorus***	29	-0.7	strong	spring	-7.3	-10.3	-0.5	1375.1	-30		-9.1	-10.4	-0.5	1238.5	-29

	A	B	C	D	E	F	G	H	J	K		L	M	N	O	P
						Air						**Soil**				
FFD mean	**Species / Cultivar**	**No. of years**	**Days per year**	**Association with temperature**	**Type of relationship**	**Stepwise days/°C**	**PSR days/°C**	***Tb***	**DD**	**θ**		**Stepwise days/°C**	**PSR days/°C**	**T_b**	**DD**	**θ**
10 Jun	*Iris sibirica*	24	0.4	none												
10 Jun	*Gladiolus illyricus*	23	-0.7	weak		-10.4	-17.9	9.5	77.1	121		-	-10.6	1.7	823.8	-18
01 Jul	***Lysimachia vulgaris***	29	0.4	strong	spring	-	-	-	-	-		-5.6	-8.4	10.5	150.3	131
09 Jul	*Lilium martagon*	22	-0.3	strong	spring	-2.2	-5.5	-	-	-		-3.4	-6.3	6.5	465.3	118
11 Jul	*Triteleia laxa*	25	-0.6	strong	spring	-8.6	-13.2	2.7	975.9	54		-4.3	-12.0	-0.5	1560.6	13
15 Jul	*Alstroemeria* sp.	26	-0.5	strong	spring	-5.2	-10.9	7.8	344.0	130		-	-	-	-	-
30 Jul	*Crinum* × *powellii*	22	-1.8	none												
09 Aug	*Crocosmia* × *crocosmiiflora*	30	-1.1	strong	spring	-9.5	-21.1	4.4	1171.0	-30		-8.5	-19.2	1.9	1599.8	-30
09 Sep	*Colchicum speciosum*	29	0.0	none												
11 Sep	*Colchicum autumnale*	27	0.3	none												
25 Sep	*Nerine bowdenii*	30	0.2	none												
06 Oct	*Crocus speciosus*	28	0.1	none												