FLOWERING NEWSLETTER REVIEW

Temperate flowering phenology

Fiona Tooke1,* and Nicholas H. Battey2
1 Eden Project, Bodelva, Cornwall, PL24 2SG
2 School of Biological Sciences, University of Reading, Reading RG6 6AS, UK

* To whom correspondence should be addressed: E-mail: ftooke@edenproject.com

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Abstract

Individuals, families, networks, and botanic gardens have made records of flowering times of a wide range of plant species over many years. These data can highlight year to year changes in seasonal events (phenology) and those datasets covering long periods draw interest for their perspective on plant responses to climate change. Temperate flowering phenology is complex, using environmental cues such as temperature and photoperiod to attune flowering to appropriate seasonal conditions. Here we give an overview of flowering phenological recording, outline different patterns of flowering, and look at the interpretation of datasets in relation to seasonal and climatic change.

Key words: Climate, flowering, life cycles, plant phenology.

Introduction

Recording when plants flower is a pastime that has appealed to people for centuries. Observations on flowering appear in datasets alongside the first croak of the common frog, the arrival of swallows, or the unfurling of oak leaves. Capturing the timing of these seasonal events is the study of phenology. Well-known recorders include Gilbert White who noted events in 18th century Selborne, England and Henry David Thoreau who recorded in Concord, USA in the 19th century. Once, phenological records were perhaps simply considered interesting but of little other value. Now, long-term datasets of seasonal events are widely sought-after for their potential to reveal how the natural world responds to climate change. Historical records have been the subject of recent analysis and several phenological recording networks have been established or revitalized in response to this resurgence of interest.

For the most part, flowering phenological data focus on first flowering dates (FFD) and records cover a wide range of species with diverse life-forms. How flowering responses may be altered by climate change is difficult to predict but of great significance with far-reaching impacts on the functioning of ecosystems, for example, through the potential de-coupling of flowering time and pollinator life cycles (Peñuelas and Filella, 2001; Memmott et al., 2007). In this paper, a brief overview of some flowering phenological records is provided and flowering life cycles and what is recorded about them are considered. Finally, we look at potential differential flowering responses to climate change.

An overview of the history of recording flowering phenology

Noting flowering times is part of a long tradition of recording seasonal events. With little need for specialist equipment or knowledge, this is an activity that has, at times, attracted large numbers of people, who have often made records as a pastime or ‘amateur’ interest (Whitfield, 2001). Its popularity as an activity has probably been greatest in the 19th century and now, at the start of the 21st century when it has become the focus of several ‘citizen science’ projects. Long-term datasets useful to research are generally considered to be those spanning 20 years or more, although Amano et al. (2010) have recently used hierarchical models and short-term records from multiple sites to estimate a 250-year index of first flowering. A few examples of long-term datasets are outlined below and some that have been used in recent research are given in Table 1.
Table 1. Examples of long-term datasets which include flowering observations and which have been used in recent research

<table>
<thead>
<tr>
<th>Recorder</th>
<th>Dataset dates</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aarne Juhonsalo and family</td>
<td>1952–</td>
<td>Oulainen-Chineva, Finland</td>
<td>Lappalainen et al., 2008</td>
</tr>
<tr>
<td>Henry David Thoreau</td>
<td>1851–1858 followed by Alfred Hosmer 1888–1902 and Primack and Miller-Rushing, 2003–2007</td>
<td>Concord, Massachusetts, USA</td>
<td>Willis et al., 2008</td>
</tr>
<tr>
<td>James McNab</td>
<td>1850–1878 followed by John Sadler 1878–1882 and Robert Lindsay up to 1895</td>
<td>Royal Botanic Gardens, Edinburgh, Scotland</td>
<td>Harper et al., 2006</td>
</tr>
<tr>
<td>Charles Robertson</td>
<td>1884–1916</td>
<td>W Illinois, USA</td>
<td>Memmott et al., 2007</td>
</tr>
<tr>
<td>Mary Manning</td>
<td>1965–</td>
<td>UK</td>
<td>Sparks and Manning, 2000</td>
</tr>
<tr>
<td>Aldo Leopold</td>
<td>1936–1947 followed by Nina Leopold</td>
<td>Fairfield Township, Sauk County, Wisconsin</td>
<td>Bradley et al. 1999</td>
</tr>
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Individuals

Robert Marsham is often seen as the founding father of British phenological recording. A tree-lover and the owner of an estate in the east of England, Marsham began his recordings of ‘Indications of Spring’ in 1736. The ‘Indications’ continued to be observed by generations of the Marsham family for 211 years, ending in 1958 when the family was advised that the data were no longer useful (Sparks and Lines, 2008). Amongst the recordings, the Marshams noted the first flowering dates of snowdrop, wood anemone, hawthorn, and turnip (Sparks and Carey, 1995). More recent examples of individuals who have kept long-term records are Richard Fitter, Mary Manning, Fred Last, and Nigel Hepper who have made records spanning 20 years or more of flowering in British gardens or countryside in Oxfordshire, Norfolk, East Lothian, and Leeds/Richmond, respectively (Last, 2001; Bisgrove and Hadley, 2002; Hepper, 2003; Sparks and Manning, 2000).

Networks

Networks of recorders have been established in a number of countries. In the UK, the Royal Meteorological Society set up a Phenological Network in 1875. Annual reports from this network were compiled by reporters, but the group was disbanded in 1947 and a final report produced in 1948. Records were sent in from 11 meteorological districts of Britain from an average of 200 observers a year but up to around 600 at the network’s peak (Jeffree, 1960). Mean flowering times of the 11 species recorded through the 58 year period are shown in Table 2 (Sparks et al., 2000). In a similar manner, the German Meteorological Service has run a phenological network since 1951. During the 1970s this network had up to 4000 recorders and currently there are around 1550 who collect data on cultivated and native plants (Estrella et al., 2007). Many other European phenological networks exist and have recently been summarized in a report by Nekovar et al. (2008).

‘Citizen science’ initiatives have recently been successful at publicizing phenology and encouraging public participation in recording. Examples of this are Plantwatch Canada (http://www.naturewatch.ca/english/plantwatch/), Project Budburst run by the USA National Phenology Network (Donaldson, 2009; http://www.windows.ucar.edu/citizen_science/budburst/), and the UK Phenology Network’s ‘Nature’s Calendar’
launched by the Centre for Ecology and Hydrology in 1998 with involvement of the Woodland Trust from 2000 (Whitfield, 2001; http://www.naturescalendar.org.uk/).

**Botanic gardens**

Botanic gardens are significant contributors to flowering phenology records. They are considered well-placed to carry out this research as they contain living collections (often long-lived), herbaria, and detailed plant records as well as public access and education provision (Harper et al., 2006; Donaldson, 2009; Primack and Miller-Rushing, 2009). At the Royal Botanic Garden Edinburgh, 250–300 accessions are monitored daily and recordings made of beginning and end dates of flowering (Harper et al., 2006). The Kew 100 programme, which began in 2000, records flowering data on 100 trees, shrubs, and bulbs at the Royal Botanic Gardens, Kew (http://data.kew.org/wild/phenology/). In both locations earlier datasets exist (Hepper, 2003; Harper et al., 2006). Many botanic gardens in Europe are also International Phenological Gardens, a garden network initiated in 1957 and co-ordinated by Humboldt University, Berlin. There are around 50 sites and these gardens grow clones of specific plants thus allowing direct comparison of flowering across a range of locations (Chmielewski and Rötzer, 2001; Primack and Miller-Rushing, 2009).

**Flowering and time**

Phenology is concerned with the timing of events. In plants, the timing of flowering is regulated by mechanisms which act to ensure that flower emergence occurs in suitable conditions. In temperate climates, the flowering process is attuned to seasons through environmental cues, particularly photoperiod and temperature. These cues for flower induction can also be involved in signalling times of dormancy to the plant. Before considering phenological records further, a brief summary of patterns of flowering in some different groups of plants is given.

Grainger (1939) observed that, ‘any attempt to elucidate the action of various factors upon the time of flowering would, moreover, seem to demand a relation to the time when the flower bud was first formed, and not only to the time when it emerged. It is known that many plants make their flower buds a considerable time before the emergence of bloom.’ His classification of flowering types reflects this, in particular in the categories of ‘direct’ and ‘indirect’ flowering, designations which recognize whether the development from initiation to emergence is uninterrupted or integrates a period of rest (Fig. 1; Grainger, 1939).

In annuals, flowering appears to be a straightforward, direct, and all-consuming process in which all meristems flower and the life cycle is completed within one year. Perennials, however, are more complex, living for years and flowering repeatedly. Although there are exceptions, such as some bamboos and monocarpic biennials including carrot and foxglove, perennials are typically polycarpic (as opposed to annuals, which are monocarpic). The polycarpic strategy allows them to retain vegetative meristems and thus the capacity for continued growth after flowering (Battey, 2000).

**Fig. 1.** ‘Direct’ and ‘indirect’ flowering, according to Grainger (1939), who dissected over 100 plants from the Huddersfield (UK) area 1937–1939. He classified coltsfoot as ‘direct’ flowering and bilberry as ‘indirect’ flowering. Top: Coltsfoot, *Tussilago farfara*. (A) Plan view of the inflorescence initial, 17 September 1938. (B) Plan view of inflorescence initial, 29 Oct. 1938: developing disk florets. (C) Side view of inflorescence 3 December 1938. The total length of the inflorescence, shown as 10 mm on 3 December, had increased to an average of 17 mm on 1 January 1939, when the florets also appeared yellow. Below: Bilberry, *Vaccinium myrtillus*. Dissection of flower initial from terminal bud of the adjoining shoot, 17 July 1938– fully-formed at this time. (Flower emergence was the following May.) Reproduced with permission from Wiley-Blackwell.
Within this group, there are diverse growth habits and cases of Grainger’s ‘indirect flowering’. In particular, there may be very long periods between flower initiation and emergence in trees and bulbs; it takes around 9-10 months for the flowering process to be completed in *Malus* (Sedgley and Griffin, 1989), whilst over a year elapses between flower initiation and emergence in *Nerine sarniensis* (Le Nard and De Hertog, 1993; Rees, 1966). These examples may be at the more extreme end of the spectrum but, in temperate fruit trees, flowers are generally initiated in the year prior to their spring emergence and bulbs may initiate the next year’s flowers shortly after those of the current year have died.

**Trees**

Dormancy in temperate tree species is described as being composed of endodormancy, regulated by physiological factors including chilling; and ecodormancy, which reflects the fact that conditions (for example, of nutrient or water availability or temperature) are unsuitable for growth. A further term, paradormancy, describes situations in which the control of dormancy in meristematic tissue is signalled or perceived at first by another part of the plant (e.g. leaves, bud scales) (Lang, 1987). The onset of dormancy is often controlled by photoperiod (short days) (Rohde and Bhatlerao, 2007), but this appears not to be the case in many Rosaceous/temperate fruit trees. Low temperatures (<12 °C) have been found to play a role in promoting dormancy of apples and pears (Heide and Prestrud, 2005). Breaking dormancy requires the completion of a period of chilling, which can be measured in hours below a certain temperature; for example, Bartlett pear and Delicious apple require around 1500 h of chilling (Sedgley and Griffin, 1989). For many cultivars, the chilling requirement falls between 1000 h and 1200 h (Barden and Neilson, 2003). Sub-optimal chilling can make budbreak protracted. Sunley *et al.* (2006) report that increasing chilling of blackcurrants and raspberries leads to more synchronous flowering.

The point at which endodormancy is completed is rarely recorded (Legave *et al.*, 2008) since, whilst buds may now have the ability to grow, unless conditions are conducive to this, the plant moves seamlessly to ecodormancy. Experimental intervention can, however, show when buds become capable of breaking dormancy (e.g. Mahmood *et al.*, 2000). Budburst, at the end of ecodormancy, occurs once a heat requirement of accumulated degree days has been met (Sedgley and Griffin, 1989). Whilst endo- and eco-dormancy are represented here as discrete phases with different temperature requirements, there is a relationship between the two (see discussion in Battey, 2000). Longer durations of chilling have been found to decrease the thermal time required for budburst (Murray *et al.*, 1989; Heide and Prestrud, 2005; Welling and Palva, 2006).

In temperate fruit trees (e.g. apples, pears, cherries, plums) dormancy through the winter interrupts the flowering process such that flowers are initiated in the summer, yet trees do not blossom until the following spring (Grainger, 1939).

**Bulbs**

In general, flower initiation in bulbs is not responsive to photoperiod and is controlled by temperature and the size of the storage organ and its available food reserves (Rees, 1992). Flower initiation times vary; in *Galanthus* and *Narcissus* flowers are initiated after the current year’s flowering is over in the spring or early summer; emergence occurs the following spring. Similarly, flower initiation in tulip takes place in mid-summer but emergence is in spring of the next year; but in *Lilium* and *Gladiolus*, flowers are initiated after shoot emergence from the storage organ, with flower emergence occurring in the summer (Rees, 1992; Le Nard and De Hertog, 1993). Summer and winter dormancy is a feature of these geophytes, which typically survive the summer underground and complete a cold requirement before above-ground growth (Rees, 1992).

**Grasses**

Temperate annual, and some perennial grasses require only long days (LD) to flower, but for most temperate perennial grasses flowering requires low temperatures or short-days (SD), followed by transition to LD for flower initiation (Heide, 1994). The primary induction by SD/low temperatures is met by autumn or winter conditions and is a vernalization or winter requirement during which there are not generally morphological changes in terms of flower initiation. Initiation typically happens during the secondary induction in the LDs of spring and summer (Heide, 1994).

In perennial grasses of Mediterranean origin, flowering in late spring is followed by summer dormancy (endodormancy), triggered by longer days and warmer temperatures. On release from dormancy by higher temperatures towards the end of summer, buds begin re-growth as the temperatures decrease in autumn (Volaire and Norton, 2006).

**Recording flowering**

Flowering phenological datasets are often composed of first flowering dates (FFD) and are, therefore, mainly records of flower emergence times. There is, however, a need to define what constitutes flower emergence, particularly when there are a large number of different recorders. In some instances observers state clearly their definition of flowering, for example, ‘visible anthers’ (Fitter *et al.*, 1995) or ‘an open flower is a flower in which stamens or stigmas could be seen without the observer pushing petals aside’ (Last, 2001). Another approach is to use a universal scale, such as the BBCH scale which is named using the initial letters of the institutions involved in its development (Biologische Bundesanstalt, Bundessortenamt, Chemische Industrie). This scale was originally drawn up to allow uniform descriptions of growth stages of agricultural crops (Lancashire *et al.*, 1991) and has been used by Menzel *et al.* (2006) to group data from various sources across Europe.

FFD constitutes the most straightforward recording activity. Other, more demanding observations relate to the
duration of flowering. Elzinga et al. (2007) outlined how flowering phenology can be recorded at different levels; population, individual plants within a population, or even flowers within an individual. So, whilst FFD might be recorded as the first flower seen (perhaps in a garden), a ‘flowering season’, as defined by Elzinga et al. is the number of days between the first and last flowering of individuals in a population. Flowering ‘spread’ or duration is recorded in some long-term datasets for perennial fruit crops, perhaps because it is seen as a better indicator of chill than a single flowering date (Sunley et al., 2006). Records for raspberry and blackcurrant cultivars over >40 year periods are held at East Malling, UK and cover first flower, full bloom, and end of flowering (Sunley et al., 2006). Blossom records of first flower (10% open), full flower (80% open), and petal fall (90% over) have been kept since 1960 for 12 apple varieties from the UK National Fruit Collections at Brogdale (M Jeger, personal communication). There are significant challenges in recording data other than FFD, for example, in gauging the percentage of flowers open, taking into account flowers dying as well as opening and monitoring populations rather than individuals.

Miller-Rushing et al. (2008) favour observations of flowering distribution, or peak or mean flowering dates, as first flowering dates represent one extreme of flowering distribution. Increases and decreases in population size can lead to earlier or later first flowering dates, respectively (see Fig. 2 for a representation). To detect changes in flowering dates, sampling needs to be fairly frequent, especially if the flowering duration is short. In one of the authors’ assessments it was found that a flowering date change of 1 d °C⁻¹ would have a 97% chance of being detected as a significant trend over a 10-year period if sampling was carried out every 2 d, but only a 54% chance of detection if sampling was every 7 d (Miller-Rushing et al., 2008).

**Alternative sources of data**

To assess trends of flowering phenology against climate change, long-term datasets are required. In the quest to uncover historical data, alternatives to numerical records have been found. Flowering herbarium specimens, photographs, and even diaries or adverts for Japanese cherry blossom festivals have been used as the basis for phenological datasets (Aono and Kazui, 2008; Miller-Rushing et al., 2006).

Where there is no history of phenological recording these alternatives could prove useful and can, as in the case of Japanese cherry flowering, give long-term datasets. Aono and Kazui (2008) were able to compile a dataset covering 60.7% of the years from 801–2005 using dates from old diaries, chronicles, adverts, and poetry. The accuracy of their data may be aided by the fact that, in Japan, cherry blossom viewing parties are usually held at full-flowering, which covers only a 2–4 d period. However, compiling data sets from alternative sources has limitations which need careful consideration. Herbarium specimens are often not from just one location. In their study of flowering phenology of coltsfoot (Tussilago farfara L.), Lavoie and Lachance (2006) needed to introduce a correction procedure to take account of different climatic conditions (snowmelt dates and urban heat island effects) across the sampling locations. Dated photographs can provide dramatic and indisputable evidence of plant developmental states at given times, and are likely to be a quite widespread resource over the last 100 years. Miller-Rushing et al. (2006) used photographs of cultivated plants at Arnold Arboretum and wild plants taken by photographer Herbert Wendell Gleason between 1900–1921 in their research. They point out, however, that these photographs were taken on one day in a flowering period and exactly when in that period is unknown. Cases in which photography is likely to be particularly useful are when repeat photographs of the same subject are taken over a period of time (Fig. 3; Willis, 1944; Sparks et al., 2006), or when the species photographed has a narrow flowering window, for example, wood anemone (Sparks, 2007). In all cases details regarding the flowering status of the plant need to be stated.

![Fig. 2. The theoretical effect of changes in population size on changes in first flowering date (Miller-Rushing et al., 2008). For the solid curves for (a) increased or (b) decreased population size, mean flowering dates are earlier than for the distribution of flowering dates for a population in a year in the past (dashed curve). Arrows indicate changes in peak and first flowering dates over time. Reproduced with permission from Wiley-Blackwell.](https://academic.oup.com/jxb/article-abstract/61/11/2853/440390?redirected=true)
Fig. 3. ‘How seasons vary’: photographic series from ‘Weatherwise’ by John Willis (1944) showing the same snowdrop clump each 1st January from 1913 to 1942. Willis described the start of 1913 as follows: ‘The year 1913, the starting-point of our pilgrim’s progress through thirty years of weather entered in a memorable fashion; for, as the photographic records of my station will show, no subsequent January has seen vegetation so amazingly advanced, not a New Year’s Day so camouflaged with flowers. Only one touch of winter swept through the year’s mild opening month, to streak the ground on the 11th with six inches of snow; while following a mild, showery January a drier and sunnier February lured vegetation to such further eager advance that the earliest spring flowers were already on the wane by the middle of the month, and daffodils were awakening in the woods weeks ahead of their time by its close’. 
Data from across Europe, from 1951–1998 have led Ahas et al. (2002) to suggest that timing of spring phases has altered over this time period, advancing by four weeks in Western and Central Europe, but being delayed by up to two weeks later in Eastern Europe. A study of 385 British plant species found that FFD was an average of 4.5 d earlier than in the previous four decades, which had shown little variation in flowering time (Fitter and Fitter, 2002).

The resurgence of interest in phenological data has been partly fuelled by the finding that there is a strong correlation between earlier flowering and warmer spring temperatures (Fitter et al., 1995; Sparks and Carey, 1995; Sparks et al., 2000). Using temperature datasets, there are opportunities to calculate trends of number of days advance (or otherwise) of flowering time per °C rise in temperature and thus patterns of flowering in relation to climate change; conversely, flowering data can be used to reconstruct past climates (Aono and Kazui, 2008). Examples of the former include the 250-year index of first flowering dates produced by Amano et al. (2010) which correlates closely with mean Central England Temperature data for February to April. Based on this study, flowering is occurring five days earlier for each 1 °C rise in temperature, while analysis of 58 years of data from the British phenological network of the Royal Meteorological Society, alongside temperature data for Central England, suggests a flowering response of 2–10 d earlier per °C (Sparks et al., 2000). The impact of a possible future climate scenario for SE England by 2100, termed the IS92a scenario, of a 3.5 °C rise in temperature, while analysis of 58 years of data from the British phenological network of the Royal Meteorological Society, alongside temperature data for Central England, suggests a flowering response of 2–10 d earlier per °C (Sparks et al., 2000). The impact of a possible future climate scenario for SE England by 2100, termed the IS92a scenario, of a 3.5 °C rise in temperature, 3 °C rise in spring, summer, and autumn temperature, and a 10% increase in rainfall has been forecast using the Marsham family dataset and Central England temperature data as the basis for predictions. Flowering of the Marsham-recorded species (snowdrop, wood anemone, hawthorn, and turnip) is predicted to be 20–25 d earlier under these conditions (Sparks and Carey, 1995).

Taken together with data on range boundaries, phenology contributes to the definition of a global ‘fingerprint’ to sum up predicted shifts in time and space of events, species ranges and abundance in response to climate change (Parmesan and Yohe, 2003; Root et al., 2003). One element of this fingerprint is a temperature-related shift of 2.3 d per decade advance in timing of spring events (Parmesan and Yohe, 2003). Flowering phenological data contributed to this global picture. The relationship between flowering and temperature data implies a slower mean rate of achievement of the chilling requirement (by 3–5 d since the 1980s) and a more rapid rate of completion of the heat requirement (by 10–13 d since the 1980s) (Fig. 4). A correlation between higher mean temperatures in February to April and earlier dates of full bloom has been detected since 1977 in the selection of apple varieties recorded at the UK National Fruit Collections, Brogdale (M Jeger, personal communication). There is a correlation between higher mean temperatures in February to April and earlier dates of full-bloom. A declining winter chill has been reported by Sunley et al. (2006) in their work on chill unit models, using raspberry and blackcurrant data from East Malling. They have discussed preliminary data suggesting the high chilling requirements (around 2500 h at <7.2 °C) of some blackcurrant cultivars are near the limits of being met by the UK climate.

**Grouping responses**

In one approach to defining a global fingerprint, Root et al. (2003) analysed spring phenological events by major taxa, classified as invertebrates, amphibians, birds, trees, and ‘other plants’, and singled out trees as statistically different from the rest with a mean shift of only 3 d earlier per decade as opposed to 5 d for the other groups. Thackeray et al. (2010) assessed phenological change for 726 terrestrial, freshwater, and marine taxa in the UK and found that the most rapid rate of change in the study period of 1976–2005, was in flowering, and fruiting dates of terrestrial plants, with flowering dates advancing particularly rapidly. Flowering phenological datasets too, reveal that some life-forms are more responsive than others to warming temperatures. Annuals have been found to flower an average of 10 d earlier than perennials and have more variable FFDs (Fitter et al., 1995; Fitter and Fitter, 2002). As groups, ‘trees’ and ‘perennials’ overlap and have a common characteristic of ‘indirect flowering’ responding to temperature over a prolonged period, such that warmer winters might be expected to reduce chilling effect and delay breaking of endodormancy. Whilst warmer springs could hasten flowering, the net effect is less than for species responding only to warmer spring temperatures. Flowering of Golden Delicious apple in France has advanced 7–8 d since the late 1980s (Legave et al., 2008). Modelling of flowering and temperature data implies a slower mean rate of achievement of the chilling requirement (by 3–5 d since the 1980s) and a more rapid rate of completion of the heat requirement (by 10–13 d since the 1980s) (Fig. 4). A correlation between higher mean temperatures in February to April and earlier dates of full-bloom. A declining winter chill has been reported by Sunley et al. (2006) in their work on chill unit models, using raspberry and blackcurrant data from East Malling. They have discussed preliminary data suggesting the high chilling requirements (around 2500 h at <7.2 °C) of some blackcurrant cultivars are near the limits of being met by the UK climate.

**Fig. 4.** Representation of time sequence of chilling and heat effects for ‘Golden Delicious’ apple trees in different locations and sub-periods (from Legave et al., 2008). Chilling accumulated from 22nd October of the year before (n–1) the flowering year (n). F1 date is the date of flowering stage when approximately 10% of flowers are open. Durations and chilling onset date estimated from chilling model simulation detailed in Legave et al. (2008). Reproduced from Legave et al. (2008) with permission from the Editor, Journal of Horticultural Science & Biotechnology.
It is apparent that species can differ markedly in their response to temperature. Research suggests, for example, that warmer summers would have opposing effects on *Daboecia cantabrica* and *Galanthus nivalis* (Harper and Morris, 2007) and that a general 1 °C warming predicts a delay of up to 6 weeks in flowering of *Petasites hybridus* but more than a 5 week advance in flowering of *Geranium robertianum* (Fitter et al., 1995). In addition, Fitter et al. (1995) found 24 species in their dataset which showed no significant relationship between flowering-time and temperature. Bradley et al. (1999) noted ‘responders’ and ‘non-responders’ in their data, classed by increases or lack of increases in earliness over 61 years of recording. These cases serve as a reminder that temperature is but one environmental parameter in flowering, and photoperiodic responses are also involved. There are also other potential non-climate related drivers of phenological change, such as population age structure or aquatic nutrient enrichment (see Thackeray et al., 2010).

Harper and Morris (2007) suggest that ‘functional groups’ of plants with shared characteristics could be identified and expected to react to climate change in a similar way. They used a provisional description of a ‘Mediterranean-type’ grouping as an example. (Plants included are not necessarily native to the region but appear to have adaptations to its climatic features). Characteristics of these plants are a relatively highly synchronized end to the reproductive phase in late spring/early summer, even though first flowering dates are highly variable across different species. It is proposed that the start of the reproductive phase in this functional group, which includes *Ulex europaeus, Viburnum tinus, Forsythia intermedia*, and *Cyclamen*, will be more responsive to climate change than the end of this phase (Harper and Morris, 2007). The approach advocated is to draw up groupings based on physiological properties. Correlation and regression analysis offers a way to identify such characteristics by discovering temperature-sensitive phases of the flowering process in different species (Harper et al., 2009).

**Life cycles and temperature**

In a theoretical approach to how temperature might affect the reproductive phase of plant development, it might be envisaged that specific events (e.g. FFD, seed set) could happen earlier or later, while life cycle phases (e.g. duration of flowering) might be shortened or prolonged to give an attenuated or extended aggregate life cycle. Alternatively the life cycle may retain its pattern and duration but shift temporally (Post et al., 2008; Steltzer and Post, 2009). Post et al. (2008) found evidence of some of these alterations in response to warming. In *Cerastium alpinum*, despite a shorter duration of the emergence phase, the aggregate life cycle retained its length. In *Salix glauca* and *Betula nana*, some or all phenological events were earlier and aggregate life cycles, shorter. Significantly altered durations of the reproductive phases of budding, flowering, and fruiting in response to experimental warming were found in winter annuals and perennials studied by Sherry et al. (2007). Of five winter annuals in the study, three showed shorter life cycles on warming (and two were unchanged) and of six perennials under the same conditions, three life cycles were longer, one shorter, and two unchanged. In some cases, even though the phenology of bud appearance was unaltered, the bud stage was prolonged, delaying fruiting and flowering (Sherry et al., 2007).

It is widely reported that temperature in the months prior to flowering correlates with flowering time (Sparks et al., 2000; Fitter and Fitter, 2002). Fitter et al. (1995) found that nearly 60% of those species in their study which flowered in January to April were affected by temperature two months before flowering and for summer flowering species, temperatures up to 4 months previously were important. Whilst the general trends are negative correlations, that is, warmer temperatures giving rise to earlier flowering, positive correlations with high temperatures in the previous autumn have also been found in both annuals and herbaceous and woody perennials (Fitter et al., 1995).

**Conclusion**

Flowering phenological datasets cover a wide range of species and locations. The existence of datasets spanning many years is testament to the commitment of recorders to capture flowering events. Flowering phenology is interdisciplinary, combining history, meteorology, seasonality, and plant physiology. Increasingly, it appears to focus on identifying trends that might help to provide a glimpse of the future in terms of the effects of climate change on plants. To date, those trends are largely quite generalized and from a plant physiologist’s perspective, it is often the anomalies that are most intriguing, offering potential insights into environmental response paths in flowering and inviting discussion as to why certain groups of plants may be responding differently to others. To allow a better understanding of the effects of changing climate, flowering phenological datasets need to include more flowering stages and records of flowering duration. In addition, recording and interpretation of climate data need to take full account of the developmental cycle underlying flower production.

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