FLOWERING AND CLIMATE CHANGE – PART II

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Part I of this paper appeared in *Sibbaldia* No.4. Part II is presented as follows:

Analysis of data from other studies of flowering and leafing phenology suggests that temperature and photoperiod can influence first-flowering date at up to nine developmental stages prior to flowering. On the assumption that not all species will be affected by environmental conditions at the same stages, it is predicted that there will be different groups of plants that can be expected to react in different ways to climate change. A provisional description is given of a group with ‘mediterranean-type’ phenology and extended flowering periods, which is expected to show extreme reaction of first-flowering date to climate change (warming winters). A second and related group is described without the extended flowering period.

INTRODUCTION

Part I of this article appeared in *Sibbaldia* No.4 (2006). It promised that Part II would describe two groups of plants – ‘summer-flowerless’ and ‘winter-flowerless’ – together with remarks on the likely effects of climate change in Scotland.

Unfortunately the material intended for Part II has mushroomed faster than it can be published. The intention now is to devote this part to the reasons why we believe there to be several functional groups of plants, each of which can be expected to react to climate change in its own characteristic way. There may be half a dozen or more of such groups that can be usefully distinguished. The remainder of this part will give a provisional description of two groups of summer-flowerless plants.

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4.1 FUNCTIONAL GROUPS

Fig. 1 summarises the results of a number of studies which show significant correlations or stepwise regression coefficients between first-flowering and first-leafing dates on the one hand and monthly mean temperatures on the other. (Henceforth the term ‘correlation’ will be used to cover both correlation and regression.) For each taxon the normal month of first flowering and first leafing is shown as a cell with a bold outline. All taxa from these studies have been included which show a significant correlation with temperature in the month of flowering/leafing or a preceding month. The deciduous trees and shrubs all leaf in April or in one case March, while first flowering ranges from December to September. Coefficients with statistical significance ($p<0.05$) are shown simply as ‘negative’ or ‘positive’ (the latter in grey cells); for the purposes of this analysis the actual values are not important.

The distribution of positive and negative correlations appears to be non-random. The most frequent effect is a negative correlation between first-flowering (33 taxa) or -leafing (13 taxa) date and temperature in the month of flowering/leafing and/or in one or more of the immediately preceding months. A ready explanation offers itself in so far as, within certain limits, development is generally accelerated by warmer conditions. In many cases this may be a straightforward consequence of the fact that most chemical reactions occur faster at higher temperatures (within the normal range of air temperatures). The common finding – in the project at the Royal Botanic Garden Edinburgh (RBGE) as well as other phenology projects – that spring-flowering plants are mostly beginning to flower earlier as winter temperatures rise is presumably an expression of these negative correlations.

While virtually all of the taxa in Fig. 1 show this negative correlation, rather fewer show a positive correlation with temperatures at some period 3–11 months before flowering (21 taxa) or leafing (7 taxa). A positive correlation means that higher temperatures are associated with later flowering or leafing. It should be noted that the date of the months showing positive correlation is not strongly correlated with the date of flowering. The positive correlations are concentrated in the period August–November, with only scattered examples earlier (May, July) and later (December, January).

Finally there is a group of negative correlations (10 taxa) in the period 6–14 months before flowering. They precede any months showing positive correlation, and are concentrated in the period April–June, with sporadic occurrences in August and September.

The positive correlations were first clearly demonstrated by Fitter *et al.* in an important study of native plants around Chinnor in Oxfordshire. They suggested that prolonged growth in autumn interferes in some way with reproductive development, and added that ‘the effect merits physiological investigation.’ More specifically we should like to suggest that there can be competition for resources between vegetative and reproductive development within the plant, such that the two functions respond differently to temperature. In this case, if higher temperatures at a given stage in development favour vegetative development over reproductive development, this could involve diversion of

	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
FLOWERING																			
Helleborus niger									**neg**										
Galanthus nivalis			neg						neg	**neg**									
Eranthis hiemalis									neg	**neg**									
Galanthus nivalis										**neg**									
Leucojum vernum					pos				neg	neg	**neg**								
Crocus aureus										neg	**neg**								
Corylus avellana		neg	neg					pos	neg	neg	**neg**								
Ranunculus ficaria									neg	neg	**neg**								
Tussilago farfara		neg.					pos		neg	neg	neg	☐							
Rhod. praecox 'Praecox'								pos		neg	neg	☐							
Narcissus pseudonarc.		pos								neg	neg	☐							
Amygdalus communis									neg	neg	neg	**neg**							
Anemone nemorosa										neg	neg	**neg**							
Pentaglottis sempervirens					pos					neg		☐							
Anemone nemorosa		neg.					pos			neg	neg	**neg**							
Brassica turnip					pos					neg	neg	**neg**							
Ribes rubrum									neg		neg	neg	**neg**						
Alliaria petiolata		neg.					pos	pos		neg	neg	neg	**neg**						
Cytisus scop. hybrids					pos						neg		☐						
Prunus padus												neg	neg	☐					
Syringa vulgaris purple												neg	neg	☐					
Aesculus hippocast.	neg.	neg.			neg.			pos				neg	neg	**neg**					
Crataegus sp		neg.										neg	neg	☐					
Cytisus laburnum											neg	neg	neg	☐					
Crataegus monogyna								pos			neg	neg	neg	**neg**					
Daboecia cantabrica				pos										☐					
Leucanthemum vulgare							pos				neg	neg	neg	**neg**					
Sambucus nigra												neg	neg		☐				
Antirrhinum majus							pos								☐				
Rosa canina		neg.									neg	neg	neg	neg	☐				
Photinia davidiana							pos								☐				
Calceolaria sp						neg	pos								☐				
Rubus sp							pos								☐				
Convolvulus sepium	neg.											neg	neg	neg	neg	☐			
Campanula rotundifolia										pos				neg	neg	☐			
Lilium candidum									pos			neg	neg		neg	☐			
Colchicum autumnale							pos	pos					neg					☐	
Hedera helix												neg	neg	neg	neg		neg	☐	
LEAFING																			
Crataegus sp						pos	pos			neg	neg	**neg**							
Acer pseudoplatanus											neg	neg	☐						
Aesculus hippocastanum					pos						neg	neg	☐						
Betula (pendula?)					pos						neg	neg	☐						
Sorbus aucuparia							pos				neg	neg	**neg**						
Carpinus betulus						pos				neg	neg	neg	☐						
Aesculus hippocastanum												neg	**neg**						
Tilia spp											neg	neg	**neg**						
Castanea sativa			pos								neg	neg	**neg**						
Acer (campestre?)											neg		**neg**						
Fagus sylvatica												neg	**neg**						
Quercus sp					pos						neg	neg	**neg**						
Fraxinus excelsior											neg	neg	**neg**						

Fig. 1 Statistically significant ($p<0.05$) correlations or stepwise regressions between first-flowering and first-leafing dates (normally occurring in the month outlined in bold) and mean monthly temperature in the same or preceding months. 'pos' – positive; 'neg' – negative. Data from Jilbert (2003), Roberts, Last & Kempton (2004), Sparks & Carey (1995), Sparks, Jeffree & Jeffree (2000).

resources from the latter to the former with a consequent retardation in flowering date. This explanation could be applicable to any plant, whether or not it has a strong chilling requirement.

Our hypothesis is prompted by the decoupling of the phenological behaviour of vegetative and reproductive shoots seen in some groups of plants. In *Colchicum*, for example, flowering occurs at a different time of year from the growing period. As a second example, even within a single species – such as *Scopolia carniolica* – some genotypes may regularly come into flower before leafing and stem elongation, thus flowering at ground level, while others regularly start to flower only after leafing and stem elongation are well advanced. It is almost as if the reproductive shoots are acting like parasites growing on the vegetative structure, and in this case it makes sense to consider the vegetative and reproductive shoots as competing for resources within the plant.

Chilling is itself a temperature effect, although it is not expected to appear in Fig. 1. Since chilling occurs over an extended period, it might be revealed by an analysis using an average winter temperature covering several months. In that case a positive correlation would be expected since, beyond a certain threshold, higher temperatures would interfere with chilling and so retard flowering if flowering occurs at all.

The early group of negative correlations in Fig. 1 may represent a temperature effect on an early stage in reproductive development, possibly in some taxa (such as Hazel (*Corylus avellana*)) the induction of reproductive development in the individual meristems.

Our analysis suggests that there may be up to four ways in which temperature can affect the date of first flowering, namely the three groups of correlations shown in Fig. 1 together with chilling. It is also known that some taxa are affected by daylength, which increases the list of environmental conditions controlling the timing of flowering to five. In addition, the lower part of Fig. 1 shows that vegetative growth is subject to two temperature effects; some species also have a chilling requirement, and some may be affected by daylength. These influences acting on the vegetative shoots on which flowers will later develop mean that, potentially at least, environmental influences acting on the vegetative shoot may ultimately affect flowering date. This brings the total number of possible developmental stages at which environmental factors might influence flowering date to nine, and there may be others.

It is likely that only a few of these would be significant in any given taxon, and it will be assumed that different combinations of environmental factors act on different taxa. To take an example from Fig. 1, it appears that *Daboecia cantabrica* is affected by higher July temperatures, which delay flowering, while *Galanthus nivalis* is affected by higher temperatures in June, which advance flowering. Thus a uniform warming of summer temperatures would be expected to produce opposite effects in the two species.

From this kind of consideration we expect different species to respond differently to climate change. There may be continuous variation between the extremes of strong retardation and strong advancement – to take just the example of first-flowering date.

We believe however that it is worth making an attempt to describe discrete groups of plants, which we call 'functional groups', each of which can be expected to respond in a characteristic way to climate change. We already have evidence, from the phenological observations made at RBGE since 2002, that some taxa are behaving differently, but only time will tell whether any functional groups we describe are in fact discrete, or instead merge into each other through a continuum of variation.

The main group selected for description in the remainder of this contribution comprises plants having what we are provisionally calling 'mediterranean-type' phenology. They have thrust themselves on our attention on account of the extreme reactions that some appear to be showing to warming winters in Scotland (although whether warming winters are the actual cause is a so far untested assumption). Our phenological data are not yet sufficient to base this classification of functional groups on detailed analysis, so it must be borne in mind that our description is provisional and relies largely on circumstantial evidence.

4.2 'MEDITERRANEAN-TYPE' PHENOLOGY: *CYCLAMEN*

The term 'mediterranean-type' phenology has been chosen to indicate that the plants in this group appear to be adapted to a Mediterranean climate of the cool moist/ warm moist/hot dry/warm moist type (see part I). However, by no means all species native to the Mediterranean area belong to this group, and some members of it are not Mediterranean plants.

The concept of 'mediterranean-type' phenology can best be introduced using a taxon that will serve as a 'type' of the group. The genus *Cyclamen* shows the main features we recognise in the group, and it has the added advantage of indicating how long-term adjustment to climate change may occur through evolution.

Fig. 2 represents data from a study in which *Cyclamen* plants were grown in an experimental garden in Montpellier with a view to comparing the foliage and reproductive phenology of 17 species in identical growing conditions (Debussche *et al.*, 2004). The foliage period – beginning and ending with 'first leaf unfolded' and 'last leaf withered' respectively – varies from 18 to 48 weeks. Of particular interest is the variance of the start and end dates respectively. 'First leaf unfolded' varies from week 26 to week 60 (numbering the weeks from 1 January at the beginning of a two-year period); the corresponding Julian dates are 182 and 421 (numbering the days through the two-year period from the same 1 January). That gives a range of 239 days (standard deviation (SD) 49.3 days). By contrast, the corresponding results for the 'last leaf withered' are week 65 to week 79, or Julian dates 452 to 551, giving a range of 99 days (SD 22.6 days). In other words, as can be seen in Fig. 2, the start date of the foliage period (the darker bars) is much more variable than the end date.

The relatively synchronised end date may reflect the adaptation of most cyclamens to the Mediterranean climate in which they grow. In warm conditions, and so long as

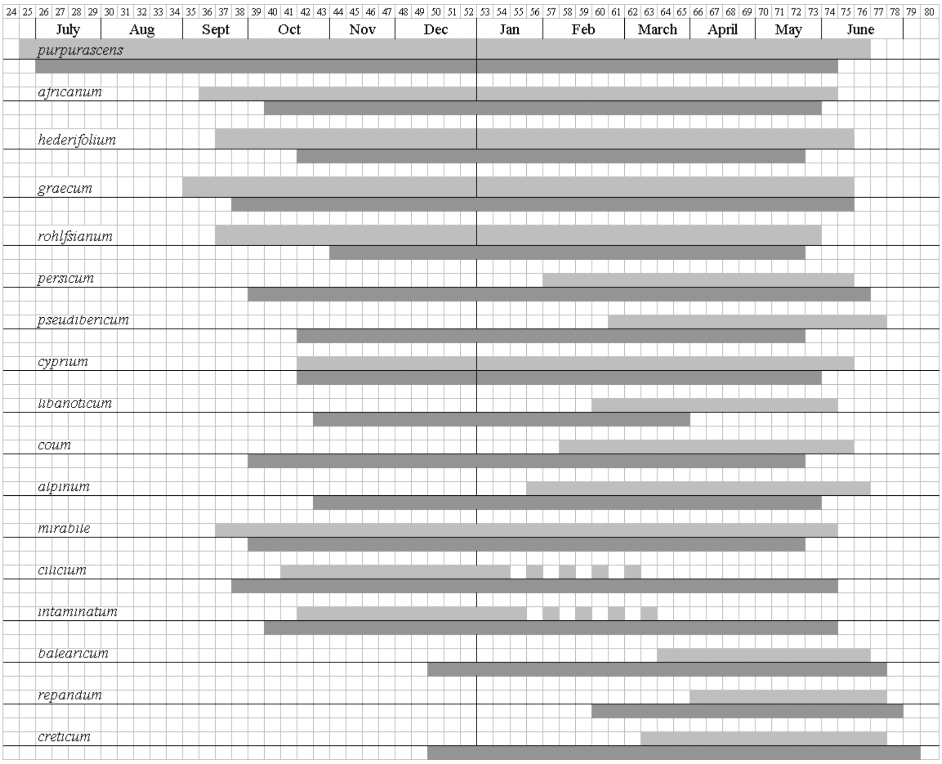


Fig. 2 Reproductive (upper pale grey bar) and foliage (lower dark grey bar) phenology of 17 species of *Cyclamen* grown in an experimental garden in Montpellier in 1999 and 2000. The reproductive period extends from 'first flower open' to 'maximum seed release', and the foliage period from 'first leaf unfolded' to 'last leaf withered'. Two species (*cilicium* and *intaminatum*) did not set seed during the trial. Weeks are numbered (top of the diagram) through the 24-month period. Data from Debussche *et al.* (2004)

soil moisture is sufficient, it would be advantageous to prolong the growing period and so accumulate maximum food reserves before summer dormancy begins at about the time that moisture becomes limiting. Selective pressure on the timing of the start of the growing period may be less intense if the start of the growing period is less critical to the plants' photosynthetic budget: the comparatively unfavourable growing conditions of autumn and winter may mean that the benefits of a long growing season are more or less balanced by the attendant risks of disease, predation and such like.

There is a similar pattern in the reproductive period, regarded as starting with 'first flower open' and ending with 'maximum seed release'. 'First flower open' varies from week 25 to week 66 (Julian dates 173–460), with a range of 287 days (SD 90.5 days); 'maximum seed release' varies from week 73 to week 77 (Julian dates 510–539), with a range of just 29 days (SD 8.7 days). The synchronisation of seed release is very striking, with the standard deviation only about one tenth of that of 'first flower open'. Again, this is clear from Fig. 2. Once more it appears that there are strong selective pressures operating in late spring and early summer, probably related to climate and involving the 'hidden phenology' reviewed in part I of this article. Detailed study would be required to unravel which physiological mechanisms and which selective pressures account for the apparent spring/summer synchronisation in both foliage and reproductive phenology. Synchronisation suggests a photoperiod effect, although such a hypothesis requires inter-year comparison within a single taxon rather than the inter-taxon comparison in Fig. 2.

While the end of the foliage and reproductive periods appear to be relatively constrained, the start of each period is much more variable between species. This is one of the main features characterising ‘mediterranean-type’ phenology. Moreover, in the group as a whole, the start date of flowering is expected to be unusually responsive to weather, and therefore may also react strongly to climate change. This possibility is illustrated in *Cyclamen* by *C. purpurascens*. Most other species are confined to the Mediterranean and Black Sea areas, and these can be assumed to correspond generally to the climate to which the ancestral *Cyclamen* was adapted – as concluded by Yesson & Culham (2006): they reconstructed the ‘ancestral’ climate as being similar to the one now found in parts of present-day eastern Greece and western Asia Minor.

The current range of *C. purpurascens* is Central Europe, which is well north of the Mediterranean zone, and subject to a continental climate. If it is assumed that its ancestor was a typical cyclamen adapted to a mediterranean climate, and that in changing its range it took in an area of more continental climate, in particular with less drought-prone summer, then comparison of *C. purpurascens* with the other species suggests how adaptation to the new climate occurred. It is noteworthy that the timing of seed release and end of the foliage period are typical of the genus. There is however a significant change in first-flower and first-leaf dates, both advancing by at least two months compared with other members of the genus, and in particular with the most closely related species (*africanum* and *hederifolium*: these three comprise the subgenus *Cyclamen*). Moreover, in its natural range, *C. purpurascens* sometimes retains leaves throughout the summer, with successive leaf generations overlapping, and there is no summer dormancy (Debussche *et al.*).

Similar comparisons could probably be made within other genera in order to trace the evolutionary history of populations as they have adapted in the long term to a new climate, especially where populations have been isolated on archipelagos such as the Azores.

As illustrated by *Cyclamen*, the defining characters of plants with ‘mediterranean-type’ reproductive phenology are a relatively tightly constrained termination of reproductive activity before mid summer, and a variable start date for the beginning of flowering after mid summer. The latter is expected to be much more responsive to weather and therefore also climate change. There is also the consequent potential for long flowering periods. Various examples from the RBGE phenology projects are now cited to illustrate how ‘mediterranean-type’ phenology is manifest in plants growing in Edinburgh.

4.3 OTHER EXAMPLES OF ‘MEDITERRANEAN-TYPE’ PHENOLOGY

(a) Gorse *Ulex europaeus*

Perhaps the clearest example of ‘mediterranean-type’ phenology in a British plant is Gorse *Ulex europaeus* (Fig. 3). Its flowering behaviour features prominently in folklore: ‘Whilst April and early May is the time when the gorse is in its full beauty, it starts flowering in February, and odd flowers may be found at almost all times – a characteristic on which is based the country saying, “When furze is out of bloom, then is kissing out of fashion”.’ (Bean 1989). *Flora Britannica* also mentions flowering as occurring ‘sporadically throughout the year’ (Mabey 1996). Cavers is rather more accurate: ‘flowers in great abundance in spring and early summer; and a second crop of blossoms follows in autumn, lasting until nipped by early frosts. In mild winters the last of the autumn flowers welcomes the first flower of the following spring’ (Cavers 1913).

Fig. 4 shows the flowering periods for all the plants monitored at RBGE. First-flowering dates range from week 36 to 62 (SD 9.8 weeks); last-flowering dates range from week 22 to 33 (SD 3.0 weeks). Thus, as in the case of *Cyclamen*, first-flowering dates are far more variable than last-flowering dates (or seed-dispersal dates in the case of *Cyclamen*, which generally has a short flowering period).

Rather than flowering occurring at almost any time of year, it appears to cease rather abruptly before mid summer. It remains to be discovered whether this is correlated with other phenological variables, such as shoot development, and/or whether it is more

Fig. 3 *Ulex europeus*, perhaps the clearest example of ‘mediterranenan-type’ phenology in a British plant.

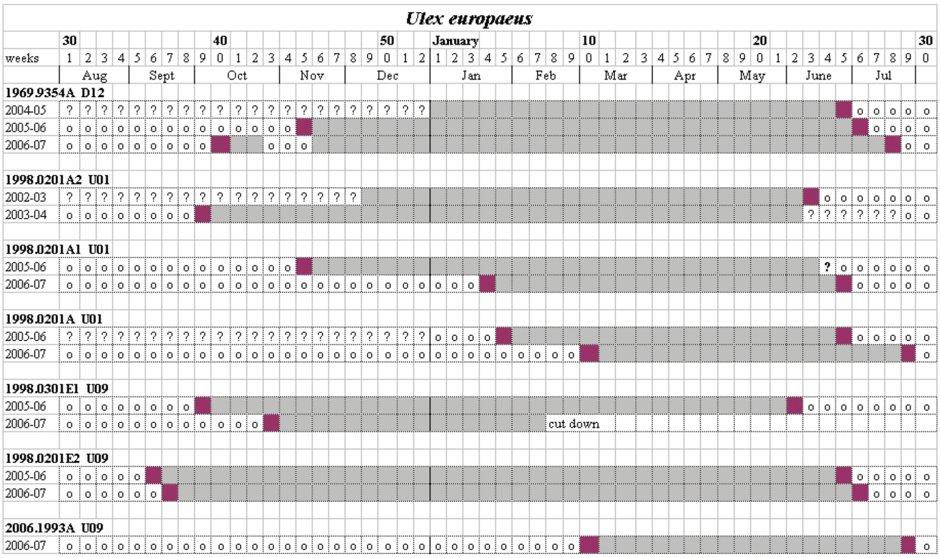


Fig. 4 Flowering periods of *Ulex europaeus* at RBGE. The individual plants are listed by their accession numbers (left). Question marks show where the plant was not being monitored; ‘o’ means no flowers open, and grey squares mean open flowers present. First- and last-flowering dates are shown as dark grey squares. The row below the ‘weeks’ row shows the months only approximately.

closely related to other reproductive functions such as seed dispersal. In Gorse this occurs by explosive dehiscence of pods in sunny weather, and it is likely that it is timed to occur at a particular time of year (summer) when weather is suitable. These questions concern the ‘hidden’ aspects of phenology, as discussed in Part I of the article.

Interestingly, this species illustrates two of the flowering patterns expected in plants within the ‘mediterranean-type’ group. Recently at RBGE flowering has occurred strongly throughout the winter season, with hardly any ‘peaking’ in spring. On the other hand, as Cavers noted, in climates involving cold winters Gorse is capable of two flowering periods, best interpreted as a potentially continuous flowering period interrupted by cold weather. We have found no evidence that Gorse, in Edinburgh, can flower at any time of the year: it seems to be a truly summer-flowerless plant, with usually no flowering from late July to early September. In 2007 about a quarter, and possibly up to a third, of bushes in Holyrood Park in Edinburgh still had a few flowers in mid July, but it is not known whether this happens every year, or is anomalous and possibly due to the exceptionally wet June in 2007.

(b) Laurustinus *Viburnum tinus*

The natural range of this species is the European Mediterranean, Lebanon, North Africa, and the Azores and Canary Islands. The literature gives the following flowering periods: in the Mediterranean area, January-June (Schönfelder & Schönfelder 1990; McMurtrie 1997); in the Iberian Peninsula, February-June (Ceballos *et al.* 1980); in France, October-June

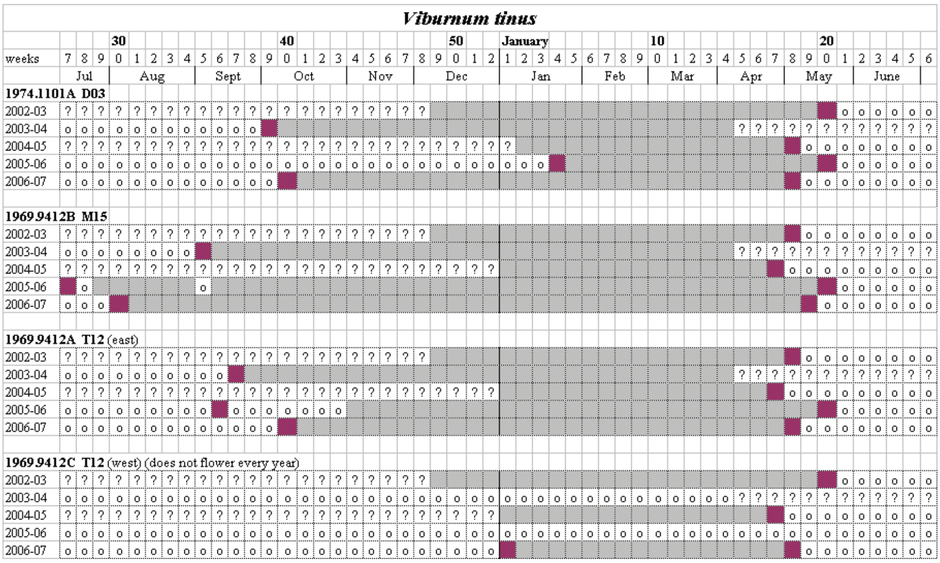


Fig. 5 Flowering periods of *Viburnum tinus* at RBGE. (For explanation, see Fig. 4)

(Guinochet & de Vilmorin 1984), or October-November (Guittonneau & Huon 1983). The subspecies *subcordatum*, endemic to the Azores, flowers there April-June (Schäfer 2002), and ssp *rigidum* on the Canaries from March to May (Kunkel & Kunkel 1974). In the Lebanon it flowers from February to April (Tohme & Tohme 2002).

The literature suggests a pattern similar to that of Gorse, in other words with very variable first-flowering dates but with flowering ending in a more synchronised fashion (often in June). This pattern also appears in our Edinburgh records (Fig. 5). Flowering begins in weeks 27-56 (SD 9.1 weeks), and ends in weeks 17-20 (SD 1.2 weeks) – well before June. Although there are few measurements to go on, the first-flowering dates appear to vary widely both within and between individual plants.

Bean interestingly comments that 'No doubt there are […] physiological variations, some races being adapted to the Mediterranean type of climate, others needing moister conditions and perhaps nearer to *V. tinus* as it existed in earlier epochs, when the climate of the Mediterranean region was rainier than it has been since the Ice Age' (Bean 1989). So here is another group of plants whose phenological variation through their geographical range might offer insight into how plants respond to climate change through evolution.

(c) <u>Spurge Laurel</u> *Daphne laureola*

Spurge Laurel ranges from Britain, Belgium and western Germany through western and southern Europe to Spain, Corsica and Macedonia. It also occurs in Asia Minor, North Africa and the Azores.

In Britain, flowering is generally recorded as March-April, although in the 19th

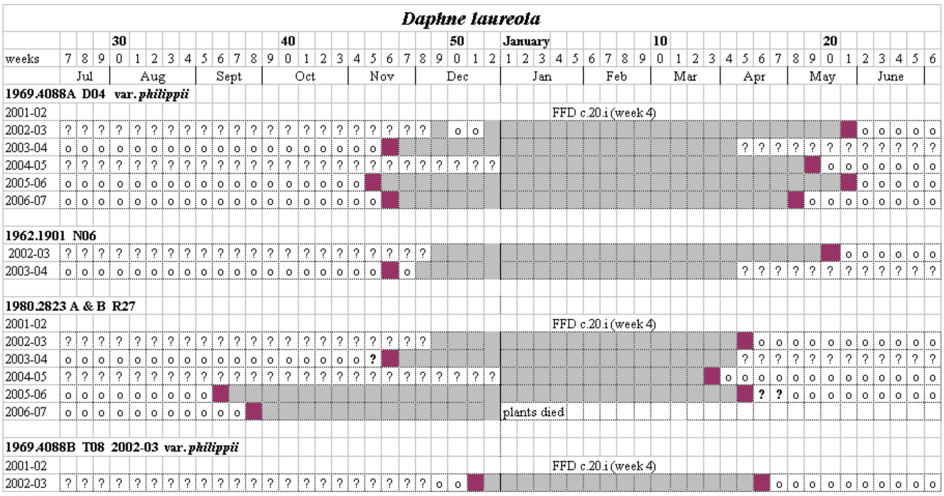


Fig. 6 Flowering periods of *Daphne laureola* at RBGE. (For explanation, see Fig. 4)

century flowering sometimes started earlier, with February-April being recorded by Babington (1843) and January–April by Hooker (1884). *Flora Britannica* notes that ‘It also flowers in winter, […] sometimes as early as mid-January’ (Mabey 1996). The cultivar ‘Margaret Mathew’ is often in flower in December (White 2006).

Flowering occurs in the Mediterranean area from February to May (Schönfelder & Schönfelder 1990), or from January or February to May or June in the Iberian Peninsula (Lopez 2002). This apparent tendency to continue flowering later in the south is taken to an extreme in the Azores, where flowering is recorded as June-July (Schäfer 2002). This may be compared with Gorse on the Azores, where it also continues flowering very late, from February to August (Schäfer 2002). Both species may have adapted there to a non-Mediterranean climate.

Generally speaking Spurge Laurel seems to have a fairly typical ‘mediterranean-type’ phenology (the Azores excepted), with admittedly a somewhat flexible end date as well as start date. The flexibility in the end date is reflected in the Edinburgh records, as seen in Fig. 6. While each individual plant is fairly consistent in its last-flowering date, there is considerable variation between plants.

The monitored plants appear to show considerable variation in the start date. Three of the plants were being monitored in early 2002, just as the Daily Project was being set up, and all three were noted as beginning to flower on about 20 January. This was in line with expectations, but it cannot be ruled out that there were flowers earlier, which had suffered from frost and had dropped off. These first-flowering dates cannot therefore be taken too seriously, since they are not supported by a long preceding run of reliable negative records.

In later years flowering has begun much earlier, commonly in weeks 45 and 46 (early November), but even in weeks 36 and 38 (early September). Like Gorse and Laurustinus, Spurge Laurel is capable of a very long flowering season, the maximum in Edinburgh so far being 32 weeks. From casual observation it seems that individual flowers last for many weeks, if not the whole of the flowering season; this is not true of Gorse, which maintains its long flowering season by sequential appearance of rather short-lived flowers. In 2007 one plant began flowering in week 31.

(d) *Pieris japonica*

As is clear from its Latin name this is not a Mediterranean plant, but is native to central and southern Japan, occupying sunny hills in Honshu, Shikoku and Kyushu (Ohwi 706). The climate is also far from being mediterranean, since humidity is high all year round, rain is at a maximum in June-July and in September, and winters can be much colder than in the Mediterranean (Arakawa 1969, vol.8). Flowering in Japan occurs in April–May (Ohwi 1965), as compared with March–April in the United Kingdom (Bean 1989; Chittenden 1981).

Nevertheless *Pieris japonica* seems to share the essential features of 'mediterranean-type' phenology. Both between and within plants there is wide variation in first-flowering dates (weeks 32–61, SD 19.9 weeks), with the exception of accession no.1934.0233A, which has remarkably consistent start dates. End-of-flowering dates are less variable (weeks 11–22, SD 3.4 weeks), but are reasonably synchronised within plants except for accession no.1969.5731A. (See Fig. 7)

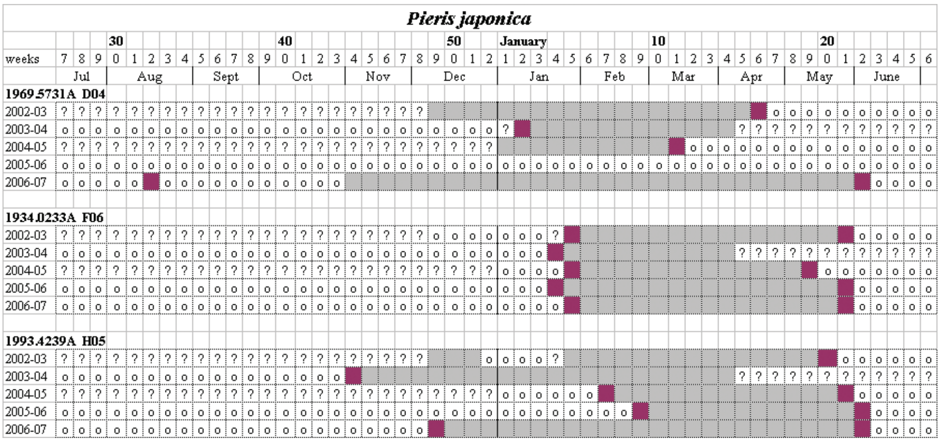


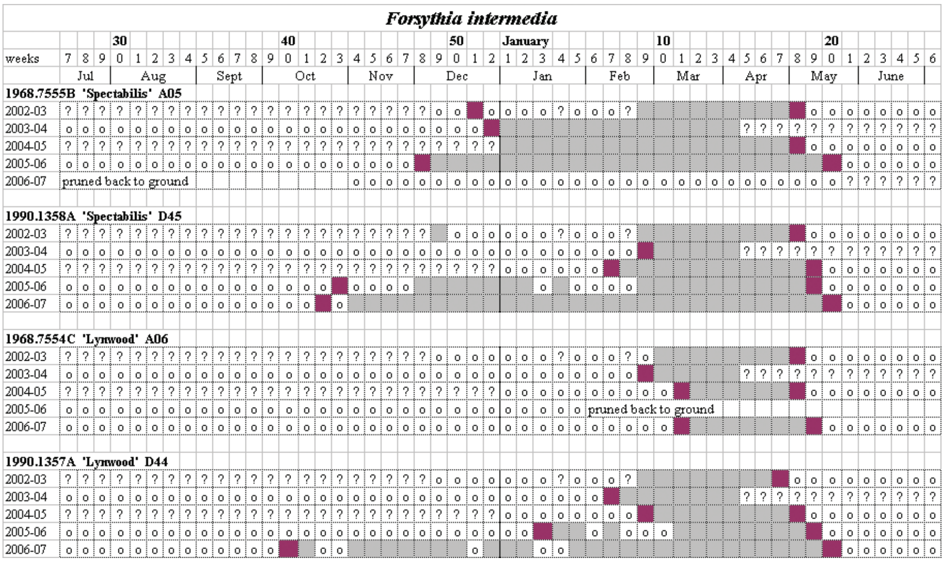
Fig. 7 Flowering periods of *Pieris japonica* at RBGE. (For explanation, see Fig. 4)

(e) *Forsythia x intermedia*

The parents of this hybrid are *F. suspensa* and *F. viridissima*. Both have wide ranges in central and eastern China, where the climate is characterised, as in Japan, by the heaviest rains occurring in the summer period (June-August, the summer monsoon) (Arakawa 1969). In China both species flower in March-April (*Flora of China*), as compared with March in the United Kingdom (Chittenden 1981).

Here again, the hybrid shows the ‘mediterranean-type’ pattern, with very variable start dates (weeks 40–63, SD 8.2 weeks) and rather well synchronised end dates (weeks 17–20, SD 0.9 weeks).

In both *Pieris japonica* and *Forsythia* x *intermedia* the early part of the flowering period can involve only part of the plant – sometimes just one branch in the *Pieris* – or sporadic flowering. So these patterns can be quite consistent with peak and/or mass flowering occurring as usual in a short period in spring. Nevertheless the variation in the first-flowering date is of biological importance in that it indicates that the plant is capable of flowering sometimes very early, and may be especially responsive to meteorological conditions. (See Fig. 8).



Forsythia intermedia

				30										40										50			January									10										20						
weeks	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
	Jul			Aug					Sept				Oct					Nov				Dec					Jan					Feb				Mar				Apr				May				June				
1968.7555B 'Spectabilis' A05																																																				
2002-03	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	o	o	■	o	o	o	o	?	o	o	o	?	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o	o
2003-04	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	?	?	?	?	?	?	?	?	?	?	?	?
2004-05	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o	o
2005-06	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o
2006-07	pruned back to ground																	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	?	?	?	?	?	?
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2005-06	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	o	o	o	o	▒	▒	▒	▒	▒	▒	▒	o	▒	o	o	o	o	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o
2006-07	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	o	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o
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2003-04	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	?	?	?	?	?	?	?	?	?	?	?	?
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2005-06	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	pruned back to ground																				
2006-07	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o
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2003-04	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	▒	▒	?	?	?	?	?	?	?	?	?	?	?	?
2004-05	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	o	o	o	o	o	o	o	o	■	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o	o
2005-06	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	▒	o	▒	o	o	o	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o	o
2006-07	o	o	o	o	o	o	o	o	o	o	o	o	o	■	▒	o	o	▒	▒	▒	▒	▒	▒	▒	o	▒	▒	▒	o	o	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	o	o	o	o	o	o

Fig. 8 Flowering periods of *Forsythia* x *intermedia* at RBGE. (For explanation, see Fig. 4)

(f) *Jasminum nudiflorum*

The sixth example is another Chinese plant – from central China, north-west Yunnan and eastern Tibet. The *Flora of China* (Wu & Raven 1996) appears to be incorrect about flowering dates in both the Chinese and English editions, describing var. *nudiflorum* as flowering in June, whereas flowering specimens in the RBGE herbarium were collected in February and March. These dates are comparable with November-February, given by Bean (1989) and Chittenden (1981). The alpine var. *pulvinatum*, on the other hand, flowers in China from April to September (Wu & Raven 1996, and RBGE herbarium specimens). This diversity of flowering phenology within one species would merit further investigation.

In Edinburgh, with one exception, the end dates are well synchronised (weeks 16–17, SD 0.5 weeks). There is a somewhat larger variation in start dates (weeks 35–43, SD 2.5 weeks), though with apparently little variation between plants. The exception is the

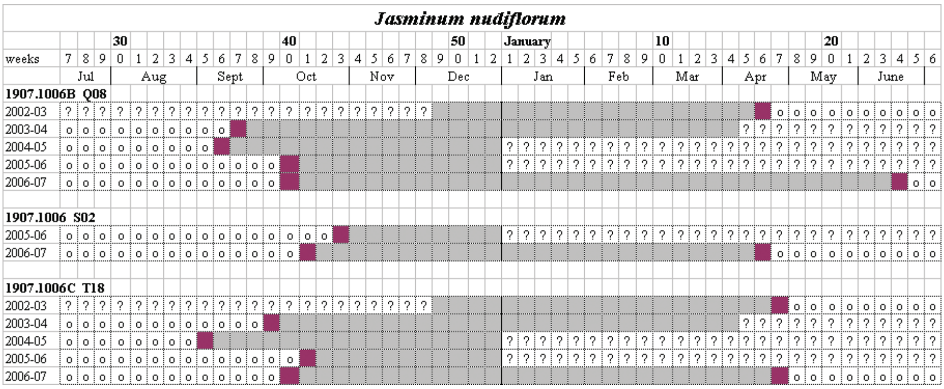

Fig. 9 Flowering periods of *Jasminum nudiflorum* at RBGE. (For explanation, see Fig. 4)

plant in bed Q08: the anomalous extension of the flowering period in 2007 may find an explanation in the fact that it was pruned back lightly in early May, after which flowering continued sporadically, with at most six flowers open at any one time. Including this anomalous flowering, the standard deviation of last-flower date becomes 3.27 weeks.

It is not certain that this species should be regarded as having ‘mediterranean-type’ phenology, but it warrants further study.

If it is accepted that the three Asian taxa are sufficiently similar in their flowering phenology to be grouped with the European species, it raises the interesting question as to how plants with such similar phenological behaviour can come from countries with such different climates. What does this tell us about the triggers being used to determine the timing of flowering, and also the adaptive significance of the behaviour in such different climates? (See Fig. 9).

4.4 TWO MORE CASES: ANOTHER FUNCTIONAL GROUP?

The six examples described above comprise plants that have extended flowering periods at an individual level as well as at the population level. These periods end in a more or less synchronised manner both within and between plants, while their start dates are far more flexible, suggesting the possibility of particular responsiveness to weather and therefore also climate change. It is possible that all these plants owe their phenological characters to the common features of (a) having an extended developmental period of the reproductive shoots, (b) the rate of this development being mainly dependent on temperature, (c) having little or no chilling requirement, and (d) end of flowering being probably dependent on photoperiod.

Two further species have also shown unusually variable first-flowering dates. Moreover these dates have advanced in a rather spectacular manner since 2002, possibly in response to the warmer winters experienced in the Edinburgh area. Data on these species have been collected only through the Daily Project, which does not measure duration of flowering, so that unfortunately diagrams of the kind given earlier cannot be constructed.

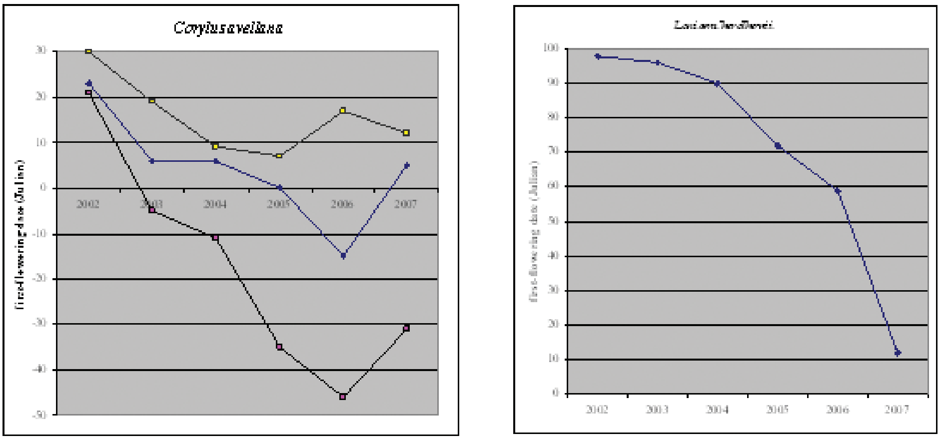

Fig. 10 First-flowering dates of *Corylus avellana* and *Lonicera korolkowii*.

Fig. 10 shows the first-flowering dates of Hazel *Corylus avellana* and a Central Asian honeysuckle *Lonicera korolkowii* as Julian dates. Positive values are days after 31 December, while negative values are counted backwards from 31 December. Each line represents an individual bush, and it can be seen that extremely rapid advancement has occurred in the honeysuckle and one of the hazels. (Interestingly the flowering of the latest hazel appears to have been delayed by the cold spring of 2006, which occurred in late January and February, while the effects of the same cold spell may explain the delayed flowering in 2007 of the two earlier-flowering bushes, which began flowering in 2006 before the cold spell.) The earliest-flowering hazel advanced on average by 16.7 days/year from 2002 to 2006, and the honeysuckle by 17.2 days/year from 2002 to 2007 (it is not clear whether it was affected by the cold period in 2006).

Although systematic observations were not made on the last-flowering dates, it is unlikely that either species has such an extended flowering period as the six examples discussed earlier. In fact the earliest-flowering hazel bush (1903.1005A) had completed flowering in 2007 earlier in the year than its first-flowering date in 2002. It is probable that, unlike the plants with typical ‘mediterranean-type’ phenology, the relatively short flowering period advances as a whole with first-flowering date (in this, resembling the cyclamens). These taxa appear to share the characteristics of the ‘mediterranean-type’ group as listed in the first paragraph of this section, and differ from them mainly in the lack of extended flowering periods with more or less synchronised end dates. It would be interesting to have measurements of the dates of fruit ripening.

4.5 DISCUSSION

Figs. 4–9 are based entirely on first- and last-flowering dates, and presence or absence of flowers in each week. It is unfortunate that they do not give any indication of the number of flowers open in each week. So a single extended flowering period as depicted in these diagrams may cover a variety of situations. At one extreme is *Forsythia* x *intermedia*,

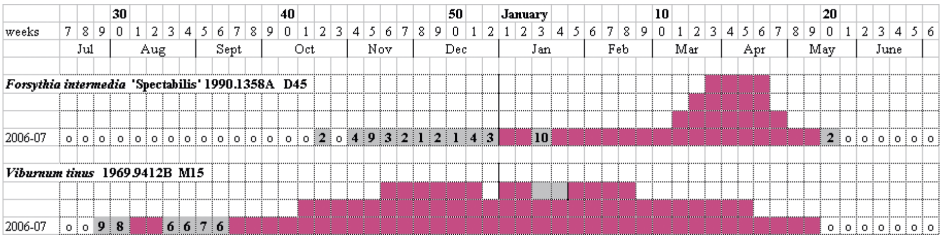

Fig. 11 Semi-quantitative diagrams of the flowering periods of two species in 2006–07. Dark grey squares form a histogram in which column height represents number of flowers on a scale 1–4, where ‘1’ = 0-25% of ‘maximum flowering’, ‘2’ = 25-50%, &c. A pale grey square on top of two dark grey squares represents an intermediate score ‘2–3’. Numbers in pale grey squares show the number of flowers (*Forsythia*) or inflorescences (*Viburnum*) where there are no more than 10.

which may flower for weeks only sporadically, with very few open at any one time. At the other extreme are *Ulex europaeus* and *Viburnum tinus*, which flower massively and steadily for months on end.

Semi-quantitative methods are now being used in the Weekly Project and the new Rhododendron Project to give an idea of when peak and/or mass flowering occur. Examples of the two extreme types are shown in Fig. 11.

While the variable first-flowering date of plants like the *Forsythia* do not appear to affect the more or less symmetrical development of flowering in the normal spring flowering period, in other plants most of the flowering period may be occupied by an extended mass flowering. Clearly it is of horticultural interest to know what ‘shape’ the flowering period takes. It will also be of interest to see how this ‘shape’ develops with climate change. Will, for instance, the *Forsythia*-type flowering period gradually change to the *Viburnum* type? Or will the symmetrical bell-shaped curve migrate to the left, meaning that the main flowering period occurs earlier? Or will a second and smaller bell-shaped curve develop in autumn, as already happens in plants like *Rhododendron decorum* and formerly occurred in *Ulex europaeus*? We now have methods which will answer these questions, and it is hoped to report results in a later article.

The period over which flowering extends has obvious implications for the quality of flowering. If there is a fixed number of flowers, all present as buds before the first-flowering date, and if each opens for a fixed time, then extension of the flowering over a longer period would be expected to lead to a decline in flowering quality in some plants: peak flowering would disappear and would be replaced by mass flowering in which only a proportion of flowers are open at any one time. However, where flower longevity is variable, and the flowers last virtually the whole of the flowering period, as in *Daphne laureola*, it may be that a longer period can only be good news.

Another consideration is the possible decoupling with foliage phenology. In *Corylus avellana* and *Forsythia* x *intermedia* flowering now sometimes begins before the leaves have fallen in the previous season, and these flowers can be considered, from a horticultural point of view, to be ‘wasted’ in so far as they are not easy to see. Yet a further possibility is that flowers opening in winter may last longer, either owing to cooler temperatures or because they take longer to be pollinated (in the case of species where pollination influences flower longevity).

To sum up, we are provisionally describing a functional group of plants with 'mediterranean-type' phenology. It is characterised by relatively invariable end-of-flowering dates in late spring or early summer, variable first-flowering dates, and the potential for extended flowering periods. They have the potential to be sensitive to climate change, and in particular to warmer winters. These species could be of particular interest to horticulturalists, in so far as they may increasingly provide colour in the winter garden, and to climatologists, in that they may be very sensitive indicators of climate change. *Erica arborea* and *Omphalodes verna* may also belong to this group.

Corylus avellana and *Lonicera korolkowii* may form the nucleus of a related group, differing mainly in the relatively short flowering period and lack of synchronised end date.

At present rather little is known about the 'hidden phenology' of these plants, but when enough data have been collected it is intended to use them for the kind of analysis summarised in Fig. 1 with a view to finding which stages in reproductive development are responsive to temperature. It must be stressed that this article describes 'work in progress', and that its conclusions are provisional. At the same time the patterns already emerging give us grounds for hoping that our approach will be productive and that phenological research will be useful to both horticulture and climatology.

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