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Rapid Changes in Flowering Time in British Plants

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The average first flowering date of 385 British plant species has advanced by 4.5 days during the past decade compared with the previous four decades: 16% of species flowered significantly earlier in the 1990s than previously, with an average advancement of 15 days in a decade. Ten species (3%) flowered significantly later in the 1990s than previously. These data reveal the strongest biological signal yet of climatic change. Flowering is especially sensitive to the temperature in the previous month, and spring-flowering species are most responsive. However, large interspecific differences in this response will affect both the structure of plant communities and gene flow between species as climate warms. Annuals are more likely to flower early than congeneric perennials, and insect-pollinated species more than wind-pollinated ones.

Climatic warming has been shown to alter the timing of important developmental or behavioral events in birds (1, 2), plants (3, 4), amphibians (5), and insects (6, 7); most studies have involved single or small sets of species. The timing of flowering is a key event for plants. It affects their chances of pollination, especially when the pollinator (for example, an insect) is itself seasonal, and determines the timing of seed ripening and dispersal: Fruit set may be pollen limited at both the start and end of the flowering period (8). Flowering time also influences animals for which pollen, nectar, and seeds are important resources (9), and earlier flowering also implies earlier activity in other processes (leaf expansion, root growth, nutrient uptake) that are important for niche differentiation among coexisting species (10, 11) and so will alter competitive interactions between species. Large changes in flowering date will therefore disrupt ecosystem structure.

We have analyzed the first flowering date for a set of 557 plant species, recorded by a single observer (R.S.R.F.) over a period of 47 years in the vicinity of a single locality in south-central England (12). We previously analyzed data for 267 of these species 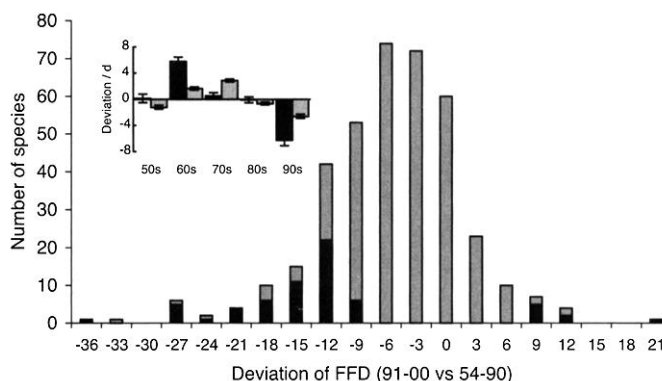for the period 1954–1989 (13), and the criteria used here were the same, except that species used were those for which data were available for more than half the years (i.e., >23) with at least four records in the period 1991–2000, giving a total of 385 species (14) [table S1 (15)].

The first flowering date (FFD) of these 385 species for the decade 1991–2000 was on average 4.5 ± 0.40 (mean ± SE; modal value = −4.0) days earlier than that for the period 1954–1990 (Fig. 1); 60 (16%) were significantly earlier ($P < 0.05$; Student's t test), with a mean deviation of −15 days. Ninety-four species (24%) had a deviation in mean FFD >0; in other words, these species showed later flowering in the 1990s than previously, but the deviation was only significant for 10 species (3%). A few species showed extreme and significant deviations in the 1990s from the long-term mean, including Lamium album (Lamiaceae; −55 days: 18 March in 1954–1990 versus 23 January in 1991–2000) and Cymbalaria muralis (Scrophulariaceae; −35 days: 15 April versus 11 March). L. album is a species that used occasionally to flower through the winter and now routinely does so; earlier floras give the FFD as March (16), April (17), or May (18, 19). One species, the introduced shrub Buddleja davidii (Buddlejaceae), was strongly delayed in the 1990s, by 36 days compared with the 1954–1990 mean. These data are similar to, but more marked than, those seen in a study of 100 species over 30 years (1970–1999) in Washington, DC (20): 89% were advanced and 11% retarded, with an overall mean advancement of 2.4 days in 30 years, and extreme shifts of −46 to +10 days.

FFD showed little variation in flowering time during the first four decades of the period studied (Fig. 1, inset), but there has been a major shift in FFD since the 1980s. We have explored the impact of climatic variables on these changes by using the data from the Central England Temperature (CET) Record (21) and the North Atlantic Oscillation (NAO) (22, 23). Correlations with CET data were stronger than with NAO data in all cases. We grouped species by the month of their mean FFD and determined

Fig. 1. Frequency distribution of deviations in FFD in the decade 1991–2000 from the mean over the period 1954–1990. Categories are 3-day periods; numbers represent the lower bound of each category. Solid values of the column represent species for which the deviation was significantly different from zero. Negative values indicate earlier flowering than the 1954–1990 mean, positive values later flowering. Two species with extreme deviations [L. album (−55 days) and B. davidii (+36 days)] have been omitted for clarity. (**Inset**) Mean deviation of the FFD for each decade from the long-term mean (1954–2000); solid bars represent species flowering in spring (January to April); open bars denote summer-flowering species (May to August). Error bars represent standard errors.

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Table 1. Regressions of mean FFD deviation (1991–2000 versus 1954–1990) of species flowering in different months on mean monthly temperature. The month giving the best relation with FFD deviation was determined by calculating the correlation matrix of FFD deviation with mean temperature of all 12 months before the month of FFD. Regression equations were then calculated between the mean FFD deviation and the mean temperature for that month, with data for all 47 years (1954–2000). The regression coefficient b represents the number of days by which flowering was advanced (negative) by a 1°C increase in mean monthly temperature. Species are grouped according to their mean FFD (1954–2000). All regression equations had F-values >30 and all were significant at $P < 0.001$. Too few species had a mean FFD in either January or August to be included in the analysis.

Month of mean FFD	No. of species	b	R^2 (%)	Month for which mean temperature was used as independent variable
February	12	−6.0	61	January
March	22	−4.5	42	February
April	63	−4.3	53	March
May	105	−2.0	50	February
June	108	−1.7	43	February
July	67	−2.8	41	June

the correlation between mean deviation in FFD of each group and mean monthly temperature of each of the previous 12 months. Regression of mean FFD deviation on the best-correlated month showed that for species flowering in spring (February, March, and April), FFD was more than 4 days earlier for each degree °C increase in the temperature of the previous month (Table 1). For species flowering in May and June, February temperature had the greatest effect, but these species are less sensitive to temperature than spring-flowering species.

It is difficult to detect systematic or biological patterns in most phenological data sets, because their small size precludes phylogenetically robust analyses. We used various statistical tests and phylogenetically independent contrasts (PICs) to look for evidence that phylogeny, life-form, geographical distribution, or pollination mechanism can explain the very large variation in sensitivity of FFD among species seen in Fig. 1. There was no taxonomic pattern to the data above the genus level; in the 13 families (in two subclasses) that were represented by at least two genera each with more than one species, differences among subclasses, superorders, and families were not significant (24).

Of the 57 species flowering significantly earlier in the 1990s, 26% were woody, compared with 11% of the entire set of 385 species, a significant discrepancy ($\chi^2 = 7.18, P < 0.05$). However, 64% of the woody species in the set flowered before 1 May, as compared with 24% of nonwoody species, suggesting that this pat-

Table 2. Deviations of FFD in 1991–2000 from the 1954–1990 mean in the 15 genera containing both annuals and perennials. Biennials have been classified as annuals when they are typically short-lived, sometimes flowering in their first year, following Clapham et al. (19). For analysis of phylogenetically independent contrasts (PICs), the mean value for each group of species within a category (genus and life-form) was used.

Genus	Annuals	FFD deviation	Perennials	FFD deviation
Alopecurus	myosuroides	−4	geniculatus	−5
			pratensis	−4
Bromus	hordeaceus	−3	erectus	−1
Cardamine	hirsuta	−25	pratensis	−9
Cerastium	glomeratum	−13	fontanum	−6
			tomentosum	−3
Crepis	vesicaria	−7	biennis	0
	capillaris	0		
Euphorbia	exigua	−10	amygdaloides	0
	helioscopia	−32		
Fallopia	convolvulus	−4	japonica	+4
Galium	aparine	−7	odoratum	−1
			saxatile	−10
			uliginosum	−7
Geranium	dissectum	−3	phaeum	−7
	rotundifolium	+6	pyrenaicum	−10
	robertianum	+1		
Hordeum	distichon	−3	secalinum	−3
	murinum	−16		
Melilotus	albus	−2	altissimus	+4
			officinalis	−1
Myosotis	arvensis	−10	scorpioides	−4
			sylvatica	−11
Sonchus	asper	−11	arvensis	−7
	oleraceus	−12		
Trifolium	campestre	+3	medium	−1
	dubium	0	pratense	−1
			repens	−3
Veronica	arvensis	+5	beccabunga	−2
	hederifolia	−18	chamaedrys	+3
			filiformis	−2

tern occurred because early-flowering species were most affected by warming (Fig. 1, inset). Annuals flowered 10 days earlier than perennials (25) but did not differ in mean deviation. Nevertheless, in a PIC analysis of the 15 genera with both types, annuals showed a greater (−7.8 days) deviation in FFD in the 1990s than perennials (−3.2 days) in 12 genera (Table 2) ($t_{21} = 2.12, P = 0.046$).

Both pollination mechanism and geographical distribution explain part of the variation. The index of geographical distribution used was the N-S index from the Ecological Flora Database (26). Both the mean FFD for the period 1954–2000 ($r_{383} = 0.24, P < 0.001$) and the absolute deviation of the N-S index from the mean value for the full set of species ($r_{354} = 0.16, P = 0.002$) were correlated with the deviation; the further the center of the distribution of the species is from the locality, the less likely it therefore is to respond to warming by earlier flowering (27). Both variables (mean FFD and N-S index) were used in an analysis of covariance to test the influence of pollination mechanism (15). Insect-pollinated species showed a significantly greater deviation than wind-pollinated ones (−4.8 days versus −3.5 days), and there was a significant interaction between pollination

mechanism and mean FFD: Whereas the deviation in FFD for wind-pollinated species was unaffected by flowering season (Fig. 2A), insect-pollinated species that flowered early were much more sensitive to warming than those that flowered later (Fig. 2B). This distinction suggests that responsiveness is a character that has itself responded to selection.

These data confirm studies (4, 13, 28, 29) suggesting that FFD is sensitive to temperature. Some of those studies have shown a temporal trend, implying that climate warming is changing phenology progressively. In an analysis covering all of Germany in the period 1951–1996 (30), early spring phenophases advanced by up to 6 days in the second half of the period (1974–1996), a slower rate than we observed, whereas olive phenology in the Mediterranean has advanced by about 6 days per °C, comparable to our own findings (31). Our data show that a powerful climate-warming signal has become established during the 1990s, the warmest decade on record. Temperature (or possibly a climate variable correlated with temperature, such as sunshine hours) is a key determinant of flowering time: Recent rapid shifts in FFD coincide with the marked warming identifiable in the CET record since about 1975. The lack of a

Fig. 2. Relation between mean FFD deviation (1991–2000 versus 1954–1990) and the long-term mean FFD (1954–2000) for (**A**) wind-pollinated (anemophilous) species and (**B**) insect-pollinated (entomophilous) species. The fitted regression line in (B) is the deviation = (0.063 × mean FFD) − 14.1 ($F_{1,290}$ = 30.55, $P < 0.001$).
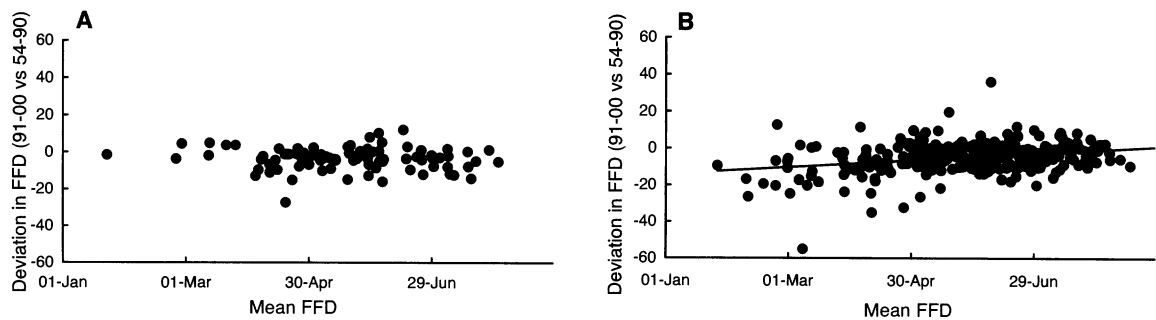

Table 3. Pairs of species known to form hybrids in which actual changes in mean FFD between 1954–1990 and 1991–2000 have led to flowering being more or less synchronous and therefore hybridization more or less likely. Net change is the number of days by which FFD have become more (positive) or less (negative) coincident. All values are rounded to the nearest day.

Species	Mean FFD 1954–1990	Mean FFD 1991–2000	Change (days)	Net change (days)
More likely				
Rumex sanguineus	27 June	15 June	−12	+13
R. obtusifolius	30 May	1 June	+1	
Mentha aquatica	6 August	31 July	−6	+11
M. arvensis	25 June	31 July	+5	
Potentilla reptans	17 June	6 June	−11	+7
P. erecta	13 May	10 May	−4	
Silene dioica	27 April	30 April	+3	+5
S. latifolia	15 May	12 May	−2	
Less likely				
Viola odorata	9 March	21 February	−17	−15
V. hirta	25 March	23 March	−2	
Linaria repens	9 July	9 July	0	−8
L. vulgaris	27 June	19 June	−8	

taxonomic pattern in the data permits extrapolation to the wider British flora; on the basis of the 16% of species that flowered significantly earlier in the 1990s, 150 to 200 species may now be flowering on average 15 days earlier in Britain now than in the very recent past.

The distinct responses to warming of functional groups of plants will disrupt communities, altering competitive and other interactions. An important vegetation type in the area studied is calcareous grassland classified as type CG2 in the UK National Vegetation Classification (*32*), which includes 57 species in the data set. If these species are ranked according to FFD in 1954–1990 and in 1991–2000, the average change in rank between the two lists is 2.6, with several species exhibiting rank changes of eight or nine places. There may also be evolutionary consequences: Table 3 lists six pairs of species, all of which form natural hybrids (*33*). Four of these are more likely to flower synchronously now than formerly, increasing the probability of hybridization, and two are less likely to, reducing it. These phenological changes, therefore, combined with more obvious consequences of climate change such as changes in geographic range (*34*), will alter population-level interactions (*35*) and community dynamics and have profound ecosystem and evolutionary consequences (*36, 37*).

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24. We used a nested analysis of covariance for the following families (number of genera and species are in parentheses): Asteraceae (10, 26), Boraginaceae (2, 5), Brassicaceae (2, 4), Caryophyllaceae (3, 8), Fabaceae (5, 14), Juncaceae (2, 5), Lamiaceae (2, 5), Orchidaceae (2, 5), Poaceae (12, 28), Polygonaceae (3, 11), Rosaceae (6, 17), Salicaceae (2, 8), Scrophulariaceae (4, 14). The covariate (earliest flowering date) was significant ($F_{1,153}$ = 6.14, P = 0.015), as were genera within families ($F_{42,98}$ = 1.75, P = 0.012), but families (tested against genera) were not ($F_{12,42}$ = 1.18, P = 0.323), nor were subclasses (dicotyledons Magnoliidae versus monocotyledons Liliidae: $F_{1,11}$ = 0.01). Only 1 order had more than 2 families with sufficient data, and within the Liliidae, there was only 1 suitable family in the Orchidales; superorders were therefore tested within the Magnoliidae only, but again there was a significant difference only at the genus level (superorders: $F_{2,7}$ = 0.60, P = 0.563).
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7 March 2002; accepted 22 April 2002