

GLOBAL WARMING AND FLOWERING TIMES IN THOREAU'S CONCORD: A COMMUNITY PERSPECTIVE

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Abstract. As a result of climate change, many plants are now flowering measurably earlier than they did in the past. However, some species' flowering times have changed much more than others. Data at the community level can clarify the variation in flowering responses to climate change. In order to determine how North American species' flowering times respond to climate, we analyzed a series of previously unstudied records of the dates of first flowering for over 500 plant taxa in Concord, Massachusetts, USA. These records began with six years of observations by the famous naturalist Henry David Thoreau from 1852 to 1858, continued with 16 years of observations by the botanist Alfred Hosmer in 1878 and 1888–1902, and concluded with our own observations in 2004, 2005, and 2006. From 1852 through 2006, Concord warmed by 2.4°C due to global climate change and urbanization. Using a subset of 43 common species, we determined that plants are now flowering seven days earlier on average than they did in Thoreau's times. Plant flowering times were most correlated with mean temperatures in the one or two months just before flowering and were also correlated with January temperatures. Summer-flowering species showed more interannual variation in flowering time than did spring-flowering species, but the flowering times of spring-flowering species correlated more strongly to mean monthly temperatures. In many cases, such as within the genera *Betula* and *Solidago*, closely related, co-occurring species responded to climate very differently from one another. The differences in flowering responses to warming could affect relationships in plant communities as warming continues. Common St. John's wort (*Hypericum perforatum*) and highbush blueberry (*Vaccinium corymbosum*) are particularly responsive to changes in climate, are common across much of the United States, and could serve as indicators of biological responses to climate change. We discuss the need for researchers to be aware, when using data sets involving multiple observers, of how varying methodologies, sample sizes, and sampling intensities affect the results. Finally, we emphasize the importance of using historical observations, like those of Thoreau and Hosmer, as sources of long-term data and to increase public awareness of biological responses to climate change.

Key words: climate change; Concord, Massachusetts; flowering times; global warming; Henry David Thoreau; phenology.

INTRODUCTION

It is astonishing how soon and unexpectedly flowers appear, when the fields are scarcely tinged with green. Yesterday, for instance, you observed only the radical leaves of some plants; to-day you pluck a flower.

—Henry David Thoreau (Thoreau 1962)

Climate change is already affecting biological systems worldwide (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). Several studies have detected effects of climate change on changes in species distributions (Grabherr et al. 1994, Parmesan et al. 1999), rates of extinctions (McLaughlin et al. 2002, Pounds et al.

2006), the storage of carbon in plants and soils (Shaver et al. 2000), and the timing of life history or phenological events (Menzel and Fabian 1999, Inouye et al. 2000, 2003, Primack et al. 2004). Of these biological responses to climate change, changes in the timing of phenological events are the most widely reported and probably the most easily detectable (Parmesan and Yohe 2003, Root et al. 2003). Climate-related changes in phenology, some quite dramatic, have been observed on every continent and in the oceans (e.g., Menzel and Fabian 1999, Inouye et al. 2000, Schwartz and Chen 2002, Edwards and Richardson 2004, Gordo et al. 2005, Barbraud and Weimerskirch 2006, Beaumont et al. 2006).

In most instances, phenological events, such as flowering, bird migration, and amphibian reproduction, are now occurring earlier than in the past (Parmesan and Yohe 2003, Root et al. 2003). However, it is clear that species' phenologies are changing at different rates. In some cases, different phenological events are changing at different rates even within a single species or individual plant or animal (Post et al. 2008). These changes have

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the potential to alter relationships among many species (Stenseth and Mysterud 2002, Visser and Both 2005) and could alter species' exposures to abiotic factors such as frost (Inouye 2008). Some changes in intertrophic interactions are already evident (Inouye et al. 2000, Edwards and Richardson 2004, Both et al. 2006). For plants, studies have shown significant variation in the rates at which flowering times are changing across species (Fitter et al. 1995, Bradley et al. 1999, Sparks et al. 2000). For example, in England, some species are flowering more than a month earlier than they did 50 years ago, while other species' flowering times are not changing (Fitter et al. 1995). From these findings arise several questions: Why do species respond differently to climate change? Can we better characterize these differences? What species, or groups of species, are most (or least) sensitive to changes in climate? More specifically, does season of flowering or growth form explain any of the variation we see in the responses of individual species to variations in climate?

The answers to these questions could impact on individual performance (Gross and Werner 1983, Parra-Tabla and Vargas 2004) and population and community dynamics (Inouye et al. 2000, Visser and Both 2005). Rare and endangered species that do not adapt to these changes could face extinction. Unfortunately, the number of species included in most historical data sets has limited previous studies. To our knowledge, only one major study has examined the responses of enough plant species (in this case, 243) to search for biological patterns that might explain differences in species' responses (Fitter et al. 1995, Fitter and Fitter 2002). That study showed that 16% of species flowered significantly earlier in the 1990s than in previous decades. Early-flowering species, annuals, and insect-pollinated species showed the greatest sensitivity to climate change (Fitter and Fitter 2002). Although their findings are significant, the observed trends may be valid only for Europe or central England, where the study took place.

The purpose of our study was to characterize how flowering times respond to variations in climate in North America. To this end, we analyzed data from a previously unstudied record of first flowering dates in Concord, Massachusetts, USA. Our data set is unique in several aspects. First, it spans an exceptionally long period of time—155 years from 1852 to 2006—which we accomplish by combining three individual sets of observations. Second, our data set includes observations on over 500 plant taxa, which allows us to identify patterns that occur at the community level. Finally, our data set begins with the observations of Henry David Thoreau, the famous naturalist, philosopher, and author of the widely read book *Walden*, which could make these results particularly relevant to a nonscientist audience. With this unique set of data, we investigated abiotic factors contributing to variation in flowering responses to climate change. We tested the hypothesis that climate

change has altered phenology, and we identified potential mechanisms responsible for these phenological changes.

METHODS

Since the 1850s, several botanists have recorded flowering times in Concord, Massachusetts, USA. These records began with the work of Henry David Thoreau, who observed the first flowering dates (FFD) of over 500 species of plants in Concord from 1852 to 1858 (Thoreau 1962; unpublished tables courtesy of B. P. Dean). Alfred Hosmer, a shopkeeper and amateur botanist, continued these observations of FFDs in Concord for over 700 plant taxa in 1878 and 1888–1902 (Hosmer 1878–1903). Thoreau's and Hosmer's records included the flowering times of plants in all habitat types. Later, from 1963 to 1993, Pennie Logemann, a Concord landscape designer, maintained records of flowering times for over 250 species of plants that occurred on her property, which consisted primarily of forest and wetland. Each of these botanists observed new taxa in flower several days per week during the flowering season. Thoreau intended to write a book about phenology, but did not complete it before his death (Thoreau 1993, 1999). We do not know why Hosmer kept phenological records, as he never wrote any papers based on his observations other than those intended to update the flora of Concord (Hosmer 1899*a, b*). Logemann made phenological calendars as an aid for designing gardens. We know that each of these naturalists had a good working knowledge of the flora of Concord, because of their abilities to distinguish taxa that differ in subtle characteristics (Eaton 1974).

We made our own observations of flowering times in Concord from 2003 to 2006. We purposefully used methods similar to those of the previous naturalists, particularly Thoreau and Hosmer. Two or three days a week from March to October, we recorded plants in flower across Concord. We observed over 500 species in flower. For the analyses in this study, we did not use the observations we made in 2003, because at that time we were still learning the locations of the plants in Concord and frequently missed the earliest flowering dates.

We analyzed in detail the FFDs for 43 common, early-flowering species for which we had the most flowering data. For these species, we included observations made by Thoreau (six years, 1852–1858), Hosmer (16 years, 1878 and 1888–1902), and ourselves (three years, 2004–2006), for a total of 25 years of observations. For each species, we had FFD data for at least 19 of the 25 years. Because we did not have observations for each species in each year, we calculated the difference between the FFD in each year and the FFD in the benchmark year of 1893, a year for which we had observations for all 43 species. This calculation minimized biases caused by different species missing from each year. We used regression analysis to determine the relationship between FFD and mean monthly temper-

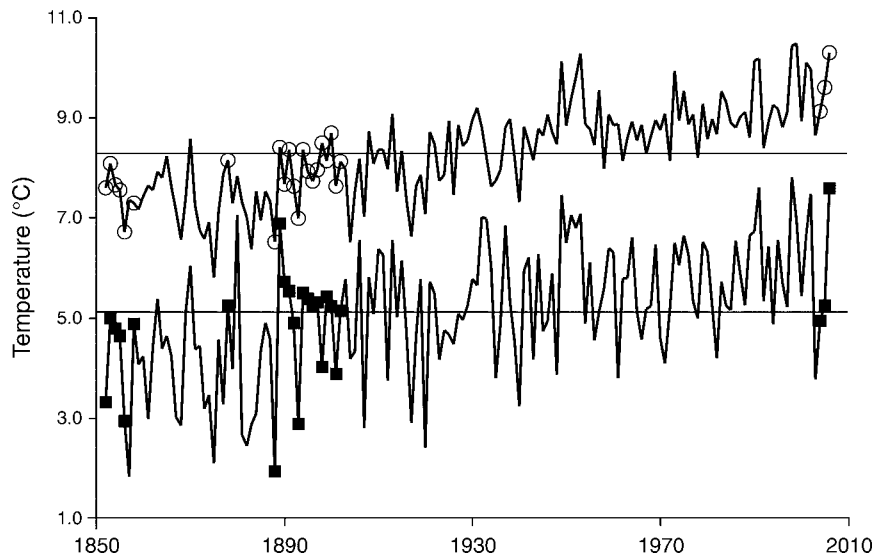


FIG. 1. Temperatures at Blue Hill Meteorological Observatory (33 km southeast of Concord, Massachusetts, USA) from 1852 to 2006. The upper line and open circles represent mean annual temperatures. The lower line and solid squares represent mean monthly temperatures in January, April, and May, temperatures that were highly correlated with flowering times for many species. Horizontal lines show long-term means for each (annual = 8.3°C; Jan, Apr, May = 5.1°C). Circles and squares show years with flowering data.

atures. Logemann observed first flowering dates for eight of these species in at least nine years during the period 1963–1993. We included her observations in regressions for these eight species.

For a broad survey of flowering phenology, we analyzed the records of the 296 taxa (293 species, three distinct subspecies) of flowering plants for which Hosmer had made an observation in each of 15 years, 1888–1902. We compared FFD in each year with mean monthly temperatures. For each taxon, we correlated the FFD with the mean monthly temperatures of the month of flowering and each of the 11 preceding months. From those correlations, we found the months for which the mean temperatures were best correlated with FFD. We also correlated each FFD with the mean temperature for January and the two months preceding flowering, as temperatures in those months were often significantly correlated with FFD. Following the example of Fitter et al. (1995), we used standard deviations about the mean FFD as a measure of interannual variation in flowering time. We then used the regression analyses and standard deviations to compare several groups of taxa—e.g., plants that flower in different months; native and nonnative taxa; and annuals, perennial herbs, and woody plants—in order to find patterns that might explain the overall variation in response to year-to-year changes in climate.

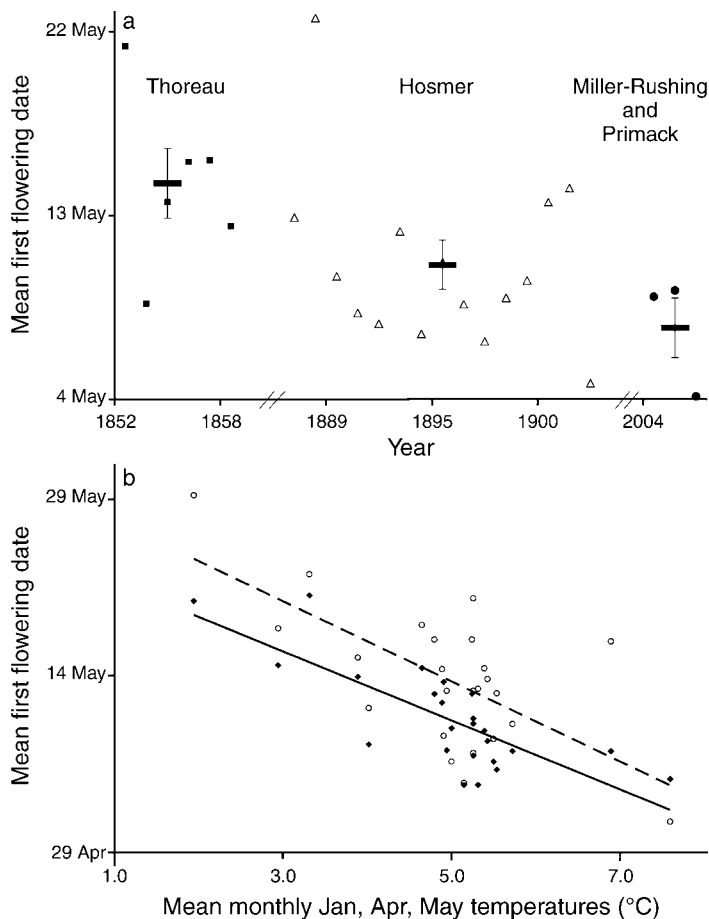
For our analysis, we used dry bulb air temperatures recorded in a standardized way at Blue Hill Meteorological Observatory in Milton, Massachusetts, USA (33 km southeast of Concord). Unfortunately, the weather records for Concord were not complete for the time period between 1888 and 1902. However, we correlated

the available Concord temperature records (1931–1949) with those for Blue Hill Observatory and found that mean monthly temperatures for each year had a correlation coefficient of 0.995 or higher. Thus, we are confident that the temperature in Concord was closely related to that at Blue Hill Observatory.

RESULTS

For 43 common, spring-flowering species (33 native, 10 nonnative), we combined 25 years of observations by three different observers (Thoreau, Hosmer, and ourselves) that span the years 1852–2006. Over this time, mean annual temperatures in Concord rose by 2.4°C and mean monthly temperatures in January, April, and May rose by 2.3°C, as determined by linear regression (Fig. 1). Our analysis of these observations showed that these plants have flowered progressively earlier over the past 150 years (Fig. 2a). For the 43 species, the mean FFD during Thoreau's observations (1852–1858) was 14 May, whereas the mean FFD for our observations (2004–2006) was 7 May, seven days earlier. The mean FFD for Hosmer (1878, 1888–1902) was 10 May, intermediate between Thoreau's and our own observations. The differences in FFDs among the three time periods were highly significant as determined by two-way ANOVA, considering time period (Thoreau, Hosmer, and ourselves) and species as factors ($P < 0.001$). The FFD for some species changed dramatically from 1852 to 2006. For example, highbush blueberry (*Vaccinium corymbosum*), a native shrub, and yellow wood sorrel (*Oxalis europaea*), a native herb, are now flowering 21 and 32 days earlier than they did 150 years ago, respectively.

FIG. 2. Change in mean first flowering dates (FFD) for 33 native and 10 nonnative species (a) over time and (b) in response to warming mean monthly temperatures in January, April, and May. (a) Symbols correspond to observers and time periods: solid squares for observations by Henry David Thoreau (1852–1858), open triangles for observations by Alfred Hosmer (1878, 1888–1902), and solid circles for our observations (2004–2006). Solid horizontal bars with standard error bars represent the mean FFD for each observer. Each point (other than solid bars) was calculated by using the difference between when a species flowered in a particular year and when it flowered in the benchmark year of 1893, when all species were observed. Then we averaged these differences among species; each point represents the mean difference in FFD from 1893 for all species observed in a particular year. (b) Solid diamonds and the solid line represent mean FFD for 33 native species. Open circles and the dashed line represent mean FFD for 10 nonnative species. Means were calculated as described for (a), as differences from FFD in 1893. Lines are best-fit regressions. Natives flowered 2.93 days earlier per 1°C warming ($R^2 = 0.609$, $P < 0.001$). Nonnatives flowered 3.40 days earlier per 1°C warming ($R^2 = 0.428$, $P < 0.001$).



The earlier flowering times were strongly correlated with warming mean monthly temperatures in January, April, and May over that time period. On average, plants flowered 3.07 days earlier for each 1°C increase in mean monthly temperatures, as determined by linear regression (43 species, $R^2 = 0.609$, $P < 0.001$; Fig. 2b). The changes in FFD for native (33 species, 2.93 days earlier per 1°C, $R^2 = 0.596$, $P < 0.001$) and nonnative (10 species, 3.40 days earlier per 1°C, $R^2 = 0.428$, $P < 0.001$) were virtually identical. Average January, April, and May temperatures were 4.3°C during Thoreau's observations, 5.0°C during Hosmer's observations, and 5.9°C during our own observations.

Of these 43 common species, Logemann observed eight, all native, in at least nine years (1963–1993). Inclusion of her observations improved the ability of temperature to explain FFDs for three species—shadbush (*Amelanchier canadensis*), bunchberry (*Cornus canadensis*), and wild strawberry (*Fragaria virginiana*)—as indicated by R^2 values from the flowering-temperature relationship; R^2 values increased when her observations were included. FFDs of three species were not correlated with temperature, with or without Logemann's observations, and Logemann's observations did

not improve the explanatory power for the remaining two species.

For our broad survey of 296 species that Hosmer observed from 1888–1902, mean FFD ranged from 4 March, for skunk cabbage (*Symplocarpus foetidus*), to 14 August, for swamp rose mallow (*Hibiscus palustris*). Some species, such as witch hazel (*Hamamelis virginiana*), flowered earlier or later, but Hosmer's records for those species were not complete. Most plant taxa flowered in May (82), June (86), and July (76); fewer taxa flowered in March (2), April (32), and August (18); and the mean flowering date for all plants was 12 June.

On average, the Concord plants observed by Hosmer responded to each 1°C increase in mean January, April, and May temperatures by flowering 3.28 days earlier (296 taxa, $R^2 = 0.84$, $P < 0.001$). Of the 296 taxa we examined, 279 (94%) flowered earlier in years with warmer mean monthly temperatures in January and the two months prior to flowering, as indicated by negative correlations; 168 (57%) showed significant ($P < 0.05$) correlations between FFD and mean monthly temperatures. No taxon showed a significant trend toward later FFD with warmer mean monthly temperatures. For 20 taxa, mean monthly temperatures explained more than 60% of the variation in FFDs ($R^2 > 0.60$; Table 1). For

TABLE 1. The 20 taxa with first flowering dates (FFD) best predicted by mean monthly temperatures in January and the two months prior to flowering, out of a sample of 296 taxa.

Species	Common name	R ²	Change	Mean FFD	SD
<i>Hypericum perforatum</i> †	common St. John's wort	0.73	-3.5	21 Jun	5.1
<i>Cichorium intybus</i> †	chicory	0.70	-3.5	30 Jun	5.1
<i>Amelanchier canadensis</i>	shadbush	0.70	-3.4	2 May	5.6
<i>Viola pubescens</i>	downy yellow violet	0.69	-4.5	9 May	7.3
<i>Vaccinium corymbosum</i>	highbush blueberry	0.67	-5.6	8 May	9.3
<i>Erigeron pulchellus</i>	Robin's plantain	0.66	-5.8	21 May	9.6
<i>Kalmia polifolia</i>	pale laurel	0.66	-3.2	12 May	5.3
<i>Chelidonium majus</i> †	celandine	0.66	-4.3	13 May	7.2
<i>Chamaedaphne calyculata</i>	leatherleaf	0.65	-3.2	22 Apr	5.7
<i>Melampyrum lineare</i>	cowwheat	0.64	-3.4	16 Jun	5.2
<i>Vaccinium vacillans</i>	late low blueberry	0.64	-4.6	4 May	7.7
<i>Lysimachia terrestris</i>	swamp candles	0.64	-4.5	25 Jun	6.8
<i>Maianthemum canadense</i>	Canada mayflower	0.63	-3.4	18 May	5.8
<i>Rhododendron nudiflorum</i>	pink azalea	0.63	-4.5	26 May	7.7
<i>Iris versicolor</i>	larger blue flag	0.63	-4.0	1 Jun	6.1
<i>Cornus canadensis</i>	bunchberry	0.62	-4.4	22 May	7.6
<i>Ranunculus bulbosus</i> †	bulbous buttercup	0.62	-5.1	4 May	8.8
<i>Viola cucullata</i>	marsh blue violet	0.61	-3.2	27 Apr	5.8
<i>Houstonia caerulea</i>	bluets	0.61	-4.2	18 Apr	7.6
<i>Ligustrum vulgare</i> †	privet	0.60	-6.2	23 Jun	9.8

Notes: Change is given as days/°C. $P < 0.001$ for all taxa shown. Negative change indicates a change toward earlier FFD in warmer years.

† Nonnative species.

example, 73% of the variation in the FFD of common St. John's wort (*Hypericum perforatum*) was explained by changes in mean monthly temperatures in January, April, and May. Two other species sensitive to mean monthly temperatures, privet (*Ligustrum vulgare*) and robin's plantain (*Erigeron pulchellus*), each responded to each 1°C increase in temperatures by flowering about six days earlier.

Because taxa respond more to temperatures in individual months rather than annual temperatures

(Fitter et al. 1995, Sparks and Carey 1995), we examined the relative importance of each month's mean temperature in predicting changes in mean FFD. Of the 221 taxa with FFDs that were significantly correlated with the mean temperature of at least one month ($P < 0.05$), 116 (52%) were correlated with mean May temperatures, while 100 (45%) were correlated with mean January temperatures (Fig. 3). The FFDs of 162 (73%) taxa were correlated with the mean temperatures either in the month of flowering or in one of the two months prior to

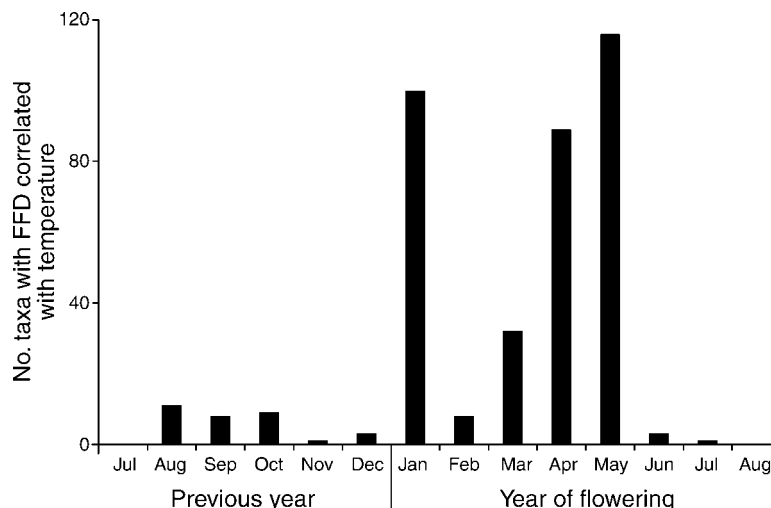


FIG. 3. Frequency with which each month's mean temperature was significantly correlated with the first flowering date (FFD) of a taxon. Only significant correlations are shown ($P < 0.05$). The pattern is consistent whether the number of taxa or the percentage of possible occurrences is considered. The FFDs for a total of 221 taxa were significantly correlated with mean temperatures in at least one month. We tested correlations between FFD and temperatures in the month of flowering and in the 11 preceding months. Months are shown as occurring during the year of flowering or during the previous calendar year.

flowering. Fig. 3 shows three peaks where months were relatively important in predicting FFD compared to nearby months: large peaks in April, May, and January of the flowering year. A small number of species had FFDs correlated with temperatures in August, September, and October of the year prior to flowering. This pattern, which is consistent whether absolute number of occurrences or percent of possible occurrences are considered (data not shown), suggests that many species are particularly sensitive to cold January temperatures and to warming temperatures early in the spring or just prior to flowering.

The peak in January is particularly striking, because FFDs were often significantly correlated with mean January temperature, but very rarely correlated with the adjacent months, i.e., December of the previous year and February of the flowering year. Mean January temperatures were significantly correlated with FFDs for equal percentages of all growth forms (approximately 33% each of annuals, perennial herbs, and woody shrubs). It is possible that these correlations were due to severely cold temperatures in January. January was the coldest month in eight out of the 15 years that Hosmer kept records (1888–1902).

Due to the large number of taxa included in our analysis, we were also able to examine the effects of season of flowering, growth form, nativeness, and habitat on responses to climate change. We found that FFDs for early-flowering (March, April, May, June) taxa were more correlated with mean monthly temperatures than were FFDs for late-flowering (July, August) taxa as shown by regression analysis (296 taxa, $P < 0.001$; Fig. 4). In other words, the mean FFDs of early-flowering taxa were better predicted by and more responsive to mean monthly temperatures than were late-flowering taxa. Even though FFDs of early-flowering species were more correlated with temperature, we found that late-flowering taxa had greater standard deviations about their mean flowering dates than did early-flowering taxa, as determined by regression analysis ($P = 0.016$).

When we analyzed the same relationship according to growth form, we found that growth forms differed significantly in their patterns. The standard deviations of annuals were not significantly affected by season of flowering (18 taxa, $P = 0.120$); late-flowering perennial herbs had greater standard deviations than early-flowering taxa (194 taxa, $P < 0.001$). Woody plants, however, displayed an opposite trend: early-flowering taxa had greater standard deviations than late-flowering ones (66 taxa, $P = 0.032$). Because the majority of taxa in the data set were perennial herbs (65%), it is likely that the relationship between standard deviation and mean FFD for perennial herbs drove the trend seen when all taxa were considered together. In addition, on average, annuals showed a marginally significantly greater standard deviation about their mean FFDs than did perennial herbs (11.2 compared to 8.7 days, $t = 1.92$,

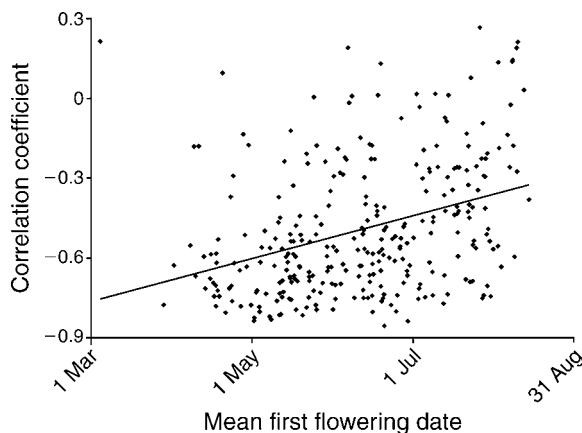


FIG. 4. The relationship between mean first flowering date (FFD) from 1888 to 1902 and the correlation between FFD and mean monthly temperatures in January and the two months prior to flowering for 296 plant taxa. Each point represents one taxon. Negative correlation coefficients indicate earlier flowering in warmer years. Slope = 0.003, $R^2 = 0.141$, $P < 0.001$.

two-tailed $P = 0.07$), which in turn showed a significantly greater standard deviation than did woody plants (8.7 compared to 7.4 days, $t = -2.77$, two-tailed $P = 0.006$). That is, life-form explained, in part, why some taxa had more year-to-year variation in flowering compared to others.

We found that nonnative taxa did not differ from native taxa in their flowering responses to temperature. Both native (239 taxa) and nonnative (54 taxa) taxa showed a great deal of variation of response, but neither standard deviations about mean FFDs (8.6 vs. 9.2 days, $t = -0.971$, two-tailed $P = 0.33$) nor correlations with mean monthly temperatures (correlation coefficients of -0.490 vs. -0.523 , $t = 0.863$, two-tailed $P = 0.39$) differed significantly between the two groups. Similarly, habitat (aquatic, forest, grassland, roadside, wetland) did not explain any of the variation in flowering responses to temperature.

The FFDs of many closely related (i.e., within the same genus) and co-occurring species responded to changes in temperature at very different rates. For example, black birch (*Betula lenta*) and gray birch (*Betula populifolia*), which occur in many of the same habitats in Concord, show very different responses to temperature (Miller-Rushing and Primack, *in press*). Black birch flowered 2.83 days earlier for each 1°C increase in January, March, and April temperatures ($R^2 = 0.376$, $P = 0.015$), whereas gray birch FFDs showed no relationship with temperature ($P = 0.535$). In an even more dramatic example, rough-stemmed goldenrod (*Solidago rugosa*) flowered 11.17 days earlier for each 1°C increase in January, May, and June temperatures ($R^2 = 0.554$, $P = 0.001$), whereas the FFDs of lance-leaved goldenrod (*Solidago graminifolia*) and most other goldenrods showed no relationship with temperature ($P = 0.535$). Among the 52 genera for which Hosmer

observed more than one species, 31 (60%) contained at least one species with FFDs significantly correlated to mean monthly temperatures in January and the two months prior to flowering and at least one species with FFDs that were not correlated with temperature. Of the 25 genera for which Hosmer observed just two species, 10 (40%) contained one species with FFDs significantly correlated to mean monthly temperatures and one species with FFDs not correlated to temperature.

DISCUSSION

On average, plants in Concord appear to flower now seven days earlier than they did when Thoreau made his observations (1852–1858). Most of this change in flowering time is probably due to rising winter and spring temperatures. Temperatures in eastern Massachusetts have increased more rapidly than in many other areas of the world due to the combination of global warming and the urban heat island effect (New England Regional Assessment Group 2001). The rate at which Concord plants responded to warming—3.3 days earlier flowering for each 1°C increase in mean monthly temperatures in January, April, and May—fits well with findings in Europe (Sparks and Carey 1995, Chmielewski and Rötzer 2001, Fitter and Fitter 2002) and North America (Schwartz and Reiter 2000, Cayan et al. 2001).

We also found that mean monthly temperatures in January and the two months immediately preceding flowering were significantly correlated with the FFDs for many species. It is known that plants respond to temperatures from the previous fall (Fitter et al. 1995). Cooling temperatures in the fall and winter often contribute to the vernalization process, in which colder temperatures lead to increased competence and earlier flowering (Chuine 2000, Sung and Amasino 2004). However, we found that colder January temperatures were correlated to later flowering times. One reason for the discrepancy could be the difference between climate patterns in the northeastern United States and Western Europe, the site of many previous studies of plant phenology (e.g., Fitter et al. 1995, Sparks et al. 2000). Winter temperatures in Western Europe's maritime climate tend to be significantly milder than those in the continental climate of the northeastern United States (Hartmann 1994, Seager et al. 2002). For an average of 12 days in each January (1963–2006), there is no snow cover in Concord to insulate plants from the extreme cold. Thus, overwintering plants and seeds in the northeastern United States may be much more susceptible to damage from January's extreme cold temperatures than are plants in Western Europe. It is also possible that the phenologies of species in colder climates may simply be particularly sensitive to climate (Thórhallsdóttir 1998).

In another surprising finding, early-flowering perennial herbs had FFDs that displayed less interannual variability than did those of late-flowering taxa, although the variation in early-flowering taxa was more

closely linked to mean monthly temperatures (Fig. 2). Previous studies have found individual examples of highly variable flowering times in late-flowering perennial herbs, such as bird's foot trefoil (*Lotus corniculatus*; Ollerton and Lack 1998), but we do not know of previous evidence suggesting that it may be a widespread pattern. Woody species showed the more usual pattern of greater interannual variation in flowering times for early-flowering species rather than late-flowering species (Fitter et al. 1995, Post and Stenseth 1999). It seems that the flowering times of many late-flowering perennial herbs may have been linked to an indicator, or set of indicators, that were more variable than mean monthly temperatures, or that late-flowering perennial herbs have inherently variable flowering times. Possibilities of non-temperature indicators for flowering times include phenomena such as rainfall, shading, and land use. It is also possible that monthly temperatures were too coarse to have a detectable effect on flowering times for these species, and that daily temperatures may be more appropriate. Further study is clearly necessary to isolate the factors responsible for the high variation in the flowering dates of late-flowering perennial herbs. Intriguingly, Rich et al. (2008) found additional differences between woody and herbaceous species in a piñon–juniper woodland suggesting that herbaceous species are more responsive to environmental variation than are woody species.

The flowering times of several species appear sensitive enough to changes in temperature that they could serve as indicator species and be used to measure biological responses to changes in climate over time. Among the species in our study, two particularly common species—common St. John's wort (*Hypericum perforatum*) and chicory (*Cichorium intybus*)—both had high correlations with mean monthly temperatures ($R^2 > 0.60$) and had mean FFDs that advanced more than three days per 1°C increase in temperature (Table 1). Although these species are nonnative, they are both common in urban and rural areas across the United States and easy to identify. Common and widespread native species, such as highbush blueberry (*Vaccinium corymbosum*), Canada mayflower (*Maianthemum canadense*), and larger blue flag (*Iris versicolor*; see Plate 1) could also serve as indicator species (Table 1). Before these species are utilized as indicator species across their ranges, however, we suggest that studies determine if their sensitivity to changes in temperatures is consistent across their ranges. Their usefulness as indicators for interacting species should also be tested, as Both et al. (2006) have shown that phenological changes may differ among different parts of a food chain.

Our study suggests that flowering times are changing at different rates for several closely related, co-occurring species, such as those within the genera *Betula* and *Solidago*. As the timing of flowering and other correlated life history traits change for these species, interactions among the species will also change. Un-



PLATE 1. The first flowering dates of larger blue flag (*Iris versicolor*) were highly correlated with changes in temperature in Concord, Massachusetts (USA). The flowering date of this species may provide a good indicator of biotic responses to climate change. Photo credit: A. J. Miller-Rushing and R. B. Primack.

doubtedly, these changes will be to the advantage of some species and disadvantage of others, although it is difficult to predict the winners and losers. It is also clear that the net effect of phenological changes on the fitness of individuals or species will depend on complex, timing-based interactions, sometimes spanning multiple trophic levels (Stenseth and Myserud 2002, Visser and Both 2005). For example, plants with particularly rapid responses to changes in temperature could flower before the emergence of their pollinators, thus decreasing their chances of reproductive success (Kudo et al. 2008). In other cases, plants may become more susceptible to frost events or benefit from the lengthening of the growing season (Inouye 2008, Kudo et al. 2008). As studies like ours identify the species most sensitive to changes in climate, researchers can specifically include these species in their examinations of the ecological and evolutionary impacts of non-synchronous shifts in flowering times.

In many instances, the best long-term phenological data may contain observations made by several observers over long periods of time, as in our study. In these cases, researchers must be mindful of the different time periods and the methods that various observers might use, including sampling effort (days/week, hours/day, total area examined) and definitions of what constitutes an open flower. For example, the statistical power of our analysis was limited because of the heterogeneity of our data, with only three years of recent observations. In

such a circumstance, one anomalous year could alter results. In our case, mean January, April, and May temperatures in 2004 and 2005 were colder than most years since 1990 (Fig. 1). Thus, our estimates of changes in flowering times are probably quite conservative. In addition, we, Thoreau, and Hosmer observed flowering times throughout Concord, while Logemann observed flowering times only on her property in Concord. Because Logemann observed a smaller area and fewer plants, the first flowering dates she observed for many species were later than they were for the other observers (data not shown). Many phenological records document changes in first observations, such as first flowering dates rather than mean flowering dates. Changes in population size or sampling effort can affect these first observations independently of changes in the changes in the population mean (Tryjanowski and Sparks 2001). If populations decline over time or if sampling intensity declines, first observations can occur later even when the population mean does not change. Similarly, if populations increase over time or if sampling intensity increases, first observations can occur earlier even when the population mean does not change. Based on Hosmer's descriptions of species abundance, population sizes in Concord remained fairly constant over the last century for 32 of 43 of the main study species. Population sizes declined over time for the remaining 11 species, meaning that estimates of changes in

flowering times are probably overly conservative for these 11 species. Clearly, it is critical that researchers combine phenological data with descriptions of observation methods and changes in population sizes. Given these caveats, however, observations made by different individuals, or even using different methods, can yield surprisingly high quality, consistent results (Miller-Rushing et al. 2006).

Because of the clear ecological and evolutionary importance of phenological responses to climate change, we suggest that researchers increase efforts to collect long-term phenological data via new projects and searches of historical records. Many Long-term Ecological Research (LTER) sites, as well as other research sites, already collect such data. In addition, phenological data sets already exist in many libraries, herbaria, museums, and private homes (Ledneva et al. 2004, Primack et al. 2004, Miller-Rushing et al. 2006). Thoreau's and Hosmer's records were freely available at various libraries, but had never been previously analyzed. Logemann quite willingly shared her notebooks and charts, which she kept in her home. By using such pre-existing records and adding new sites for phenological studies, researchers could greatly enhance our understanding of how phenological changes vary according to location and species and how they might affect other aspects of ecology and evolution (Betancourt and Schwartz 2005).

In addition, evidence of phenological changes can improve public awareness of the effects that climate change is already having on biological systems. People can see changes in phenology in their immediate environment: plants flowering in gardens, fruits ripening, and birds arriving at bird feeders. We believe that building on the observations of a well known figure such as Thoreau can show that plants are responding to climate change and increase the potential for public outreach. Other studies of changes in phenology made by famous individuals such as Aldo Leopold (Bradley et al. 1999), or in well-known locations such as Washington, D.C. (Abu-Asab et al. 2001) and Boston (Primack et al. 2004, Miller-Rushing et al. 2006) generate similar public interest. Thoreau was keenly aware of the importance of educating people about environmental issues. He helped his townsmen to appreciate wild nature, and he encouraged them to protect it. He wrote, "I think that each town should have a park, or rather a primitive forest of five hundred or a thousand acres, either in one body or several, where a stick should never be cut for fuel, nor for the navy, nor to make wagons, but stand and decay for higher uses—a common possession forever, for instruction and recreation." Residents of Concord and the government have followed this advice; about 40% of Concord's land is preserved in parks and protected areas. With the help of these protected areas, we have been able to continue the same observations of flowering times made by Thoreau at the same localities in Concord. We now hope that

Thoreau's observations and our own work will promote broad discussion of the effects of climate change on biological systems. Only with an understanding of the changes taking place can people make informed decisions regarding climate change.

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