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PHOTOGRAPHS AND HERBARIUM SPECIMENS AS TOOLS TO DOCUMENT PHENOLOGICAL CHANGES IN RESPONSE TO GLOBAL WARMING[1]

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Global warming is affecting natural systems across the world. Of the biological responses to warming, changes in the timing of phenological events such as flowering are among the most sensitive. Despite the recognized importance of phenological changes, the limited number of long-term records of phenological events has restricted research on the topic in most areas of the world. In a previous study in Boston (*American Journal of Botany* 91: 1260–1264), we used herbarium specimens and one season of field observations to show that plants flowered earlier as the climate warmed over the past 100 yr. In our new study, we found that two extra years of data did not strengthen the explanatory power of the analysis. Analysis of herbarium specimens without any field data yielded results similar to analyses that included field observations. In addition, we found that photographs of cultivated and wild plants in Massachusetts, data similar to that contained in herbarium specimens, show changes in flowering times that closely match independent data on the same species in the same locations. Dated photographs of plants in flower represent a new resource to extend the range of species and localities addressed in global-warming research.

Key words: Arnold Arboretum; climate change; Concord, Massachusetts; flowering times; global warming; herbarium specimens; phenology; photographs.

Global warming is already affecting natural processes around the world. For example, glaciers are melting, species are shifting their ranges poleward and up mountain slopes, and some species are going extinct (Walther et al., 2002). Of the biological responses to warming detected to date, changes in phenological events are among the most sensitive (Parmesan and Yohe, 2003; Root et al., 2003). In England plants are now flowering as much as a month earlier than they did 50 yr ago (Fitter et al., 1995). In addition, across Europe leaves are emerging an average of 6 d earlier now than they did 30 yr ago (Menzel and Fabian, 1999). In Massachusetts, we have observed similar trends toward earlier flowering, bird migrations, and frog reproduction in recent, warmer years (Ledneva et al., 2004).

It is clear that current changes in plant phenology will have widespread impacts on critical ecosystem processes such as carbon sequestration (Barford et al., 2001; White and Nemani, 2003), ecosystem–atmosphere interactions (Fitzjarrald et al., 2001), and trophic interactions (Inouye et al., 2000; Visser and Both, 2005). For example, in the Netherlands, dramatic declines in some populations of pied flycatchers (*Ficedula hypoleuca*) have been attributed to changes in the time-sensitive relationships between oak tree leaf out, caterpillar emergence, and bird breeding times (Both et al., 2006).

Most studies that have documented the impact of climate change on phenological events have relied on long-term written records (e.g., Inouye and Mcguire, 1991; Sparks and Carey, 1995; Bradley et al., 1999; Fitter and Fitter, 2002; Molau et al., 2005). Although many such records have been found and analyzed in Europe, they are still too rare in other locations around the world to provide adequate data to answer fundamental questions regarding how phenological events are changing and how they will continue to change as a result of climate change. In order to answer questions regarding changing phenologies, scientists must maximize the amount of reliable data available in terms of lengths of records, numbers of species, and geographic locations.

We previously demonstrated that herbarium specimens collected over many years could be combined with a single baseline season of field observations to provide a source of data for changes in plant flowering times (Primack et al., 2004). Because studying data from herbarium specimens is new in phenological studies, it is not clear what the strengths of these data are. For example, is it possible to use only data from preserved specimens, without any field observations, to demonstrate flowering responses to climate change? Does including more years of baseline field observations improve estimates of trends toward earlier flowering of plants using herbarium specimens? That is, by obtaining 3 years of observations of current flowering, can we more precisely describe the effects of climate change on these plants? Or are plant flowering times and order of flowering among multiple species so consistent from year to year that one year of baseline data sufficiently describes the flowering time of individual plants?

Photographs could provide a similar source of data for measuring changes in plant flowering times. Like herbarium specimens, dated photographs of plants in flower provide an estimate of the peak flowering date of an individual. Photographs also offer the benefit of being substantially more common than herbarium specimens or observations collected by individual scientists. Collections of photographs that include phenological phenomena can be found in museums,

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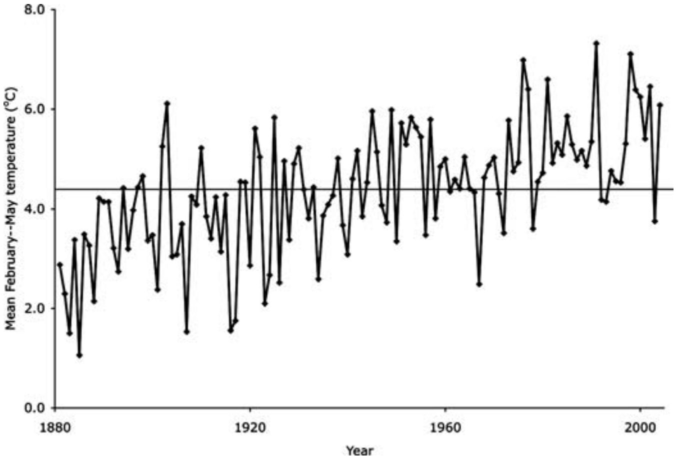

Fig. 1. Mean temperatures in February, March, April, and May from 1881 to 2004 as recorded at Blue Hill Meteorological Observatory in Milton, Massachusetts. The horizontal line represents the long-term mean February–May temperature (4.4°C).

libraries, universities, or private holdings. Other fields of science have used abundant photographic records to document changes in soil (Trimble and Crosson, 2000) and vegetation (Rogers et al., 1984; Moiseev and Shiyatov, 2003) and to calculate the rate of retreat of glaciers (Harrison, 1974). Recently, Sparks et al. (2006) used fixed-date photographs to document changes in plant development in response to weather conditions. Expanding the use of dated photographs to document changes in flowering times, or other phenological events, could provide valuable new data for studying changes in response to climate change.

Here we address questions regarding herbarium specimens as a source of phenological data by comparing them with 3 years of field observations of living plants, each of which is represented by at least one herbarium specimen at the Arnold Arboretum of Harvard University in Boston. We also examined two collections of dated photographs of flowering plants, one of cultivated plants at the Arnold Arboretum and one of wild plants in Concord, Massachusetts. Overall, we tested the utility and outlined the strengths of using data that capture point records of historical flowering events.

MATERIALS AND METHODS

Climate data**—**We obtained temperature data from Blue Hill Meteorological Observatory in Milton, Massachusetts. From 1881 to 2004, mean February–May temperatures at the site warmed 2.5°C ($P < 0.001$) as determined by ordinary least squares (OLS) regression (Fig. 1). The observatory is located approximately 8 km south of the Arnold Arboretum and 33 km southeast of Concord, Massachusetts. The Blue Hill weather record is one of the longest continuous records of weather observations in the United States.

Herbarium specimens**—**In 2004 and 2005 we observed the flowering times of 120 individual woody plants growing at the Arnold Arboretum, each of which had been observed in 2003 as described by Primack et al. (2004). These 120 individual plants represented 42 species. We had previously selected these plants because each of them was represented by at least one herbarium specimen in full flower from a year in the past. In total, the 120 plants that we observed in all 3 years were represented by 177 herbarium specimens collected from 1881 to 2002. In 2004 and 2005 our observations began in April and were conducted weekly, usually by two observers. Of the 229 individual plants that we monitored in 2003 (Primack et al., 2004), 109 were not included in this study due to plant death, removal from the Arboretum, a nonflowering year, or a shorter field season in 2005 that did not include certain early flowering plants.

For each plant, we determined a single Julian date of full flower in each year. This date could have missed the true flowering peak by an average of 3.5 d due to sampling just once a week. In cases for which plants were in full flower on multiple dates, we calculated the mean date of full flowering. Full flowering was defined as occurring when more than 50% of flower buds were open on a given individual.

We used correlation analysis to compare the flowering dates of plants in 2003, 2004, and 2005 to see if dates of full flowering were consistent among years. We also compared flowering dates observed in the field with flowering dates as determined by herbarium records. For each of our field observations we subtracted our observed full-flowering date from the date that the matching herbarium specimens were collected. This subtraction provided an estimate of the change in plant flowering dates for each individual. We used OLS regression to examine how flowering dates changed over time for all plants on average. We also used OLS regression to determine how changes in flowering times compared to changes in mean temperatures in February to May over the last 120 yr. We performed four separate regressions for changes over time, including one for each year of field observations and another using the mean date of full flowering averaged across the 3 yr (2003–2005) that we made observations. We performed another four regressions to demonstrate the relationship between flowering times and temperatures. We compared the results to determine whether the rate of change in flowering times indicated by the regressions differed among the years in which we made field observations. We also tested if multiple years of observation improved the estimates of changes in flowering times.

In addition, we tested whether herbarium specimens alone, without field observations, could demonstrate the effects of temperature on flowering times. Among the 229 individual plants used in our previous study (Primack et al., 2004), we found 74 from which herbarium specimens had been collected in flower in 2 or more years, for a total of 216 herbarium specimens. Within the herbarium record of each individual, we compared the differences in the flowering dates with differences in mean February–May temperatures in the years in which those specimens were collected. Specifically, we subtracted the Julian flowering date of the later specimen (say 1960) from that of the earlier specimen (say 1930). We then calculated the difference in February–May temperatures between the years in which the specimens were collected. In the hypothetical case described, we would have subtracted the mean February–May temperature of 1960 from that of 1930. If temperatures affected flowering times, we would have expected to see a negative correlation between the difference in plant flowering times and the difference in temperatures. That is, if 1960 were warmer than 1930, we would have expected, on average, for plants to flower earlier in 1960 than in 1930.

Photographic data**—**We examined two records of photographs. The first of these records contained 251 dated images of cultivated woody plants in flower at the Arnold Arboretum. The Arnold Arboretum photographs were taken for a wide variety of projects and purposes from 1904 to 2004. The Arboretum catalogued many of the photographs taken by staff photographers in a central collection, but staff members and amateur photographers also took and held many of the photographs. Unlike the herbarium specimens, these photographs were not associated with particular individual plants on the grounds of the Arboretum.

The second record contained 34 dated photographs of 17 species of wild plants in flower in Concord, Massachusetts. The photographs included images mostly of wildflowers, but also of trees and shrubs. The Concord photographs were taken by the landscape photographer Herbert Wendell Gleason and spanned the years from 1900 to 1921 (Robbins-Mills Collection of Herbert Wendell Gleason Photographic Negatives, 1899–1937, William Munroe Special Collections, Concord Free Public Library).

First, we examined the collection of photographs taken at the Arnold Arboretum. We began with the assumption that, on average, the photographs represented the mean flowering of a species in a particular year. We had previously validated a similar assumption using herbarium specimens (Primack et al., 2004). For each photograph, we calculated how much earlier or later a plant flowered in a historical year than it did in the benchmark year of 2003 (Fig. 2A). We then used OLS regression to estimate the rate that flowering dates changed over time and also in relation to mean temperatures from February to May. We validated the magnitudes of the changes in flowering times by comparing them to trends taken from our previous study, which used

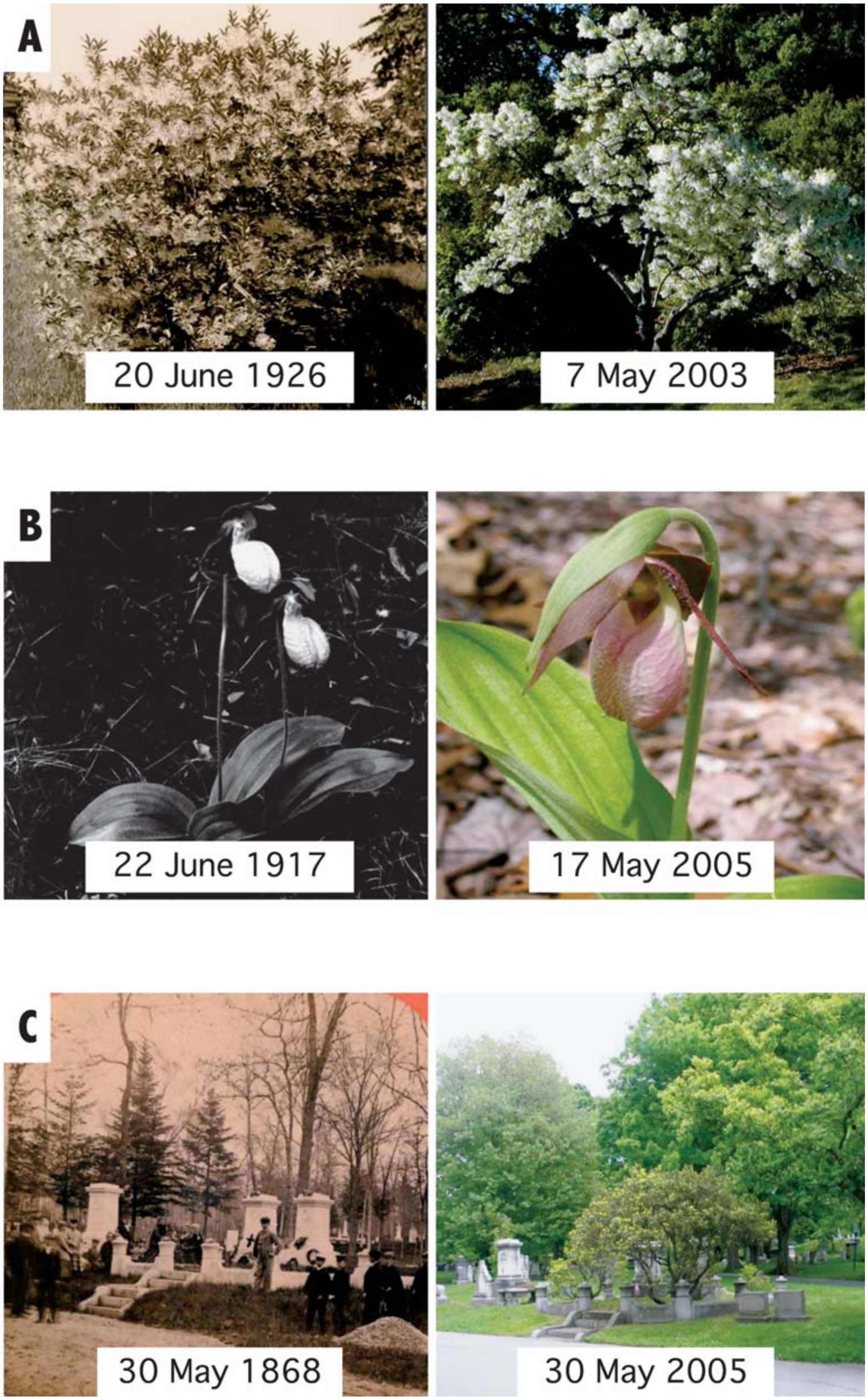

Fig. 2. Representative comparisons of historical and recent photographs of phenological events. (A) Fringe trees (*Chionanthus virginicus* L.) flowered later in 1926 (mean February–May temperature = 2.5°C) than in 2003 (3.8°C) at the Arnold Arboretum in Boston. (B) Wild specimens of pink lady's slipper (*Cypripedium acaule* Ait.) flowered later in 1917 (1.8°C) than in 2005 (4.7°C) in Concord, Massachusetts. (C) Leaf-out at Lowell Cemetery in Lowell, Massachusetts. Trees lack leaves in the 1868 (1.9°C) photograph. The same trees were fully leafed in 2005 (4.7°C). Left to right, photographs were taken by (A) E. H. Wilson, R. Mayer, (B) H. W. Gleason, A. J. Miller-Rushing, (C) unknown, and R. B. Primack.

TABLE 1. Comparison of regression results showing change in flowering dates over time. For each year shown, we subtracted that year's peak flowering date from the date that a flowering specimen of that plant was collected in the past. This subtraction provided an estimate of the change in plant flowering dates. We then used ordinary least squares regression to estimate the rate of change in flowering dates over time. SE represents the standard error of the regression coefficient. Negative regression coefficients indicate earlier flowering over time. $N = 177$ for all regressions shown.

Data	Regression coefficient (d/yr)	SE	P	R^2
2003 + herbarium specimens	−0.059	0.020	0.003	0.048
2004 + herbarium specimens	−0.043	0.020	0.030	0.026
2005 + herbarium specimens	−0.042	0.019	0.030	0.027
Mean of 3 yr + herb. sp.	−0.048	0.019	0.010	0.037

herbarium specimens and field observations to document changes in flowering times for the same species in the same location (Primack et al., 2004).

Second, to demonstrate the generality of the technique, we analyzed the collection of Gleason's historical photographs of wild plants flowering in Concord, Massachusetts. We compared the dates of the photographs to our observations of mean plant flowering times from the same species in Concord in 2005 (Miller-Rushing and Primack, unpublished data). We calculated mean flowering times in Concord in 2005 from our own field observations, which we made two to three times per week. Thus, for each photograph we had a measure of how much earlier or later a plant species flowered in a historical year than it did in the benchmark year of 2005 (Fig. 2B). We then used OLS regression to document how flowering times changed over time and also in relation to mean temperatures from February to May. We validated the magnitude of the temperature response by comparing it to trends taken from observations of 13 of the same species' first flowering times made by the botanist Alfred Hosmer in Concord each year from 1887 to 1903 (Hosmer, A. W. Alfred W. Hosmer Botanical Manuscripts, 1878–1903, William Munroe Special Collections, Concord Free Public Library).

Comparing regressions—To determine if two trends were identical, we used a multiple regression test on both sets of data together, with the sets distinguished by a dummy variable:

$$\text{Flowering date} = \beta_0 + \beta_1\text{Temperature} + \beta_2\text{Dummy} + \beta_3\text{Dummy} \times \text{Temperature} + \mu. \quad (1)$$

If β_3 were significantly different from zero, then the test would suggest that the two sources of data did not demonstrate the same relationship between temperature and flowering times. If β_3 were not significantly different from zero, then the test would suggest that the photographs and the independently collected observations were statistically indistinguishable.

RESULTS

Herbarium specimens—There was a strong correlation among flowering dates of plants at the Arnold Arboretum in 2003, 2004, and 2005 ($r > 0.94$ for all comparisons among years). Plants flowered in essentially the same order each year. On average, plants flowered earliest in 2004 (day 145 or May 24) and latest in 2003 (day 156 or June 5). In 2005 plants flowered on June 2 (day 153) on average.

We tested whether the rate of change in flowering times estimated by OLS regression differed depending on which year of field observations we used as a benchmark in our calculations. We also tested whether multiple years of observation improved the estimates of changes in flowering times. In regressions for each year of field observations, we found significant trends toward earlier flowering from 1881 to 2002 (Table 1; $P < 0.05$ for all years). The rate of change in flowering times estimated by the regressions varied from 0.42 ± 0.19 (using 2005 field observations) to 0.59 ± 0.20 d (using 2003 field observations) earlier per decade. When we used the mean flowering times over the 3 yr of field observations, we estimated that plants flowered about 0.48 ± 0.19 d earlier each decade. The results among the 3 yr of field observations showed a consistent pattern of earlier flowering over time, indicating the robustness of our method.

We also determined how flowering times changed in response to warming temperatures in February–May using each of three benchmark years. In each case, mean February–May temperatures explained a significant amount of the variation in flowering times (Table 2; $P < 0.001$, $0.29 > R^2 > 0.23$ for each regression). The rate of change in flowering times varied from 3.7 ± 0.5 (using 2004 field observations) to 4.2 ± 0.5 d (using 2003 field observations) earlier per 1°C increase in mean February–May temperatures. When we used the mean flowering times over the 3 yr of field observations, we estimated that plants flowered about 3.9 ± 0.5 d earlier for each 1°C increase in mean February–May temperatures. The explanatory power of the model did not improve appreciably when we used the mean flowering times over the 3 yr of field observations ($R^2 = 0.29$) instead of just one year of field observations. Again, these results demonstrated the robustness of the basic approach of using herbarium specimens and one season of field observations to document changes in flowering time caused by warming.

These rates of change in flowering times in response to warming temperatures compare favorably with previously documented changes in flowering times, which demonstrated that plants are flowering 2–10 d earlier per 1°C increase in temperature (Fitter et al., 1995; Sparks and Carey, 1995; Sparks et al., 2000; Cayan et al., 2001). To test further if the results were reasonable, however, we estimated the change in flowering times in response to temperature for the 3 yr for which we made field observations, without using data from herbarium specimens. OLS regression on flowering times during these 3 yr indicated that plants flowered 4.7 ± 0.1 d earlier for each 1°C increase in mean February–May temperatures (Table 2; $P = 0.012$). The regression based on 3 yr of field observations is not particularly reliable, but the similarity between the results from herbarium specimens and the results from field observations is noteworthy.

Multiple regression indicated that temperature affected flowering times, with plants flowering relatively early in warm years ($P < 0.001$). When we accounted for the effects of temperature, plants actually tended to flower slightly later over time. Using multiple regression with the mean flowering times for the plants over the 3 yr of field observations and the herbarium records, plants flowered 0.76 ± 0.20 d later per decade and 5.4 ± 0.6 d earlier for each 1°C increase in mean February–May temperatures ($P < 0.001$ in both cases). Mean February–May temperatures at Blue Hill Observatory warmed 2.5°C from 1881 to 2002 ($P < 0.001$). In the particularly cold springs of 1881, 1893, 1901, and 1916 (mean February–May temperatures $< 3.0°C$), plants flowered 8 d later than on average. In the particularly warm springs of 1981, 1998, 1999, 2000, and 2002 (mean February–May temperatures $> 6.0°C$), plants flowered 6 d earlier than on average.

We also tested the ability of herbarium specimens alone, without field observations, to demonstrate changes in flowering times. We compared the flowering dates of herbarium specimens for each plant from which there were two or more

Table 2. Comparison of regression results showing change in flowering times in response to mean temperatures from February to May. For each year shown, we subtracted that year's peak flowering date from the date that a flowering specimen of that plant was collected in the past. This subtraction provided an estimate of the change in plant flowering dates. We then used ordinary least squares regression to estimate the rate of change in flowering times in response to mean February–May temperatures. We performed a similar regression using just the mean flowering dates as determined by the 3 yr of field observations, without herbarium specimen data, and as determined by herbarium specimens alone, without field observations. The R^2 value for the regression with field observations alone is very high because the three points fell along a straight line. SE represents the standard error of the regression coefficient. Negative regression coefficients indicate earlier flowering in warmer years.

Data	N	Regression coefficient (d/°C)	SE	P	R^2
2003 + herbarium specimens	177	−4.20	0.50	<0.001	0.29
2004 + herbarium specimens	177	−3.91	0.51	<0.001	0.25
2005 + herbarium specimens	177	−3.69	0.50	<0.001	0.24
Mean of 3 yr + herb. sp.	177	−3.94	0.46	<0.001	0.29
Field observations alone	3	−4.73	0.09	0.012	>0.99
Herbarium specimens alone	142	−5.92	0.71	<0.001	0.34

specimens. Using just these herbarium specimen data, OLS regression indicated that plants flowered 5.9 ± 0.7 d earlier for each 1°C increase in mean February–May temperatures ($P < 0.001$). According to the test in equation (1) this rate of change differed statistically from the rate determined using herbarium specimens and the mean flowering dates for the 3 yr of field observations ($P = 0.018$). Although the rates of change were statistically different, they were relatively similar in magnitude (5.9 compared to 4.7 d earlier for each 1°C increase in mean February–May temperatures).

Photographs—The photographic record of cultivated plants at the Arnold Arboretum indicated that plants are flowering about 11 d earlier on average over the last 100 yr (Fig. 3; $R^2 = 0.08$, $P < 0.001$). Multiple regression, using time and temperature as explanatory variables, demonstrated that this change in flowering time was due to warming mean temperatures from February to May. That is, the coefficient on the time term was not significantly different from zero ($P = 0.56$), while the coefficient on the temperature term was highly significant ($P < 0.001$). Plants flowered 3.9 d earlier for each 1°C increase in mean February–May temperatures ($R^2 = 0.27$, $P < 0.001$). The magnitude of the flowering response to warming temperatures closely matched the response of the same species in the same location as determined by our previous study of herbarium specimens at the Arnold Arboretum (Primack et al., 2004). Mean February–May temperatures at Blue Hill Observatory warmed 2.1°C from 1904 to 2004 ($P < 0.001$). In the particularly cold springs of 1916, 1923, 1924, and 1926 (mean February–May temperatures < 3.0°C), plants flowered 9 d later than average. In the particularly warm springs of 1976, 1977, 1981, 1991, 2002, and 2004 (mean February–May temperatures > 6.0°C), plants flowered 2 d earlier than average.

We tested the generality of this method by examining a photographic collection of wild species in Concord, Massachusetts. OLS regression using these data indicated that flowering times did not change from 1900 to 1921 ($P = 0.72$), which is reasonable because temperatures at Blue Hill Observatory did not warm over that time period (change in mean February–May temperatures = −0.03°C, $P = 0.97$). The photographic record demonstrated, however, that plants flowered 5.3 d earlier for each 1°C warming of spring temperatures (Fig. 4; $R^2 = 0.28$, $P = 0.001$). That is, plants flowered earlier in warm years, such as 1903, than in cool years, such as 1916. Specifically, in the particularly cold springs of 1901, 1916, 1917, and 1920 (mean February–May temperatures < 3.0°C), plants flowered 8 d later than average. In the particularly warm spring of 1903 (mean February–May temperatures > 6.0°C), plants flowered 8 d earlier than average.

We verified our regression results for wild plants by comparing them to results from an analysis of an independently collected set of unpublished observations of flowering times in Concord (A. W. Hosmer, Alfred W. Hosmer Botanical Manuscripts, 1878–1903, William Munroe Special Collections, Concord Free Public Library). Hosmer's observations indicated that the same species flowered 4.8 d earlier for each 1°C warming of spring temperatures ($R^2 = 0.08$, $P < 0.001$). To determine if the two trends differed significantly, we used the multiple regression test described in equation (1). The resultant β_3 was not significantly different from zero ($P = 0.84$), while both β_1 and β_2 were different from zero ($P < 0.001$ in both cases). This result for β_3 indicated that the trends from the photographs and the independently collected observations were statistically indistinguishable. The result for β_2 reflected the difference in methods between our calculations of changes in Hosmer's observations of first flowering dates and Gleason's photographs of peak flowering dates.

We also noted an example of how photographs may be used to document changes in the phenology of leaf out as well as flowering. We obtained a striking photograph (held by Janet Heywood of Mount Auburn Cemetery) taken in the Lowell Cemetery in Lowell, Massachusetts, on Memorial Day, 30 May 1868 (Fig. 2C, left). In the photo, the trees have not leafed out yet, despite the late date. In addition, people are wearing heavy clothing. A photograph taken on the same date in 2005 at the same location shows that the trees are fully leafed out (Fig. 2C, right). At least two of the large, leafless trees in the 1868 photo are still alive and had fully leafed out in 2005 but are not seen in the 2005 photo due to intervening trees. These two trees appear in the 1868 photograph directly above the far left and far right large rectangular stones. An exceptionally cold spring probably caused the delayed leaf-out in 1868. The mean temperature from February to May of that year was 2.2°C lower than the average over the past 150 yr and 2.7°C colder than February–May 2005.

DISCUSSION

Our results indicate that collections of photographs and herbarium specimens can provide valuable sources of data to document changes in flowering times. Specifically, photographs and herbarium specimens provide robust estimates of the date of peak flowering date. When analyzed, they demonstrate rates of change in flowering times that are statistically indistinguishable from independently collected data sets, including direct field observations. Moreover, these results hold true for both wild and cultivated plants.

Because photographs and herbarium specimens are far more

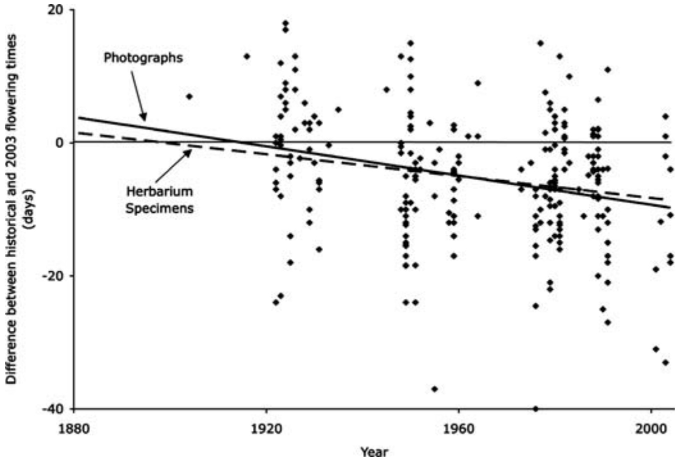

Fig. 3. Changes in flowering times of woody plants at the Arnold Arboretum of Harvard University in Boston for the period 1904–2004. Each point represents the difference between the date a historical photograph showed a specimen in flower and the date that the same species was in flower in 2003 (historical date − 2003 date). Negative values indicate historical flowering times that were earlier than flowering times in 2003. Solid line represents the best fit via ordinary least squares regression (slope = –0.11 d/yr, $R^2 = 0.08$, $P < 0.001$). For comparison, the dashed line represents regression using independent data from herbarium specimens and field observations in 2003 (slope = –0.08 d/yr, $R^2 = 0.06$, $P < 0.001$) (Primack et al., 2004). The individual data points from the herbarium specimen data are not shown.

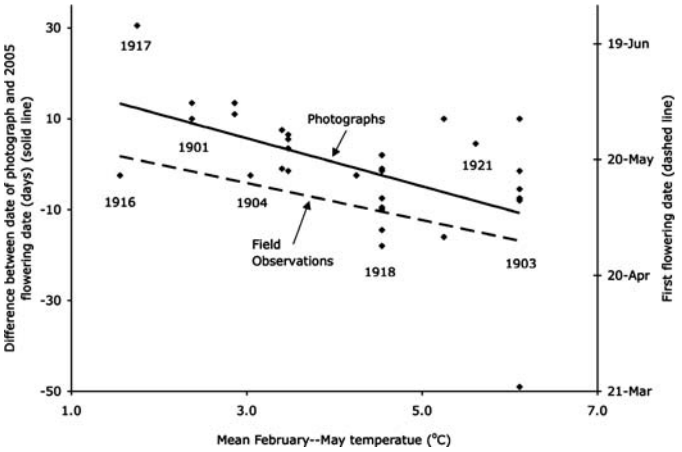

Fig. 4. Changes in flowering times in response to changes in mean spring (February–May) temperatures for wild plants in Concord, Massachusetts for the period 1900–1921. Each point represents the difference between the date a historical photograph showed a specimen in flower and the date that same species was in flower in 2005 (historical date – 2005 date). Negative values indicate historical flowering times that were earlier than flowering times in 2005. Solid line represents the best fit via ordinary least squares regression (slope = –5.3 d/°C, R^2 = 0.28, P = 0.001). Dashed line represents regression using independent data from field observations of first flowering dates collected by A. W. Hosmer between 1887 and 1903 (slope = –4.8 d/°C, $R^2 = 0.08$, $P < 0.001$). The individual data points for Hosmer's observations are not shown. If the point in the bottom right is removed, the trend remains significantly different from zero ($P = 0.003$) and not significantly different from the trend determined from the field observations ($P = 0.69$). Although the y-axes are different, the slopes for the two regression lines are in the same units, change in flowering date (days) per change in mean spring temperatures (°C).

abundant than are scientists' field observations, these records could dramatically increase the amount of reliable data available for phenological studies. Photographs and herbarium specimens contain long-term phenological data on large numbers of species in locations across the world. Collections of photographs and herbarium specimens are also common. They are often held in large collections in libraries, universities, museums, botanical gardens, and private collections. Photographs are particularly abundant and can contain information about many phenological events other than flowering, such as leaf-out, bird migration, and spring emergence of many organisms.

It is important to recognize, however, that use of herbarium specimens and photograph collections in phenological research is subject to strengths and limitations that differ from the strengths and limitations of observations collected by scientists in the field. We explored some of these strengths and limitations in our current study. We found three particularly important results. First, plants flowered in almost exactly the same sequence in all 3 yr that we made field observations. Molau et al. (2005) found a similar pattern for plants in Sweden. As a result, field sampling for a second and third year did not provide much additional information beyond that gained in one field season, when the field data were combined with a large historical data set (e.g., herbarium specimens). Second, we demonstrated that the response of flowering times to changes in temperature as measured by herbarium specimens and photographs combined with field observations statistically matched changes measured by field observations alone. Third, we found that herbarium specimens alone, without field observations, can show that flowering times respond to changes in temperature. The magnitude of the response measured with herbarium specimens alone was statistically different from the responses shown by studies on herbarium specimens combined with field observations. Even so, the results from herbarium specimens alone were similar to those that included data from field observations (Table 2).

This third finding, that herbarium specimens may be useful without field observations, is particularly surprising. Each herbarium specimen provides only an approximate record of the peak flowering date of the plant. In the case of plants with long flowering periods, a specimen could be collected several weeks earlier or later than the actual peak of full flower date. This uncertainty is significantly greater than the uncertainty contained in our weekly observations, which would have missed the peak full-flowering date by 7 d at most. When comparing two herbarium specimens to each other, the uncertainty associated with each sample could increase dramatically and obscure any trends showing earlier flowering times in warmer years. Despite these concerns, our findings demonstrate that herbarium specimens provide a robust measure of peak flowering times, at least with relatively large sample sizes.

In addition to the strengths of herbarium specimens and photographs as sources of phenological data, we note some factors that researchers must consider when using these types of data. For example, the number of photographs taken or herbarium specimens collected in any particular year can vary substantially. In the Arnold Arboretum photograph study, there were six periods with an especially large number of photographs. These periods corresponded to the periods that the Arnold Arboretum employed photographers. Also, photographs and herbarium specimens represent an observation of flowering on only one day during a multiday flowering period. Thus, results based on photographs or herbarium specimens may also be influenced by the tendency of one photographer or collector to photograph or collect plants as soon as they start to flower, or by another individual who tends to photograph or collect plants later when they have more flowers open (Lavoie and Lachance, 2006). These limitations did not substantially affect the results of our study, as demonstrated by the validation using independently collected data. Researchers who use photographic records in climate change research must consider these limitations, however, when determining the appropriate analysis and interpretation of results.

When interpreting our quantitative results, it is important to recognize that our regression analyses assumed implicitly that the flowering times of all the plants we observed changed at similar rates. We made this assumption for simplicity, even though we know that it is not true. The flowering times of different species have changed at different rates in response to climate change (Fitter et al., 1995; Sparks and Carey, 1995; Bradley et al., 1999). The differences between the rates at which flowering times have changed for different species added variation to our results and reduced the explanatory power of our regressions. To improve explanatory power, studies could examine changes in flowering times of single species (e.g., Lavoie and Lachance, 2006). Despite this added variation, we found a strong signal indicating that, on average, plants are flowering earlier now than in the past because of warmer temperatures.

Our findings and those of others (Menzel and Fabian, 1999; Chmielewski and Rotzer, 2001; Lavoie and Lachance, 2006), indicate that botanical gardens can serve as particularly valuable sources of long-term data to describe how plants are responding to climate change. Because of the sensitivity of plant phenological events to climate change (Root et al., 2003) and the importance of phenological events such as flowering, we suggest that botanical gardens actively collect phenological data on plants in their collections. Under ideal circumstances, staff could make direct observations of key phenological events such as leaf bud burst, flowering, fruiting, and leaf senescence. We have shown that alternative methods, however, such as the regular collection of herbarium specimens and photographs, can provide sufficient information to show phenological responses to climate change.

In conclusion, photographic and herbarium records provide novel and useful tools to examine long-term trends in phenological events and how they relate to climate change. They are abundant, and, as we have shown, they are also reliable. Analysis of such collections should dramatically increase our understanding of how climate change affects biological systems at many previously unexamined localities and for a wide range of species.

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