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Herbarium specimens demonstrate earlier flowering times in response to warming in Boston[1]

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Museum specimens collected in the past may be a valuable source of information on the response of species to climate change. This idea was tested by comparing the flowering times during the year 2003 of 229 living plants growing at the Arnold Arboretum in Boston, Massachusetts, USA, with 372 records of flowering times from 1885 to 2002 using herbarium specimens of the same individual plants. During this period, Boston experienced a 1.5°C increase in mean annual temperature. Flowering times became progressively earlier; plants flowered 8 d earlier from 1980 to 2002 than they did from 1900 to 1920. Most of this shift toward earlier flowering times is explained by the influence of temperature, especially temperatures in the months of February, March, April, and May, on flowering time. Plants with a long flowering duration appear to be as useful for detecting responses to changing temperatures as plants with a short flowering duration. Additional studies using herbarium specimens to detect responses to climate change could examine specimens from specific, intensively collected localities, such as mountain peaks, islands, and unique habitats.

Key words: Arnold Arboretum; climate change; flowering times; herbarium specimens; phenology; temperature.

Phenological observations provide one of the best biological indicators of climate change (Schwartz, 1999; Peñuelas and Filella, 2001). A growing number of papers have demonstrated phenological responses, such as earlier dates for flowering and bird migration, to changes in temperature at specific localities (e.g., Inouye and McGuire, 1991; Oglesby and Smith, 1995; Sparks and Carey, 1995; Ahas, 1999; Bradley et al., 1999; Fitter and Fitter, 2002). These phenological changes have been shown to impact interspecific interactions and evolutionary processes (Harrington et al., 1999; Inouye et al., 2000; Bradshaw and Holzapfel, 2001; Visser and Holleman, 2001). Phenological responses to climate change have been shown to exist at the global scale (Myneni et al., 1997; Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). Each of these studies relies upon long-term data sets typically created for the specific purpose of measuring phenology. Unfortunately, these data sets are rare and often difficult to find, and long-term phenological data are not available for many regions and species.

To supplement this small number of specialized historical records, biological collections from museums, herbaria, zoos, botanical gardens, and research stations may provide data for examining patterns of response to changing climate. Data from such collections has many advantages over the more conventionally used historical data sets:

1. Although most current long-term phenological studies are confined to Europe and North America, herbarium and museum samples have been collected from locations across the globe, and zoos and botanical gardens are similarly dispersed.
2. Collection records at herbaria and museums often extend back more than 100 yr, providing information for a significantly longer period than do most long-term data sets that have been analyzed.
3. Many of the recent analyses of historical phenology records have been limited by data sets that include a relatively small number of species. However, the records of museums and herbaria often include samples from a large number of species.
4. Historical data sets often describe only the beginning of reproduction for an entire population, the timing of which could be altered by changes in population size as well as climate (Sparks, 1999; Tryjanowski and Sparks, 2001). On the other hand, many specimens are collected at the peak of reproduction—especially plants, which are often preserved at the flowering stage—a time that is resistant to changes in population size.
5. Plants grown in controlled conditions may experience reduced fluctuations in nutrient availability, competition, and herbivory, factors which may impact a species' response to climate change. Thus, specimens taken from botanical gardens might better show the impacts of various climatic variables on phenology, while controlling for other factors.

If records from these collections could be used to detect patterns of species response to climate change, we would have a greatly expanded range of data for research.

The purpose of this project was to test whether herbarium records could be used to detect long-term changes in flowering times and the responses of numerous species to changes in springtime temperature. As far as we know, this is the first attempt to use museum specimens for this purpose. To accomplish this, we compared the current flowering dates of marked individuals with their past flowering dates using herbarium specimens collected over the last century at the Arnold Arboretum in Boston, Massachusetts, USA.

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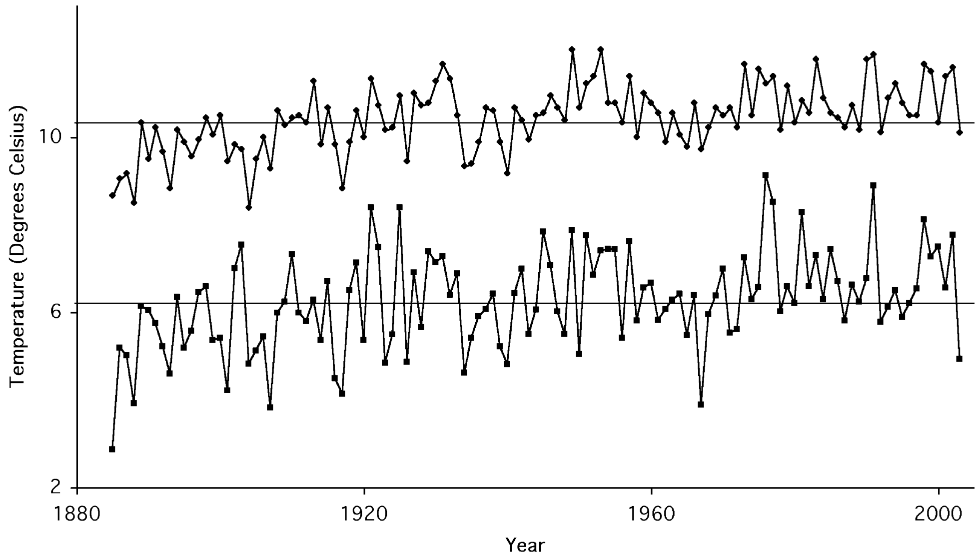

Fig. 1. Boston temperatures from 1885 to 2003 as reported by National Oceanic and Atmospheric Administration (2004). The top series (diamonds) represents mean annual temperatures. The bottom series (squares) represents mean temperatures in February, March, April, and May. The two horizontal lines represent the long-term mean temperatures for each series (annual = 10.3°C; Feb–May = 6.1°C).

MATERIALS AND METHODS

The Arnold Arboretum, managed by Harvard University, is the oldest arboretum in the United States. It has a collection of 15 000 living woody plants and an associated herbarium of 80 000 specimens, many of which were taken from numbered plants still growing on the grounds. Herbarium specimens are dried, flattened plant specimens, mounted on sheets, with label information describing when and where they were collected. Often plants are collected in full flower for use in later studies of plant taxonomy and morphology. After examining these herbarium specimens and using our knowledge of species biology, living plants were selected for study based on the following criteria: (1) plants that produce conspicuous, easily recognizable flowers; (2) plants that have an abrupt onset and fairly rapid decline of flowers, i.e., bloom for a relatively short time; (3) plants that represent wild species (either native or introduced) rather than cultivars and hybrids, to minimize unknown alterations of plant physiology; and of greatest importance, (4) only individuals for which there was at least one herbarium record of that plant in peak flower (at least half of the flowers were open) were selected for this study. Using these criteria, we selected 229 living plants for which there were 372 herbarium records of time of flowering between 1885 and 2002 (see Supplemental Data accompanying the online version of this article); some individual plants were represented by more than one herbarium specimen. These plants were contained in 37 genera. Genera that had at least 10 individuals in the sample are *Amelanchier*, *Cornus*, *Corylopsis*, *Enkianthus*, *Halesia*, *Magnolia*, *Malus*, *Prunus*, *Rhododendron*, and *Syringa*. All specimens are woody plants, including trees, shrubs, and vines. Individual plants are grown well spaced in conditions considered ideal for the species, which includes mulching, weeding, and pesticide and fertilizer applications when needed.

During the spring and summer of 2003, the same two people observed these individually numbered plants weekly between 13 April and 14 July. The observers determined the current peak flowering date and duration of flowering for each plant. Plants were recorded as being in one of four stages: not flowering, almost in full flower, full flower, or past full flower. A plant in full flower was defined as having at least 50% of its buds in full bloom and as being suitable for making a herbarium specimen. Once a plant was recorded as past flower, it was no longer observed.

A single Julian date of full flower was determined for each plant in 2003, although this date could have missed the true flowering peak by 3–4 d due to sampling just once a week. In cases when full flowering was observed on multiple dates, the mean of the Julian dates for those days was used. Once the date of full flowering was determined for each plant in 2003, these dates were compared with flowering dates based on the herbarium records. For each record, the Julian date of peak flowering in 2003 was subtracted from the Julian date of the past flowering date to estimate a change in plant flowering dates. In effect, the flowering dates of 2003 were used as a standard against which flowering times in other years were compared. The spring (February through May) of 2003 was colder than any previous year since 1967 and was more typical of temperatures early in the 20th century. Using these changes in flowering dates for individual plants, we used multiple regression analysis to examine how flowering times across all species have changed over time and how this change compares to the trend of warming spring temperatures in Boston. We estimated the following equation: $\Delta FT = \acute{\alpha} + B_1\Delta Temp + B_2\Delta Time + \mu$, where ΔFT, $\Delta Temp$, and $\Delta Time$ are the difference between the flowering time, temperature, and years, respectively, in 2003 and a past year in which a herbarium specimen was collected. $\acute{\alpha}$ is a constant, B_1 and B_2 are regression coefficients, and μ is a normally distributed random error term.

Over the last 100 yr, Boston has experienced an annual temperature increase of 1.5°C (Fig. 1), which has been due to regional climate change and the urban heat island effect (New England Regional Assessment, 2001). We hypothesized that, given this warming trend, analysis of herbarium samples would demonstrate that plants are responding to a warmer climate by flowering earlier. We believed that the main drawback of using herbarium samples to determine peak flowering date would be the deviation between the dates of collection and peak flowering; that is, people in the past might have collected specimens early or late in the flowering season, obscuring trends in flowering times. We investigated this area further in our analysis.

RESULTS

Over the last 100 yr (without considering temperature as an explanatory variable), plants are flowering progressively earlier, about 8 d earlier on average (Fig. 2). As seen in Fig. 2, the flowering times of plants from 1900 to 1920 are indistinguishable from their flowering times in the cool year of 2003, while plants flowering during the warmer years of 1980 to 2002 flowered much earlier than they did in the 2003 benchmark year.

We were concerned that three factors—outlying data points, non-normal distribution of collection effort, and errors associated with collection times of herbarium specimens—could

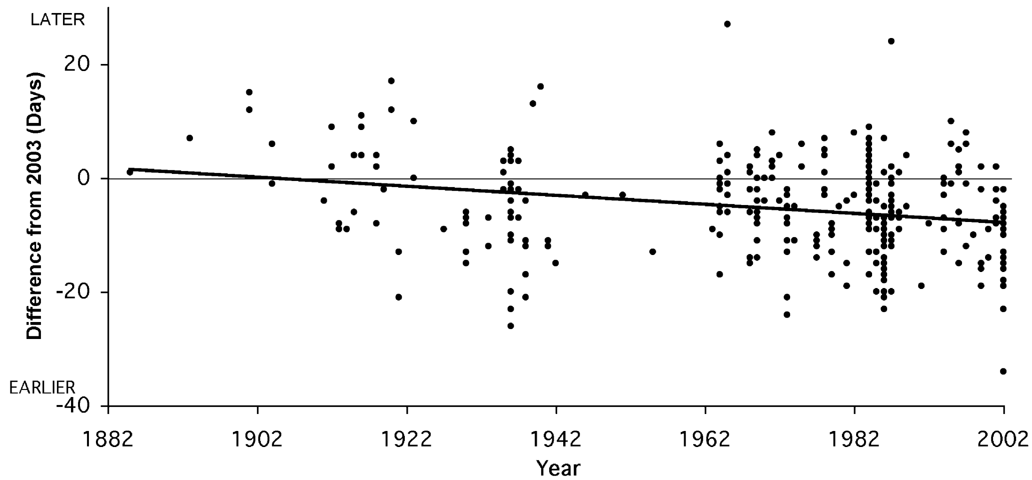

Fig. 2. Changes in flowering times of plants at the Arnold Arboretum over time: number of days plants flowered earlier or later in the past than they did in 2003 calculated as the Julian date the herbarium specimen was collected subtracted from the peak flowering date in 2003. Negative values indicate that a plant flowered on an earlier date than that it did in 2003. The line is the best fit line for the series.

have obscured or skewed this trend. Because of the large number of data points (372 samples), the few outliers present in the data set—such as a dogwood (*Cornus mas*) that flowered 27 d later in 1965 than in 2003 and a cherry tree (*Prunus apetela*) that flowered 24 d later in 1987 than in 2003—did not significantly affect the trend toward earlier flowering. Additionally, although herbarium samples were collected more actively in some decades than others—with a gap in collecting from 1940 to 1960—the overall tendency toward earlier flowering time in recent years was not affected. When the groups of herbarium samples on either side of the gap in the record are analyzed separately, observations in both periods demonstrate significant trends toward earlier flowering (1885–1955, $P < 0.001$; 1960–2002, $P < 0.001$).

In addition to the trend toward earlier flowering over time, the herbarium records demonstrate that plant flowering times are highly responsive to changes in average temperatures in the 4 mo (mean temperature in February, March, April, and May) before and during flowering ($P < 0.001$; Fig. 3). Flowering times are sensitive to relatively small shifts in temperature, advancing 3.9 d per 1°C increase in mean spring temperature (when controlling for time). This rate of advancement agrees with the findings of other studies, which have observed flowering times to be 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). Given that temperatures in February through May have warmed approximately 1.5°C over the past 100 yr (Fig. 1), warming temperatures seem to have caused the Arboretum plants to flower approximately 5 d earlier over the past 100 yr. The multiple regression results also showed that time (after controlling for changes in temperature) showed a significant relationship with flowering time, with plants flowering earlier over time ($P < 0.001$).

We examined possible sampling errors associated with herbarium specimens. We wanted to determine if past herbarium dates for plants with a long flowering duration in 2003 would

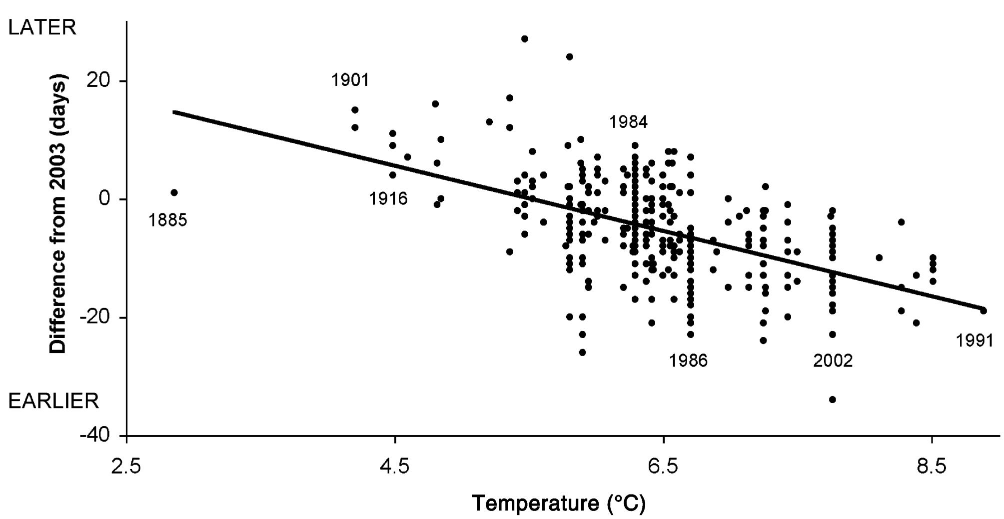

Fig. 3. Changes in flowering times of plants at the Arnold Arboretum as temperatures increase: number of days plants flowered earlier or later in the past than they did in 2003 in relation to the average temperatures in the February, March, April and May preceding flowering. Years are indicated for certain years with many specimens and years with extreme temperatures. The line is the best fit line for the series.

deviate more from the 2003 peak flowering date than would those for plants with a short flowering duration in 2003. Our hypothesis was that collectors would have a period of several weeks to collect specimens from long-flowering plants, leading to more sampling variation than plants that flower for a brief duration. To test this hypothesis, we divided plants into three categories based on their flowering in 2003: rapid flowering plants (174 records) with observed peak flowering of 1 wk or less; medium-flowering plants (115 records) with 2 wk of peak flowering; and long-flowering plants (83 records) with 3 or more weeks of peak flowering. We then examined the absolute mean difference of each plant's herbarium collection date from its date of peak flowering in 2003. We calculated the mean differences for each of the three categories of plants. We found that the mean differences were essentially the same for each category of flowering duration (means and standard deviations for rapid-, medium-, and long-flowering durations are 8.2 ± 6.2, 8.0 ± 5.8, and 7.6 ± 5.7, respectively). Therefore, we concluded that, for the purposes of this study, collection bias did not affect data from plants with a long flowering duration.

DISCUSSION

Using the herbarium records of the Arnold Arboretum from 1885 to 2002 and observations from one field season in 2003, we were able to demonstrate a significant response of plant flowering time to changing spring temperatures over the past century. Specifically, plants are now flowering earlier because of warmer spring temperatures, as shown by multiple regression.

We believe that four primary factors contributed to our ability to show this response. First, the large number of samples used from the Arboretum herbarium (372 specimens) appears to have overcome any possible error introduced by collection dates that vary from peak flowering date. Second, the samples come from one relatively homogenous location—that is, the Arboretum grounds contain no significant shifts in elevation, and land use has remained the same. These characteristics minimized sampling errors that might have hidden the effects of climate change. Third, we were able to compare past flowering times from herbarium samples with the current flowering time of the same plants that are still living on the Arboretum grounds. Thus, we were able to observe the flowering phenology of each individual plant for one field season (2003). That one year of data became our reference year, to which we compared the historical flowering times and from which we were able to establish trends in flowering date over time and temperature. By using tagged plants, we were able to eliminate the variation in flowering time among plants of the same species caused by genetic and environmental variation.

Fourth, our study benefited from the excess warming in Boston caused by the urban heat-island effect. Between 1885 and the present, the time covered by our study, the mean annual temperature of the rural areas of Massachusetts warmed by 0.7°C (Keim et al., 2003), while the city of Boston warmed by 1.5°C, as the city surfaces were covered by more buildings and paved surfaces. The extra warming almost certainly made the trend toward earlier flowering time in Boston more visible than it would have been in other, less urbanized areas of the United States (Roetzer et al., 2000). Such earlier flowering has similarly been noted in other urban centers, such as the Washington, D.C., area (Shetler and Wiser, 1987). However, the large sample size used in our study would have likely allowed us to detect earlier flowering with even less warming than the 1.5°C warming experienced by Boston.

When we used multiple regression to control for temperature, plants were still flowering earlier over time. Therefore, factors other than temperature at the Boston weather station were also affecting flowering times. These factors could include temperature in other months of the year and other climatic variables, such as rainfall and humidity. Local conditions within and around the Arboretum may also affect flowering times. For example, increased paving of roads within the Arboretum and construction of buildings on adjacent land may have caused localized warming. Finally, if plants were flowering over a longer period as they increased in size and age and were consistently collected at the beginning of their flowering period, there could be a false trend toward earlier flowering over time. Further investigations are needed in order to determine the relative importance of these factors.

Our results suggest that other museum and herbarium collections could be utilized to measure the effects of climate change on phenological events. We believe that many such intensive collections exist at other institutions. Collections may also exist in a much more dispersed form, with samples having been collected from one location by many individuals and now being held at various storage sites. Certain localities with unusual concentrations of endemic or rare species have been intensively collected by biologists at many periods in the past, especially mountain peaks, islands, swamps, lake shores, and dunes. For example, biologists have collected extensively from many isolated natural areas—e.g., the top of Mount Washington in New Hampshire, the Florida Everglades, the northern tip of Newfoundland, and Stewart Island off the southern coast of New Zealand.

If information on flowering time from one of these locations could be gathered into one data set, an analysis could reflect the responses of native species to climate change. We believe that many such data sets from around the world could be assembled, covering the last 100–150 yr. Using such data, analyses could allow scientists to clarify the extent and character of local variation in natural responses to climate change. Furthermore, this would improve predictions of the effects that future climate change might have on biological communities. Using herbarium specimens from the Arnold Arboretum and 1 yr of observation, we have been able to demonstrate a clear pattern of earlier flowering over time and earlier flowering in response to warmer spring temperatures.

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