Flowering phenology change and climate warming in southwestern Ohio

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Abstract Global surface temperature has increased markedly over the last 100 years. This increase has a variety of implications for human societies, and for ecological systems. One of the most obvious ways ecosystems are affected by global climate change is through alteration of organisms' developmental timing (phenology). We used annual botanical surveys that documented the first flowering for an array of species from 1976 to 2003 to examine the potential implications of climate change for plant development. The overall trend for these species was a progressively earlier flowering time. The two earliest flowering taxa (*Galanthus* and *Crocus*) also exhibited the strongest shift in first flowering. We detected a significant trend in climate suggesting higher temperatures in winter and spring over the sampling interval and found a significant relationship between warming temperatures and first flowering time for

some species. Although 60% of the species in our study flowered earlier over the sampling interval, the remaining species exhibited no statistically detectable change. This variation in response is ostensibly associated with among-species variation in the role of climate cues in plant development. Future work is needed to isolate specific climate cues, and to link plant phenology to the physiological processes that trigger plant development.

Keywords Climate change · Global warming · First flowering · Minimum temperature

Introduction

Reports issued over the past 20 years by the Intergovernmental Panel on Climate Change (IPCC) have been increasingly clear about changes currently occurring in Earth systems (Houghton et al. 2001). Most recently, the Fourth Assessment Report (AR4) concluded that “warming of the climate system is unequivocal” (Solomon et al. 2007, p. 7) and that “observational evidence from all continents and most oceans shows that many natural systems are being affected by regional climate changes, particularly temperature increases” (Parry et al. 2007, p. 8). Climate warming has been shown to initiate a complex of ecological responses. In some instances, ecosystem structure may be altered substantially, and

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ecosystem-climate system feedbacks have been identified (Chapin et al. 2008). The spatial distribution of some plants is expected to shift in a warmer climate (Iverson and Prasad 1998; Walther et al. 2002; Woodall et al. 2009), and alterations in migration timing have been documented for a number of animal species (Bradley et al. 1999; Parmesan 2006). These shifts have important ecological implications as some interdependent community relationships could be disrupted (Walther et al. 2002; Parmesan 2006).

Alteration of plant phenology is one of the most readily observable ecosystem reactions to climate change. Numerous studies have indicated shifts in plant phenology related to climate warming (e.g., Orlandi et al. 2005; Nordli et al. 2008). For instance, Fitter and Fitter (2002) found an average advance of 4.5 days in flowering date among the 385 species sampled in a study from south-central England over the four decades prior to the 1990s. Bradley et al. (1999) documented overall changes of 1.2 days per decade in the phenology of various species in recent years compared to the dates measured six decades earlier. Increasingly early plant development has been documented in a number of species and study systems (Abu-Asab et al. 2001; Menzel et al. 2006; Parmesan 2006; Nordli et al. 2008).

Multi-species assessments have yielded some particular hypotheses about the nature of plant phenology change in a warming climate. First, species that flower early in the growing season tend to exhibit a greater shift in flowering time. In some species, this shift may be related to maintaining the adaptive advantage of development in advance of potential competitors in early spring (e.g., Muller 1978). Second, species' reactions to climate change are non-uniform. Bradley et al. (1999) found that while many species had substantially earlier flowering times, other species were "non-responders" that did not change in response to climate warming. The latter likely include species with flowering triggered by photoperiod. This non-uniform response across species has important ecological implications as it creates the potential for climate-response mismatches between ecologically interdependent species (Bradley et al. 1999; Walther et al. 2002; Parmesan 2006).

We examined a 28-year data set of first flowering observations in southwestern Ohio, USA. Our objective was to investigate potential influences of global change processes on plant phenology and to identify

variation in response among species. We hypothesized that (H_1) plants in our study would flower increasingly early in association with a warming climate. We further hypothesized that (H_2) plants that flower in the early spring would change more substantially than species flowering later in the year.

Methods

Our analysis was based on flowering phenology observations on a species rich 0.5 hectare tract in Beavercreek, OH (39°73'N, 84°04'W) from January 1976 through 2003 (Carol Graff, personal communication). The observations were made every day through spring and summer of each year. A transit was made each morning along a path that circles through the property. Additional observations were made in secondary transits during most days (Carol Graff, personal communication). Across the sampling period, 270 different taxa of both native and cultivated species were observed, though most were observed only a few times, and many were taxonomic varieties. Because we were specifically interested in long-term changes in flowering phenology, in our analyses we only included taxa that occurred in ≥ 16 of the observation years.

For the purposes of analysis, first flowering dates were converted to ordinal date (mathematical sum of days beginning at 1 January). Simple linear regression analysis was used to test the hypothesis of no change in first flowering date (for each taxon individually) over the sampling interval. In this analysis, year was the independent variable, ordinal date of flowering was the dependant variable, and the regression was considered significantly different from zero at $P \leq 0.05$.

Daily climate data were obtained from the National Climate Data Center for the weather station at the Dayton International Airport (Co-op ID #332075; located at 39°54'N, 84°13'W). The weather station is located approximately 35 km from the site of observations. We analyzed mean daily maximum and minimum temperature for each month. A linear regression analysis was performed on the raw monthly data to test the statistical significance of any deviation over time of the temperature trend from zero. Regressions were considered significantly different from zero at $P \leq 0.05$, and highly significant at $P \leq 0.01$. Since we were interested in potential influences of

temperature changes during the period for which we had observations, we used temperature data for the period 1976–2003.

Results

We found 15 taxa with at least 16 observations over the 28-year sampling period (Table 1). These included ornamental species, natives to the region, exotic ornamentals, and a variety of life forms including both woody and herbaceous species. First flowering dates ranged from early March through early August (Table 1).

In support of our first hypothesis (H_1), 9 of the 15 taxa we tested (60%) had a statistically significant negative slope (Table 1; Fig. 1) indicating earlier flowering. For instance, *Crocus*, *Galanthus* and *Phlox* were the three taxa with the most strongly negative slope (Fig. 2) and the regression for each of these was highly significant ($P < 0.001$, for all three). In contrast, species such as *Ranunculus*, *Centaurea* and *Ageratum* did not exhibit detectable changes over the sampling period (Fig. 2).

We found some support for our hypothesis (H_2) that species flowering earlier in the year would have the strongest change in flowering date. *Galanthus* and

Crocus had the two most negative slopes, indicating the most substantial shift in flowering time, and were also the two earliest flowering species (Fig. 1). Considering only species that flowered before June (ordinal date ~ 150), there was a highly significant positive relationship ($P = 0.003$; $r^2 = 0.6$) between flowering date and flowering date change, where species that flowered later in the year also had a less negative slope (Fig. 1; relationship not shown). An analysis that included the whole data set, though, suggested no relationship ($P = 0.3$; $r^2 = 0.08$), and this was largely caused by two taxa (*Phlox* and *Hosta*) that had significantly negative slopes, but were late flowering species (Fig. 1).

Over the sampling period there was a distinct trend in temperature, with increasingly warm temperatures especially apparent for months early in the year (Table 2). Although there was substantial annual variability, mean minimum temperature exhibited a significant (increasing) trend for January, February and June ($P < 0.05$; Fig. 3). We also detected a significant trend in mean minimum temperature averaging December through February (Table 2). Mean maximum temperatures in January also increased significantly (Table 2).

Early season temperature changes were strongly correlated to changes in first flowering date of early

Table 1 First flowering date change of plant species monitored for 28 years in southwestern Ohio, USA

First flowering		Taxon	First flowering change		
Date (mean)	Ordinal day (mean $\pm$ SE)		Days/year (slope)	r^2	P
02 March	61 $\pm$ 2.8	<i>Galanthus</i> sp. (snowdrop)	−1.10	0.36	0.001
06 March	65 $\pm$ 3.2	<i>Crocus flavus</i> (crocus)	−1.22	0.33	0.001
27 March	86 $\pm$ 2.0	<i>Forsythia</i> sp. (forsythia)	−0.18	0.02	0.468
18 April	108 $\pm$ 1.5	<i>Viola pubescens</i> (yellow violet)	−0.58	0.35	0.001
19 April	109 $\pm$ 1.5	<i>Malus</i> sp. (crab apple)	−0.45	0.25	0.014
23 April	113 $\pm$ 1.6	<i>Ajuga reptans</i> (ajuga)	−0.19	0.04	0.336
25 April	115 $\pm$ 1.3	<i>Delphinium consolidate</i> (larkspur)	−0.37	0.20	0.019
27 April	117 $\pm$ 2.2	<i>Dicentra spectabilis</i> (bleeding heart)	−0.37	0.18	0.047
27 April	117 $\pm$ 1.2	<i>Geranium maculatum</i> (wild geranium)	−0.19	0.06	0.243
05 May	125 $\pm$ 1.9	<i>Ranunculus</i> sp. (buttercup)	0.16	0.02	0.488
13 May	133 $\pm$ 2.3	<i>Centaurea cyanus</i> (bachelor's button)	0.23	0.04	0.440
19 May	138 $\pm$ 1.6	<i>Hemerocallis lilioasphodelus</i> (daylily)	−0.40	0.16	0.044
14 July	195 $\pm$ 2.2	<i>Phlox</i> sp. (phlox)	−0.91	0.50	<0.001
08 August	220 $\pm$ 1.9	<i>Ageratum</i> sp. (ageratum)	0.18	0.02	0.475
11 August	223 $\pm$ 2.3	<i>Hosta plantaginea</i> (giant white hosta)	−0.64	0.20	0.039

Fig. 1 First flowering date change (ordinal date) over a 28-year (1976–2003) observation period in southwestern Ohio, USA. Flowering date change represents the slope of the linear regression between first flowering date and year. Darkened symbols represent slopes that were statistically different from zero ($P < 0.05$), and the horizontal dashed line represents no change

flowering species (Fig. 4). Mean minimum temperatures for December–February were significantly, and negatively, related to first flowering date in *Galanthus* ($P < 0.001$; $r^2 = 0.61$) and *Crocus* ($P = 0.001$; $r^2 = 0.33$) (Fig. 4). These two species were the earliest flowering species and also exhibited the strongest shifts in flowering (Table 1; Fig. 1). First flowering dates for *Galanthus* ($P < 0.001$; $r^2 = 0.66$) and *Crocus* ($P < 0.001$; $r^2 = 0.39$) were also

significantly related to mean maximum temperature over the same 3 months (Fig. 4).

Discussion

A warming global climate has the potential to substantially influence the structure, composition, and function of ecosystems (Parmesan 2006; Chapin

Fig. 2 Response of first flowering date (ordinal date) of selected taxa over a 28-year (1976–2003) observation period in southwestern Ohio, USA. Column of figures on the left represents the three species with the most negative slopes (all significant at $P \leq 0.001$; solid lines) indicating increasingly early flowering. Figures on the right represent the three most positive slopes (none statistically significant, dotted lines). Panels in each column are ordered from earliest to latest flowering

Table 2 Temperature trends from 1976 to 2003 in southwestern Ohio, USA

Month	Minimum (°C/year)	Maximum (°C/year)
December	0.04	0.00
January	0.19*	0.18*
February	0.17**	0.12
March	−0.01	−0.04*
April	0.04	0.01
May	0.02	−0.05*
June	0.06*	−0.03*
July	0.01	−0.03*
August	0.04	0.02
December–February	0.10*	0.13**

Slope of the linear regression values for raw data are given (* $P < 0.05$; ** $P < 0.01$)

Fig. 3 Temperature trend for selected months over a 28-year (1976–2003) observation period in southwestern Ohio, USA

et al. 2008). Alteration in the timing of plant phenology is one important potential impact of a warming climate (Bradley et al. 1999; Fitter and

Fitter 2002; Primack et al. 2004; Orlandi et al. 2005). Our data supported the hypothesis (H_1) that first flowering time was increasingly early over the last three decades and was related to an overall trend of increasing seasonal temperature. Of the species in our study, 60% exhibited significantly earlier flowering over the study period. Abu-Asab et al. (2001), similarly, found an increasingly early flowering time for a variety of species correlated with an increase in minimum temperatures in the Washington, DC area. Similarly, Houle (2007) found an advance of 2–6 days per century in a study of flowering phenology in eastern Canadian forest species. That study found that a shift of 2–3 days was correlated with a change of 1°C of temperature rise, and showed a stronger effect on species found in Montreal, a large urban area which experiences a heat-island effect (Houle 2007). Our data add to a growing body of work (e.g., Fitter and Fitter 2002; Parmesan and Yohe 2003; Nordli et al. 2008) that indicates plant phenology is changing markedly in association with a warming climate.

In addition to the overall trend of increasingly early flowering, we hypothesized (H_2) that early flowering plants would exhibit a more marked change in phenology than later flowering species. Hypothetically, early-spring flowering species, which exploit a narrow window in time before leaf-out of other species, would have evolutionary pressure to track climatic conditions and begin development at the earliest opportunity. A number of studies have supported this concept (e.g., Abu-Asab et al. 2001; Fitter and Fitter 2002; Walther et al. 2002). For instance, Parmesan and Yohe (2003) found that 62% of early spring phenophases shifted earlier in response to climate warming. We found some support for this postulate as the earliest flowering species also exhibited the strongest change in first flowering; however, two of the latest flowering species also exhibited substantially earlier flowering. Physiological work is needed to understand the mechanism(s) underlying tracking of winter temperature in early flowering species, and more survey work is needed to identify taxonomic patterns in flowering response.

Beyond variation in flowering phenology across the growing season, we found that some species responded to climate warming, while others were stable. Bradley et al. (1999), focusing only on springtime events, found that approximately one-third of the phenophases

Fig. 4 Relationship between first flowering date change (ordinal date) and mean temperature December through February over a 28-year (1976–2003) observation period in southwestern Ohio, USA. All relationships were significant at $P \leq 0.001$

they observed (including animals as well as plants) were earlier as a result of climate change, one-third were later, and one-third remained stable. In our study, plants that flowered in the range of 100–150 ordinal days (late April through early June) exhibited a variety of responses including significantly earlier flowering and non-response (Fig. 1). The cause of this variation is unknown. These species encountered identical climatic stimuli, so the cause of these differences must be linked to variation in the role of climate as a developmental trigger. We hypothesize that winter and early spring warming accelerated growth of some taxa such that they arrived at a requisite developmental threshold sooner, while other species were either (1) not accelerated by climate warming or (2) development was accelerated but flowering was unchanged because the flowering trigger was photoperiod (which is stable). Bradley et al. (1999) argue that flowering in many species is cued by photoperiod and therefore will not respond to climate warming. This suggests the possibility of a lag effect in some species that may reach a growth threshold earlier but flowering is stalled because photoperiod is unchanged. Future work is needed that focuses on the particular relationship(s) between temperature (and other climate cues),

photoperiod, developmental pathways, and physiological activity in plant species.

Climate change has wide ranging implications for ecosystems, and one of the most important is the potential for alterations in the life-history timing of individual species. Our data suggest that (1) some plant species are responding to variation in climate, (2) across the growing season the reaction is non-uniform and (3) even within season, some species react to changes in climate while others are non-responders. Given the potential importance of climate–response mismatches between community members, understanding the basis of plant phenology response is an important next step for research (Parmesan 2006). In particular, we suggest that future work is needed that bridges the gap between pattern (plant phenology response) and process (plant developmental physiology) in relation to particular climatic cues.

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