

SHIFTS IN THE FLOWERING PHENOLOGY OF THE NORTHERN GREAT PLAINS: PATTERNS OVER 100 YEARS¹

KELSEY L. DUNNELL² AND STEVEN E. TRAVERS²

Department of Biological Sciences, North Dakota State University, Dept. 2715, P.O. Box 6050, Fargo, North Dakota 58108-6050 USA

- *Premise of the study:* Climate change is associated with phenological shifts in an increasing number of organisms worldwide. However, accurate estimates of these shifts are dependent on long-term data sets that include phenological observations from before annual average temperatures began to rise.
- *Methods:* We compared the first flowering times of native prairie plants between 2007 and 2010 with historical data recorded by O. A. Stevens from 1910 to 1961. By merging climate variable data from the same time period, it also was possible to correlate first flowering dates with associated climate variables.
- *Key results:* Over the past 100 years, spring temperatures in the Red River Valley near Fargo, North Dakota, USA, have increased, and growing seasons have lengthened significantly. Seventy-five percent of the 178 species observed by Stevens had flowering times that were sensitive to at least one variable related to temperature or precipitation. Over the past 4 yr, 5% to 17% of the species observed have significantly shifted their first flowering time either earlier or later relative to the previous century.
- *Conclusions:* The results of this study indicate that as spring temperatures in the northern Great Plains have increased and the growing season has lengthened, some spring flowering species have advanced their first flowering time, some fall species have delayed their first flowering, and some species have not changed. Given the importance of flowering timing for reproductive success, the changing climate in the Great Plains is expected to have long-term ecological and evolutionary consequences for native plant species.

Key words: climate change; flowering; Minnesota; North Dakota; phenology; prairie.

The timing of flowering of plants is a potentially powerful determinant of the fitness of individuals (Rathcke and Lacey, 1985). Ecological relationships between plants and pollinators or plants and herbivores depend on complex dynamics of synchronicity among multiple species (e.g., the simultaneous availability of mature floral structures and visiting pollinators). Waser (1979) found that seed set per flower in ocotillo, *Fouquieria splendens*, is greatest for flowers that bloom at the same time that hummingbirds are migrating through the region. Further, while studying *Impatiens pallida*, Schemske (1984) found strong evidence that in some populations, early summer flowering increases fitness relative to later flowering because of increasing levels of herbivory in mid and late summer. However, as a result of changes in the global climate over the past 100 yr, the phenology of many plant species is changing (Schwartz, 1994; Walther et al., 2002; Root et al., 2003; Menzel et al., 2006; Schwartz et al., 2006; Cleland et al., 2007). Because of the importance of the timing of reproductive phases for the reproductive success of plants, we need to understand the relationship between climate change and plant phenology if we are

to understand ecological and evolutionary dynamics of future plant communities. As temperatures rise and precipitation patterns change, understanding the specific cues for phenological phases becomes more important.

There is strong evidence that regional temperature increases over the past 100 yr are caused by increasing concentrations of greenhouse gases in the atmosphere, which trap reflected radiation (Nicholls, 1996; Kaufmann and Stern, 1997; Barnett et al., 2001; IPCC, 2007). The rate of warming of the globe from 1976 onward has been greater than at any other time in the last 1000 yr (Walther et al., 2002). Moreover, if atmospheric CO₂ concentrations continue to increase as they have, the environmental conditions that many species have evolved under will soon be significantly different.

Understanding how plants will adapt to these rapidly changing climate conditions in the future depends in part on understanding phenological shifts that have already occurred. However, long-term data sets of flowering patterns before temperature increases in the 1970s are rare. Results of some studies indicate that many plant species in northern latitudes in Europe and Asia have advanced their flowering periods in concert with increasing temperatures over the past several decades (Sparks and Carey, 1995; Ahas et al., 2002; Scheifinger et al., 2003; Wielgolaski and Inouye, 2003; Chen et al., 2005; Menzel et al., 2006; Zheng et al., 2006; Gordo and Sanz, 2009; Primack et al., 2009). Evidence for advancement in flowering periods in North America has also been found at northern latitudes (Bradley et al., 1999; Miller-Rushing and Primack, 2008; Miller-Rushing and Inouye, 2009) or montane regions (Inouye et al., 2002; Inouye et al., 2003; Inouye, 2008; Forrest et al., 2010; Lambert et al., 2010) where growing seasons are constrained by severe seasonality. There is also some indication that late-flowering

¹Manuscript received 16 September 2010; revision accepted 14 February 2011.

The authors thank T. Owen and A. Akyüz for their assistance in obtaining climate data for this study, D. Rehder for his observations, and the Minnesota Nature Conservancy for their support. M. Otte, A. Akyüz, G. Clambey, and E. Wolkovich provided helpful comments on an early draft of the manuscript. Funding was provided by NSF Epscor grant EPS0814442 to NDSU and the Cross Ranch Foundation.

² Authors for correspondence (Kelsey.Dunnell@ars.usda.gov, steven.travers@ndsu.edu)

species have shifted to later flowering with climate change (Sherry et al., 2007). However, long-term patterns in flowering phenology are generally understudied because of a lack of historical data on flowering patterns.

Here we present the results of a study that builds on the historical observations made in the Red River Valley region near Fargo, North Dakota, USA, by O. A. Stevens. He recorded the first flowering dates of hundreds of plant species from 1910 to 1961 in two adjacent counties, Cass County, North Dakota, and Clay County, Minnesota (Stevens, 1961; Travers and Dunnell, 2009). By comparing long-term temperature data to these flowering time observations and comparing flowering time before and after the 1970s, we examined how climate and climate change have influenced flowering phenology in the Cass/Clay County area.

The average annual temperature in Fargo and the length of growing season throughout North Dakota have increased since the 1970s (Badh et al., 2009). If this change in climate has not resulted in corresponding biological shifts, we would expect that the first flowering times of plant species in the area will not have changed on average. A field survey was conducted to test this null hypothesis. The objectives of this study were (1) to analyze Stevens' historical data of first flowering times of local plants near Fargo to look for temporal trends and relationships with climate variables and (2) to compare first flowering times of plants recorded recently (2007–2010) and historically (1910–1961).

MATERIALS AND METHODS

Climate measurements—To characterize two of the main components of climate in the northern Great Plains, temperature and precipitation, over the past century, we collected and compiled daily climate data collected in Fargo, North Dakota, USA, as part of the National Atmospheric and Oceanic Administration (NOAA) National Climatic Data Center (NCDC) observing network (<http://www.ncdc.noaa.gov/oa/ncdc.html>). These raw data included daily measures of the maximum and minimum air temperature and detectable precipitation from January 1, 1910, to the present. Snowfall was recorded as water equivalents. The data collection station was originally located in Moorhead, Minnesota (46°52'N, 96°44'W), at an elevation of 281.9 m a.s.l. However, in March of 1930, the station was moved 2.5 km to the Fargo Hector International Airport (46°56'N, 96°49'W) at an elevation of 274.3 m a.s.l.

The daily mean temperatures from these data were calculated by taking the averaging of the maximum and minimum for each day. These daily values then were used to calculate monthly and annual averages for each year from 1910 to 2009. In addition, the daily measurements of detectable precipitation were used to calculate monthly and yearly averages of precipitation per year over the same time period. Growing degree units during the months of February through May were calculated by summing the daily degree units over the course of each month with a minimum critical temperature of 1.7°C (35°F).

Flowering phenology from 1910 to 1961—To estimate the first flowering dates (hereafter FFDs) of plants in the northern Great Plains, we transcribed the handwritten notes of O. A. Stevens, an experienced botanist and a professor at North Dakota State University. O. A. Stevens observed the flowering phenology of plants in the Red River Valley area near Fargo, North Dakota, and Moorhead, Minnesota, from 1910 to 1961 (Stevens, 1961; Travers and Dunnell, 2009) and recorded the FFD of hundreds of species annually. The majority of the records were made on plants located within a 20-mile radius of the Fargo/Moorhead area (Travers and Dunnell, 2009). Stevens developed a professional interest in the timing of first flowering of prairie plant species during graduate school in Kansas (Stevens, 1917). As a result, he developed a practice of recording the first flowers seen each season during spring and summer months.

The FFDs in Stevens' handwritten notes were transcribed for a total of 448 plant species observed in adjacent Cass County, North Dakota, and Clay County, Minnesota, surrounding Fargo. The majority of plant species observed

by Stevens were native prairie and woodland species located in a 5821-acre section of native tall-grass prairie (Bluestem Prairie Preserve, Clay County, Minnesota). This patch of prairie has been managed by the Nature Conservancy since 1975 and has a rich flora of native species. Before 1975 it was uncultivated, presumably because of rocky soil. Stevens recorded the genus and species epithet of each species he observed as well as the date of the observation. If the record indicated that the observed plant was not the first flowering plant, the data were excluded from further analysis. Plant names were converted to the most recent nomenclature by comparison with synonym lists in the USDA NRCS Plants Database (plants.usda.gov). The dates of first flowering were converted to day of the year, for which January 1 of a given year is 1 to standardize the data for year-to-year comparisons. The transcribed observations began March 18, 1910, and continued through September 10, 1961. The complete data set is available at Ecological Archives (<http://esapubs.org/archive>; see Travers and Dunnell, 2009).

The FFD values observed by Stevens provide an estimate of the variability and responsiveness of flowering to environmental variables before annual temperatures in the region began increasing rapidly. We analyzed the relationship between environmental variables and FFD on an annual basis before 1962 to provide a baseline indication of which, if any, environmental variables were strong correlates of flowering time. Separate stepwise regression analyses were conducted on the first flowering data for each species. To minimize disproportionate influence of outlying values, only data from 1911 to 1961 were included in this regression analysis (1910 was not included). The initial regression model included FFD as the dependent variable and six climate variables plus year as independent variables. The independent variables derived from temperature data were calculated for each year of the observations. These variables included mean daily temperature, averaged separately for February, March, April, and May, and the day of the year of the last freeze (<0°C) in spring. An estimate of winter precipitation was included by calculating the amount of snow that fell during October through March before a given spring and converting those values to centimeters of water. Finally, the year was included as an independent variable to examine temporal patterns independent of climate. All stepwise regression analyses used the forward format and were conducted with SAS (SAS Institute, Cary, North Carolina, USA). Stepwise regressions were conducted only on those species that had been observed a minimum of 10 yr (total of 178 species). The order of predictive ability of the independent variables was determined for those variables with *P* values less than 0.05 based on decreasing magnitude of their partial *R*² values.

Flowering phenology from 2007 to 2010—To assess first flowering times of plants between 2007 and 2010, we observed plants in the same locations that Stevens had observed them in Cass and Clay counties. In addition, some species were observed in the Sheyenne National Grassland in adjacent Ransom County, North Dakota. Starting in April of each year and continuing through August, the FFD of all species was recorded. Herbaceous and woody plants in flower were recorded at Bluestem Prairie Preserve approximately twice a week and at the Sheyenne National Grassland approximately once a week during the study. We predicted that increasing annual temperatures between 1961 and 2007 have led to shifts in FFD because of dependence of flowering initiation on spring temperatures. To test this hypothesis, we first calculated 95% confidence intervals around the mean FFD values of each species between 1910 and 1961 (Zar, 1974). The FFD of each species in each year between 2007 and 2010 was compared with the mean and confidence interval of the same species between 1910 and 1961. Deviations from the mean greater than the confidence interval were considered significantly different. We adjusted for multiple tests with a Bonferroni correction (Sokal and Rohlf, 1995) by using an alpha level of 0.05 divided by the sample size 292 in the calculation of the original confidence intervals (see Discussion section).

RESULTS

Climate measurements—Daily measures of air temperature indicate that average annual temperatures in Fargo have increased over the years between 1900 and 2008 (Fig. 1). In particular, the scatter plot indicates an upswing in average temperature since the 1970s that is commensurate with global air temperature trends (IPCC, 2007). The average annual temperature within the first 9 yr of this time period (between 1900 and 1909) was 3°F lower than in the last 9 yr (between 1999 and

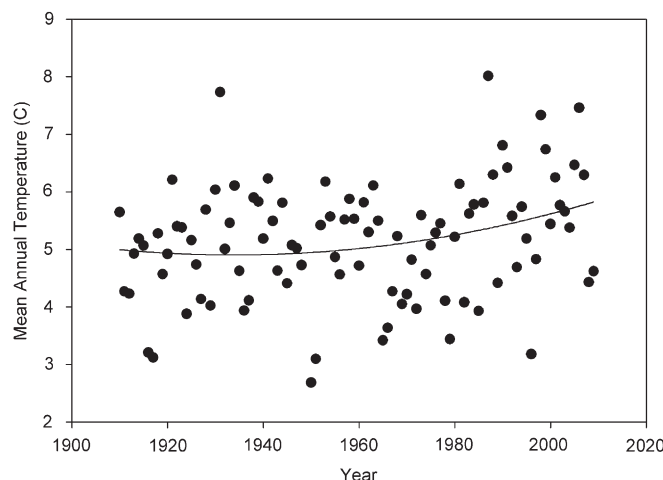


Fig. 1. Mean annual temperature (°C) at Fargo, North Dakota, USA. A quadratic regression model was significant at an alpha of 0.05 ($Y = 614 - 0.63x + 0.0002x^2$, $P = 0.029$, $df = 68$, $R^2 = 0.07$).

2008). Monthly averages of air temperature in February and May, but not in March and April, have increased over time (linear regression results: Feb: $b = 0.05^*$, $R^2 = 0.06$; March: $b = 0.01$ ns, $R^2 = 0.005$; April: $b = 0.01$ ns, $R^2 = 0.01$; May: $b = 0.03^*$, $R^2 = 0.04$; * indicates $P < 0.05$).

In concordance with the increasing annual air temperature and spring air temperature, the growing season in Fargo has increased in duration over the last 100 yr (Fig. 2). The 10-yr average of the number of days between the last frost of spring and the first frost of fall ($\leq 0^\circ\text{C}$) increased from 132 d to 154 d over the period 1910 to 2008. In particular, the growing season increased dramatically after 1970. This pattern of longer growing seasons since 1975 has been seen throughout North Dakota (Bahd et al., 2009).

Annual precipitation in the Fargo area varied considerably between 1900 and 2008 (Fig. 3). During the middle of the last century, average precipitation decreased from a high of 31 inches in 1905. However, since the 1970s, annual precipitation has increased back up to levels seen in the early 1900s. We tested linear and parabolic regression models and found a distinct improvement in fit with the squared term of the parabolic model. Seventeen percent of the variance in annual precipitation is explained by a parabolic model (Fig. 3). Precipitation in North Dakota has been cyclical over the past century, as evidenced by the pattern of variation in Fig. 3. It is not clear whether long-term changes in climate will amplify the cyclical nature of precipitation in the Fargo area or rather lead to steadily wetter conditions. The current “wet period” in the region is the longest on record.

The 4 recent years during which FFDs were observed for plants in the Red River Valley varied considerably in temperature and precipitation patterns (Table 1). Spring of the first and fourth years of the study (2007, 2010) was warmer on average than during the intervening 2 yr. In particular, March, April, and May were characterized by accumulated growing degree units in excess of the average from 1910–1961 (Table 1). In contrast, 2008 and 2009 were more typical of the period between 1910 and 1961. Precipitation in all 4 recent yr of the study was higher than average compared with 1910 to 1961. Annual precipitation values and winter snowfall values were more than twice as high as the average of the earlier century (Table 1).

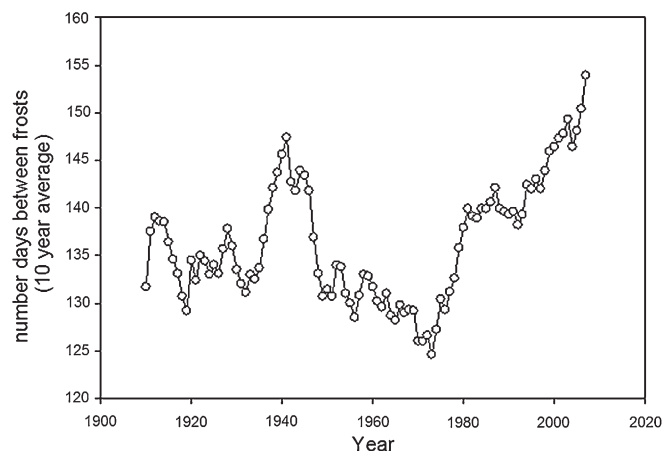


Fig. 2. Average growing season (number of days between last and first frost, 0°C) by year. Annual values were first calculated by summing the days from the last frost of spring, $<0^\circ\text{C}$, to the first frost of fall, 0°C . The plotted values represent the average of the annual values during the 10 yr before a year (e.g., 1910: mean of 1901–1910).

Flowering phenology from 1910 to 1961—A total of 753 plant species (631 herbaceous and 122 woody species) were observed by O. A. Stevens and recorded in the database of observations from 1910 to 1961 (Travers and Dunnell, 2009). Not all these species were observed every year. The number of records varied between 17 and 309 species per year, with an average of 88 species observed per year.

The responsiveness of FFD to multiple variables was analyzed for 178 species. The number of independent variables significantly associated with FFD varied among species. Twenty-two percent of the species showed no relationship between FFD and any of the independent variables (Appendix S1; see Supplemental Data with the online version of this article). In contrast, 11% of species responded significantly to three different variables, 31% to two variables, and 35% to a single variable. The overall R^2 values ranged from 0.0041 to 0.9943, depending on the species. The specific predictor of first flowering depends on the species, but the predictor that explained the greatest variation in first flowering time was most commonly

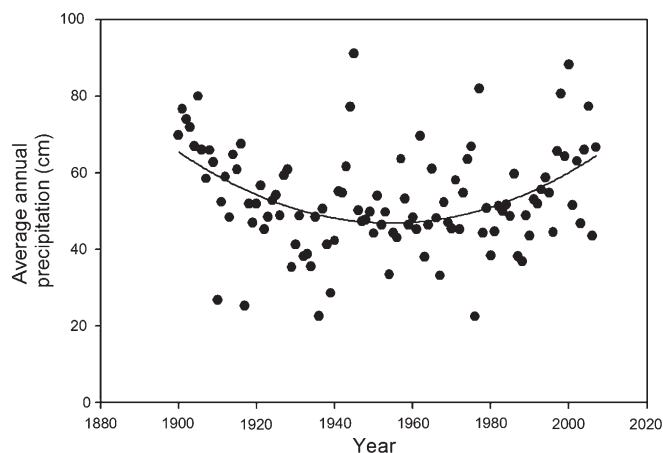


Fig. 3. Average annual precipitation (cm) at Fargo, North Dakota, USA. The solid line is the quadratic best-fit regression line ($Y = 9552 - 9.8x + 0.002x^2$, $F = 10.8$, $P < 0.0001$, $df = 108$, $R^2 = 0.17$).

TABLE 1. Climate summary in Fargo, North Dakota, USA, during the years of the study. The estimate of annual precipitation (cm) includes rainfall and snow conversion from January 1 to December 31. Winter snowfall is calculated as the number of centimeters of snow accumulated between June 30 and July 1 of the previous year. Data for the period between 1910 and 1961 include the average of the annual values during that period and the range (in parentheses).

Year(s)	Growing degree units				Annual precipitation (cm)	Winter snowfall (cm)
	February	March	April	May		
1910–1961	6.2 (0–33.8)	42.7 (2.2–166.3)	171.9 (58.9–290.8)	354.3 (220–487.5)	29.2 (22.5–91.1)	90.9 (23.6–209.0)
2007	3.1	77.2	205.8	436.9	66.6	98.5
2008	0	18.6	148.6	335.6	77.7	151.9
2009	2.8	33.3	150.8	327.5	63.2	202.4
2010	0	80.3	289.7	398.3	—	118.4

the average temperature in April, followed by May as the next most common predictor (Fig. 4).

Flowering phenology from 2007 to 2010—In 2007, 2008, 2009, and 2010, a total of 39, 93, 89, and 71 species, respectively, were observed in the study area. Overall, the percentage of species that bloomed significantly earlier or later than the mean of the early part of the century increased in warmer years (Table 1). In the two warmest years, 2007 and 2010, significant shifts in flowering time were observed in 33% and 41% of the

species, respectively. In contrast, 25% and 24% were early or late in 2008 and 2009. As expected, more species flowered early in the 2 warm years relative to the cooler years. A greater percentage of the species that deviated significantly were early in warm years (2007: 92%; 2010: 93%), relative to results in the cooler years (2008: 13%; 2009: 10%). However, in all 4 yr, some species flowered later than expected. Early-flowering species typically flowered in the first half of the growing season and late-flowering species in the second half of the growing season in all 4 yr. Regression analysis indicated significant positive

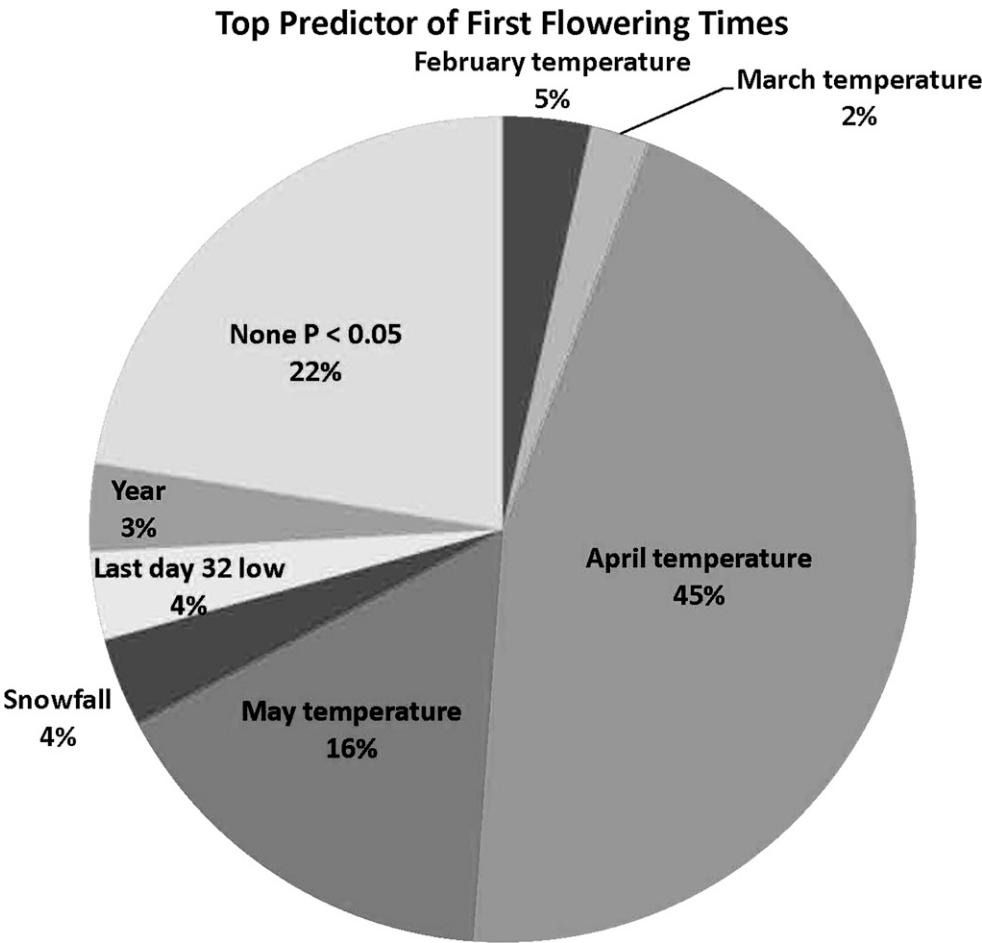


Fig. 4. Percentage of species out of 178 analyzed by stepwise regression with each of the possible independent variables as the leading predictor. The slope of the relationship between the predictor and the first flowering date could be either positive or negative.

relationships between flowering date and deviation in all years but 2007, indicating that early-flowering species flowered earlier in 2007–2010, and later-flowering species flowered later during this period (Fig. 5). We conclude that changes in population sizes of species showing significant deviations are not a likely confounding factor on observed FFD. All these species were described by Stevens as either common or frequent in the 1920s (Stevens, 1921) and were observed to be common or frequent between 2007 and 2010.

DISCUSSION

The results of this study indicate significant recent shifts in the phenological patterns for some species of flowering plants in the northern Great Plains relative to the first half of the previous century. On the basis of the mean and variance in FFD for the same species before 1961, between 24% and 41% of the species flowered either unusually early or late between 2007 and 2010 (Table 2). Warmer temperatures during 2 of the 4 recent yr of our study were associated with an increase in the total percentage of species deviating significantly from historical patterns, suggesting that temperature is playing a large role in changing flowering phenology of some species. We found strong relationships between temperature and FFD before climate change led to increasing temperatures in the latter half of the century. Therefore, we would expect plants to flower differently now that annual and spring temperatures are higher. Indeed, plots of FFD as a function of temperature in April illustrate that the earlier flowering dates of some species are consistent with the temperature dependence observed from 1910 to 1961 (Fig. 6). In contrast, for species with delayed FFD (Fig. 7), less of a relationship exists between spring temperature and FFD.

Despite the increases in annual temperatures and growing season length since 1961, it is important to note that more than half the species have not significantly changed their timing of flowering relative to the timing observed in the last century. In comparison to other studies that have found shifts in a majority of the species observed (Miller-Rushing and Primack, 2008),

the proportion of the species significantly changing phenology is low. One possible explanation is that changes in climate in the Midwestern region of the continent may be less dramatic than those in other areas. The prediction would then be that over the next several decades, more species in the northern Great Plains will show significant shifts from historical flowering patterns, as climate models predict the increase in annual temperature will continue (Easterling et al., 2000). Many of the species that have shown no significant response to increasing temperatures may have phenological patterns based on mechanisms other than temperature or precipitation. For example, if seed germination or flower bud initiation of a particular plant species began in response to a minimum critical length of day rather than to a minimum temperature, that species would be likely to flower at a relatively constant day of the year regardless of climate change.

Earlier flowering and spring green-up have been documented after 1970 in other regions of the United States and Europe (Bradley et al., 1999; Root et al., 2003; Menzel et al., 2006; Miller-Rushing and Primack, 2008). The patterns of shifted flowering phenology in this study are robust and are based on multiple decades of observation. Despite significant variation during Stevens' observations, some plants are now flowering more than 2 standard deviations (either earlier or later) than they once did.

The pattern of advanced and delayed flowering in association with extended growing seasons is consistent with observations reported in other studies (Callow et al., 1992; Taylor and Garbary, 2003). In an experimental study manipulating temperature, Sherry et al. (2007) found that plants in warmed plots flowered earlier than controls if they flowered in the first half of the growing season, and they flowered later if they flowered in the second half of the growing season. Multiple studies have found plants fruiting later over time in regions with a lengthening growing season relative to results in past years (Peñuelas et al., 2002; Menzel et al., 2006). This phenomenon may be common and suggests further shifts in plant communities associated with climate change.

The mechanism for later flowering is not clear, but it may be that in the presence of longer growing seasons and the corresponding delays in the occurrence of killing frosts in the fall, selection against late flowering and fruiting may have been relaxed. In the early part of the last century, seeds that were produced late in the season may have been destroyed by the onset of winter. However, individuals now flowering and fruiting late in the season could produce seeds that would reach maturity before winter because of a later initiation of fall. This shift in selection would lead to later-flowering individuals on average. In addition, by flowering and fruiting later, the late-flowering plant species may avoid competition with earlier-flowering species for pollinators and resources. An alternative explanation of delayed flowering with warmer springs is that species with chilling requirements are not initiating germination as early because of warmer winters (Yu et al., 2010). If increasing global temperatures lead to a reduction in the period when temperatures are low enough to satisfy a chilling requirement, we would expect those species with long chilling requirements to germinate later in warmer years.

Not all species shifted consistently between 2007 and 2010 (Table 2). Sixteen different species varied in flowering time over the 4 recent yr. In each case, the species flowered early in the 2 relatively warm years (2007, 2010) and flowered late in the cool years. As a result, the day of the year each species

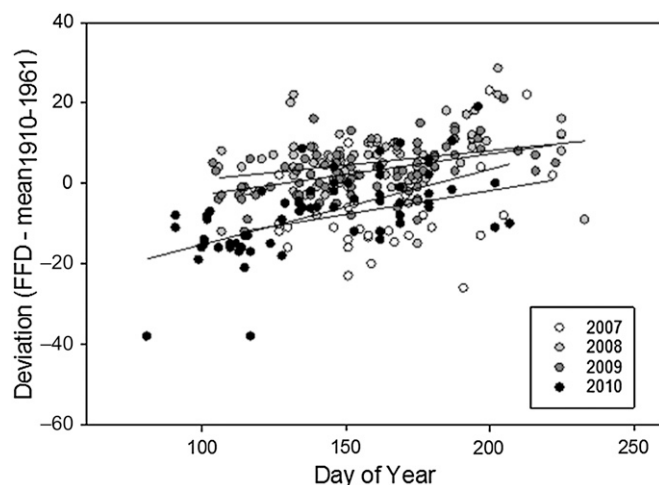


Fig. 5. The deviation in the first flowering dates (FFD) from the mean for that species between 1910 and 1960. Data for 4 recent years are labeled separately. Best-fit regression lines were calculated separately for each year (2007: $b = 0.12$, $F = 3.2$, $P = 0.08$; 2008: $b = 0.07$, $F = 8.4$, $P = 0.005$; 2009: $b = 0.1$, $F = 23.8$, $P < 0.001$; 2010: $b = 0.18$, $F = 40.9$, $P < 0.001$).

TABLE 2. First flowering dates (FFD) for plants near Fargo, North Dakota, USA, in 2007, 2008, 2009, and 2010. Deviation is the difference in the number of days from the mean from 1910–1961. Negative indicates earlier flowering. An asterisk indicates a deviation greater than the 95% confidence interval based on an alpha level of 0.0002.

Scientific name	1910-1961				2007		2008		2009		2010	
	Mean FFD	N	SE	CI(± days)	FFD	Deviation	FFD	Deviation	FFD	Deviation	FFD	Deviation
<i>Acer saccharinum</i>	99	51	0.402	4.3			107	8*	104	5*	91	-8*
<i>Corylus americana</i>	102	11	0.904	10.1			106	4	105	3	91	-11*
<i>Populus tremuloides</i>	110	17	0.817	10.2					106	-4	103	-7
<i>Thlaspi arvense</i>	110	35	0.654	9.4			132	22*				
<i>Ulmus americana</i>	110	49	0.433	4.9			114	4	107	-3	102	-8*
<i>Shepherdia argentea</i>	111	44	0.446	4.9			131	20*	117	6*	102	-9*
<i>Acer negundo</i>	115	47	0.439	4.9			121	6*	114	-1	101	-14*
<i>Populus deltoides</i>	116	42	0.454	5			113	-3	113	-3	101	-15*
<i>Sanguinaria canadensis</i>	116	16	0.756	8.5					115	-1	100	-16*
<i>Ranunculus rhomboides</i>	118	14	0.958	12.8		-2	125	7	114	-4	99	-19*
<i>Capsella bursa-pastoris</i>	119	15	0.871	10.9			107	-12*			81	-38*
<i>Androsace occidentalis</i>	122	22	0.653	7.4			120	-2	119	-3	106	-16*
<i>Ranunculus abortivus</i>	123	10	1.122	14.8			132	9	139	16*	121	-2
<i>Betula papyrifera</i>	125	33	0.477	4.9					116	-9*		
<i>Callitha palustris</i>	125	4	1.300	12.6	127	2	132	7	124	-1	110	-15*
<i>Viola papilionacea</i>	125	8	0.871	8					129	4		
<i>Celtis occidentalis</i>	126	26	0.542	5.6							110	-16*
<i>Arisaema triphyllum</i>	127	2	2.144	24.2					115	-12*	135	8.5
<i>Fraxinus lanceolata</i>	127	35	0.485	5.2								
<i>Prunus tomentosa</i>	127	10	0.938	10.3								
<i>Fragaria virginiana</i>	128	4	0.895	6			132	4			112	-15*
<i>Prunus americana</i>	129	50	0.393	4.1			138	9*			115	-13*
<i>Anelanchier alnifolia</i>	130	41	0.437	4.6			139	9*	138	9*	116	-13*
<i>Ostrya virginiana</i>	130	11	0.933	10.7					136	6*	114	-16*
<i>Uvularia grandifolia</i>	130	7	0.929	8.5			132	2	133	3	113	-17*
<i>Prunus triloba</i>	133	12	0.863	10					140	7		
<i>Cerastium arvense</i>	134	12	0.814	8.4			132	-2	134	0	117	-17*
<i>Malus sylvestris</i>	134	22	0.622	6.7			139	5				
<i>Ribes americanum</i>	134	10	0.824	8			139	5			129	-5
<i>Zanthoxylum americanum</i>	136	8	1.006	10.6			148	12.1*	138	2	115	-21*
<i>Ribes missouriense</i>	136	8	0.937	9.2			138	2	133	-3		
<i>Smilacina stellata</i>	137	11	0.806	8			142	5				
<i>Viola pedatifida</i>	137	7	1.242	15.2		-10	144	7*	134	-3	128	-9
<i>Trillium cernuum</i>	139	7	1.119	12.3	127		145	6	143	4	134	-5
<i>Allium textile</i>	139	11	0.948	11.1					152	13*		
<i>Lithospermum canescens</i>	139	7	1.074	11.4	127	-12*	136	-3	134	-5	124	-15*
<i>Lithospermum incisum</i>	140	7	1.011	10			148	8	147	7	138	-2
<i>Actaea rubra</i>	141	25	0.476	4.2			148	7				
<i>Crataegus chrysocarpa</i>	141	6	1.226	13.7			148	7				
<i>Lonicera tatarica</i>	141	30	0.488	4.8					148	7*	135	-6*
<i>Oxalis violacea</i>	141	16	0.612	5.6	130	-11*	140	-1	141	0	134	-7
<i>Sisyrinchium angustifolium</i>	141	11	0.911	10.2	151	10	147	6	138	-3	134	-7
<i>Zizia aptera</i>	142	8	0.997	10.4			148	6	147	5	146	4
<i>Aquilegia canadensis</i>	144	14	0.649	5.8					143	-1		
<i>Comandra umbellata</i>	144	4	1.561	18.1			148	4	147	2.75	138	-6.25
<i>Senecio plattensis</i>	145	11	0.714	6.3	146	1						
<i>Acer ginnala</i>	146	11	0.838	8.7					152	6		
<i>Conringia orientalis</i>	146	9	1.031	11.9			153	7				
<i>Hydrophyllum virginianum</i>	146	33	0.432	4			148	2	148	2	140	-6*
<i>Pedicularis canadensis</i>	146	3	1.328	11.4	130	-16*	144	-2	141	-5	128	-18*

TABLE 2. Continued.

Scientific name	Mean FFD	1910-1961			2007			2008			2009			2010		
		N	SE	CI(± days)	FFD	Deviation	FFD	Deviation	FFD	Deviation	FFD	Deviation	FFD	Deviation	FFD	Deviation
<i>Zizia aurea</i>	146	22	0.591	6.1	151	5	143	-3	147	1	146	0	146	0	146	0
<i>Hesperis matronalis</i>	147	11	0.831	8.5			150	3	148	1			148	1		
<i>Descurainia pinnata</i>	148	17	0.740	8.4			140	-8								
<i>Erysimum asperum</i>	148	7	0.923	8.3				0								
<i>Galium aparine</i>	148	16	0.595	5.3			148	0	149	1	146	-2	149	1	146	-2
<i>Hypoxis hirsuta</i>	148	6	1.093	10.9	146	-2		1	152	4			152	4		
<i>Viburnum lentago</i>	148	10	0.784	7.2			158	10*	159	11*			159	11*		
<i>Juglans nigra</i>	149	17	0.566	4.9			159	10*								
<i>Vicia americana</i>	150	22	0.569	5.6			161	11*								
<i>Osmorhiza longistylis</i>	151	9	0.981	10.7			161	10								
<i>Castilleja sessiliflora</i>	151	3	1.609	16.7	151	0	158	7	152	1	151	0	151	0	151	0
<i>Cypripedium candidum</i>	152	3	1.589	16.2	151	-1	147	-5	147	-5	146	-6	146	-6	146	-6
<i>Polygala senega</i>	152	3	1.355	11.8												
<i>Smilax herbacea</i>	152	10	0.871	8.9					154	2			154	2		
<i>Berteroa incana</i>	153	3	1.705	18.7					155	2			155	2		
<i>Oxytropis lambertii</i>	153	4	0.943	6.6					152	-1			152	-1		
<i>Anorpha fruticosa</i>	154	6	1.474	19.8												
<i>Erigeron philadelphicus</i>	154	9	1.089	13.2			161	7					162	8		
<i>Oxalis stricta</i>	155	6	1.206	13.2			164	9	152	-3			117	-38*		
<i>Agoseris glauca</i>	157	5	1.311	14.3			161	4								
<i>Anemone canadensis</i>	157	13	0.702	6.6			161	4								
<i>Penstemon albidus</i>	157	4	1.364	13.8	151	-6	161	4					153	4		
<i>Tragopogon dubius</i>	158	17	0.573	5	146	-11	167	10	161	4			153	4		
<i>Melilotus officinalis</i>	159	23	0.542	5.2	153	-5	163	5	168	10*			162	4		
<i>Galium boreale</i>	160	13	0.645	5.6			168	8*	168	9*			169	10*		
<i>Heuchera richardsonii</i>	160	9	1.256	17.6			168	8	152	-8			162	2		
<i>Heracleum maximum</i>	161	8	1.100	12.7					176	14.9*						
<i>Scrophularia lanceolata</i>	162	8	1.322	18.3			169	7	161	-1						
<i>Medicago lupulina</i>	162	9	0.739	6.1			164	2								
<i>Penstemon grandiflorus</i>	165	4	1.357	13.7	151	-14*	168	3	168	3			153	-12		
<i>Rosa arkansana</i>	165	14	0.583	4.7	153	-12*	168	3	175	10*			162	-3		
<i>Achillea millefolium</i>	167	8	0.941	8.1	155	-11*	168	1.5	168	1.5			162	-4.5		
<i>Asclepias ovalifolia</i>	167	5	1.199	12			185	18*	175	8						
<i>Gaura coccinea</i>	167	10	1.136	15.2	151	-16*	166	-1	170	3			169	-1		
<i>Rudbeckia hirta</i>	170	3	0.760	3.7			177	7*	175	5*						
<i>Gaillardia aristata</i>	171	5	1.519	19.2	158	-13	175	4	170	-1						
<i>Koeleria macrantha</i>	171	3	1.255	10.1					173	2						
<i>Pedimelum esculentum</i>	172	2	1.573	13	158	-13*	172	0.5								
<i>Anemone cylindrica</i>	173	5	1.156	11.1			174	1	175	2			179	6		
<i>Thalictrum dasycarpum</i>	173	4	1.566	18.2	171	-2			175	2			179	6		
<i>Apocynum cannabinum</i>	174	14	0.762	8.1			177	3	177	3			169	-5		
<i>Convolvulus arvensis</i>	174	5	1.185	11.7			177	3	188	14*						
<i>Lilium philadelphicum</i>	174	4	0.984	7.2	171	-3	181	7	181	7			179	5		
<i>Oenothera serrulata</i>	174	4	1.717	21.9			175	1								
<i>Penstemon gracilis</i>	174	12	0.946	11.5	151	-23*	172	-2	168	-6			162	-12*		
<i>Zigadenus elegans</i>	174	6	0.750	5.1	171	-3	177	3	172	-2			162	-12*		
<i>Calyptophus serrulatus</i>	175	4	1.717	21.9			203	28.5*	181	6.5						
<i>Catalpa speciosa</i>	175	15	0.704	7.1			192	17*	188	13*						
<i>Asclepias syriaca</i>	176	9	0.753	6.3			185	9*	185	9*						
<i>Onosmodium occidentale</i>	176	5	1.821	27.5			178	2	175	-1			162	-14		
<i>Potentilla pensylvanica</i>	177	4	1.445	15.5									187	10.5*		
<i>Delphinium virescens</i>	177	10	0.896	9.43	165	-11	178	1	181	4			179	2		

TABLE 2. Continued.

Scientific name	1910-1961				2007		2008		2009		2010	
	Mean FFD	N	SE	CI(± days)	FFD	Deviation	FFD	Deviation	FFD	Deviation	FFD	Deviation
<i>Campanula rapunculoides</i>	177	4	0.783	4.5	177	0	172	-5*	188	11*	169	-8
<i>Cicuta maculata</i>	177	6	0.957	8.3	200	23*	195	18	181	4	196	19
<i>Oenothera nuttallii</i>	177	6	1.456	19.3	159	-20	177	0	175	-4	169	-8
<i>Potentilla arguta</i>	179	3	2.001	25.8					175	-4	169	-10
<i>Campanula rotundifolia</i>	179	9	1.039	12					175	-4		
<i>Symphoricarpos occidentalis</i>	181	12	0.861	9.6			203	22*	188	7		
<i>Psoralea argophylla</i>	182	12	0.861	9.5	167	-14*					179	-3
<i>Pedimelum argophyllum</i>	182	12	0.761	7.5			194	12*				
<i>Rhus glabra</i>	183	3	1.920	23.7			194	11				
<i>Lygodesmia juncea</i>	184	11	0.822	8.3					205	21*		
<i>Lactuca pulchella</i>	184	3	1.427	13.1					197	13	179	-5
<i>Lobelia spicata</i>	184	5	1.649	22.6					175	-9		
<i>Chrysopsis villosa</i>	185	7	0.952	8.9	177	-8	194	9*	188	3	179	-6
<i>Anorpha canescens</i>	185	8	1.130	13.4	172	-13	190	5	196	11	179	-6
<i>Ratibida columnifera</i>	189	7	1.216	14.5			199	10	197	8	187	-2
<i>Dalea purpurea</i>	190	3	1.520	14.9			175	-15*				
<i>Panicum virgatum</i>	191	4	1.630	19.8	180	-11						
<i>Dalea candida</i>	191	2	2.144	24.1	213	22						
<i>Parnassia palustris</i>	193	13	0.836	9.4	197	4						
<i>Oenothera biennis</i>	202	5	0.868	6.3					210	8*	202	0
<i>Liatris pycnostachya</i>	209	6	1.383	17.4			225	16	216	7		
<i>Solidago missouriensis</i>	210	16	0.755	8.5	197	-13*						
<i>Helianthus maximiliani</i>	213	5	1.240	11.7			225	12.2*				
<i>Andropogon gerardii</i>	213	7	1.147	13	205	-8	225	12	216	3	202	-11
<i>Allium stellatum</i>	217	5	1.003	8.4	191	-26*	225	8			207	-10*
<i>Liatris aspera</i>	217	2	1.456	11.1			225	8		5		
<i>Liatris punctata</i>	218	13	0.782	8.2								
<i>Solidago canadensis</i>	220	11	0.664	5.4								
<i>Solidago rigida</i>	220	11	0.664	5.4	222	2	233	-9				
<i>Artemisia biennis</i>	242	2	2.060	22.3								
N						39		93		89		71
Proportion significant deviations						0.33		0.25		0.24		0.41
Proportion negative						0.92		0.13		0.10		0.93
Proportion positive						0.08		0.87		0.90		0.07

flowered varied by as much as 34 d between 2007 and 2010. These species include trees (*Acer saccharinum*, *Prunus americana*) and perennial shrubs or herbs (*Achillea millefolium*, *Amelanchier alnifolia*, *Amorpha canescens*, *Cicuta maculata*, *Echinacea purpurea*, *Liatris aspera*, *Packera plattensis*, *Penstemon albidus*, *Ranunculus rhomboideus*, *Ratibida columnifera*, *Rosa arkansana*, *Rudbeckia hirta*, *Shepherdia argentea*, and *Zigadenus elegans*).

Species that flowered consistently between 2007 and 2010 include *Androsace occidentalis*, *Campanula rotundifolia*, *Capsella bursa-pastoris*, *Cerastium arvense*, *Cypripedium candidum*, *Lithospermum canescens*, *Oxalis violacea*, *Pedicularis canadensis*, *Penstemon gracilis*, and *Populus deltoides*. These species always flowered earlier than the historical mean, but the effect was amplified in the 2 warm yr, 2007 and 2010. In contrast, consistently late-flowering species were uniformly species

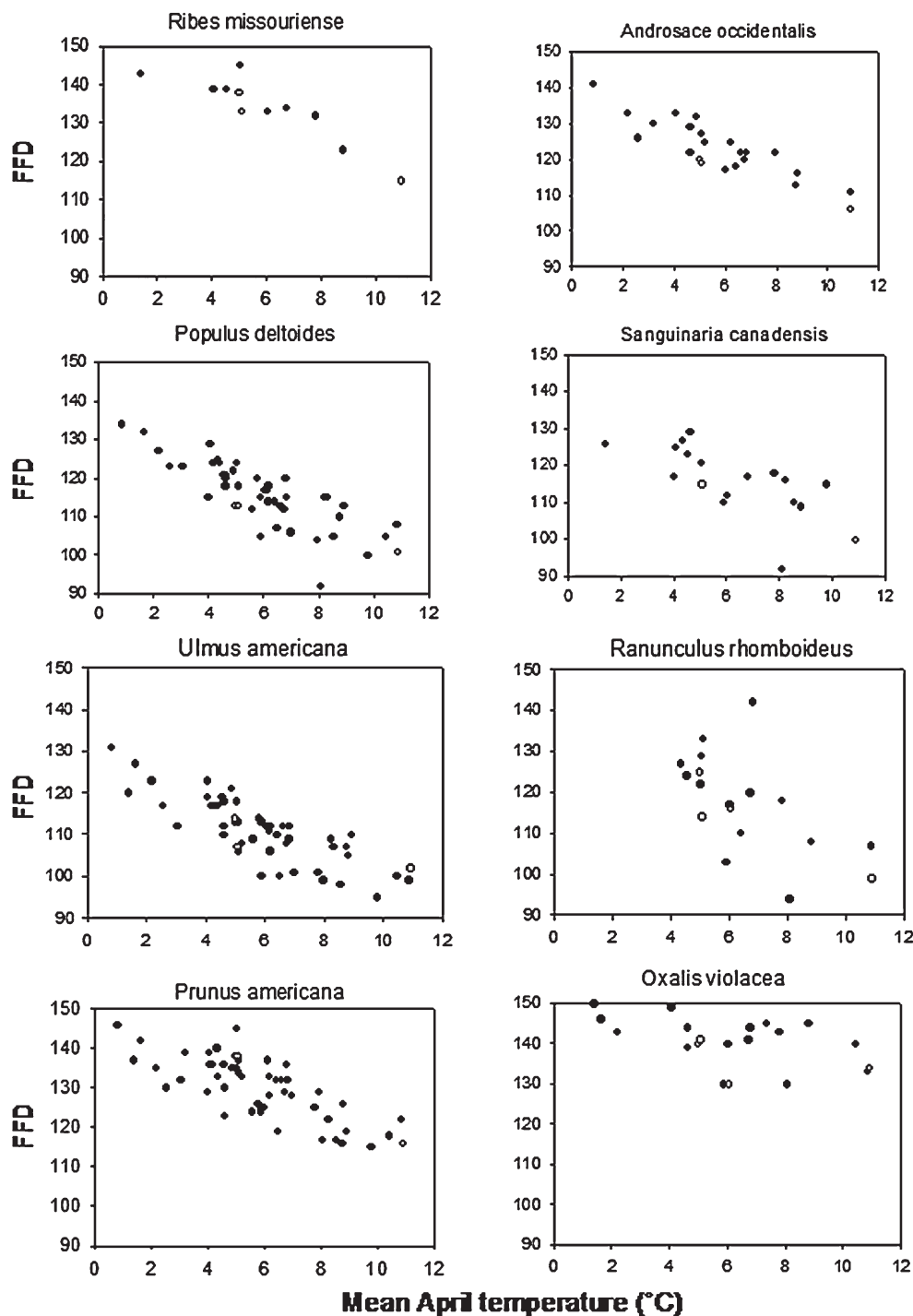


Fig. 6. Phenological patterns of eight spring flowering species. The first flowering date (FFD) is plotted against the average April temperature for that year. Black symbols indicate years 1910–1961, and gray symbols indicate years 2007–2010.

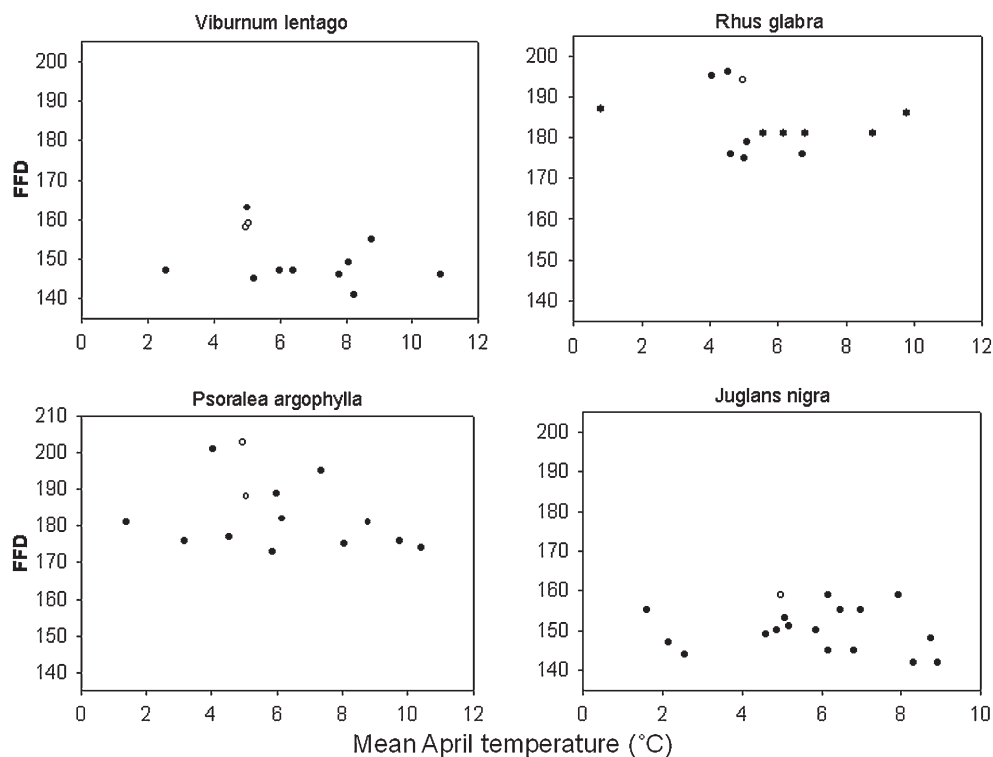


Fig. 7. Phenological patterns of four late-season flowering species. The first flowering date (FFD) is plotted against average April temperature. Black symbols indicate years 1910–1961, and gray symbols indicate years 2007–2010. These four species were chosen because they have shown significant shifts later relative to the last century.

that flowered after June 15. Species flowering later in recent years include *Asclepias ovalifolia*, *Calylophus serrulatus*, *Catalpa speciosa*, *Lilium philadelphicum*, *Melilotus officinalis*, and *Oenothera nuttallii*.

Our results are consistent with the hypothesis that plants are shifting flowering phenology in response to increased air temperatures and longer growing seasons. Climate data indicate that regional air temperatures have increased since the middle of the 1970s, resulting in earlier springs, later falls, and longer periods of above-freezing temperatures (Figs. 1, 2). In particular, the growing degree units in March, April, and May have increased over the past half century (Table 1). We have no data on flowering times of plants in the region during the initial period of temperature increase at the end of the last century (1970–1990). However, if temperatures continue to increase along the slope of the annual temperature plot for the region, we expect that in the future, many species will continue to shift their flowering times from historical patterns.

In contrast to temperature, the effects of precipitation patterns on flowering are less clear in the Red River Valley area. Although annual precipitation and winter snowfall were higher from 2007 to 2010 than the average between 1910 and 1961, there is no clear, long-term pattern in precipitation. Because of a historically cyclical pattern in rain and snowfall over the past 100 yr (Fig. 3), precipitation has followed a parabolic pattern rather than a steady increase. Nonetheless, flowering shifts over time are likely dependent on some interaction between temperatures, growing season lengths, and precipitation.

There are many implications of shifting phenology. The shifts in flowering observed in some species could alter pollinator

visitation patterns and plant reproductive success, depending on pollinator abundance, fidelity, and indirect effects from temporal changes in pollination networks (Olesen et al., 2008). Shifts in first flowering time have led to more frost damage due to earlier initiation of bud burst in frost-sensitive plants (Inouye, 2008). In the northern Great Plains, spring frosts can be severe, and early flowering increases the chances that vulnerable buds will be destroyed. Future studies are necessary to illuminate the consequences of the observed shifts in flowering phenology in this region. The consequences of different plant strategies of shifting or not shifting their flowering phenology will ultimately determine whether the species composition of the tallgrass prairie and woodlands typical of the region shift as well. However, this study represents the first step in predicting which species are more at risk for cascading ecological effects of climate change.

LITERATURE CITED

- AHAS, R., A. AASA, A. MENZEL, V. G. FEDOTOVA, AND H. SCHEIFINGER. 2002. Changes in European spring phenology. *International Journal of Climatology* 22: 1727–1738.
- BADH, A., A. AKYUZ, G. VOCKE, AND B. MULLINS. 2009. Impact of climate change on the growing seasons in select cities of North Dakota, United States of America. *International Journal of Climate Change: Impacts and Responses* 1: 105–117.
- BARNETT, T. P., D. W. PIERCE, AND R. SCHNUR. 2001. Detection of anthropogenic climate change in the world's oceans. *Science* 292: 270–274.
- BRADLEY, N., A. LEOPOLD, J. ROSS, AND W. HUFFAKER. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences, USA* 96: 9701–9704.

- CALLOW, J. M., H. KANTRUD, AND K. F. HIGGINS. 1992. First flowering dates and flowering periods of prairie plants at Woodworth, North Dakota. *Prairie Naturalist* 24: 57–64.
- CHEN, X. Q., B. HU, AND R. YU. 2005. Spatial and temporal variation of phenological growing season and climate change impacts in temperate eastern China. *Global Change Biology* 11: 1118–1130.
- CLELAND, E. E., I. CHUINE, A. MENZEL, H. A. MOONEY, AND M. D. SCHWARTZ. 2007. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22: 357–365.
- EASTERLING, D. R., G. A. MEEHL, C. PARMESAN, S. A. CHANGNON, T. R. KARL, AND L. O. MEARNES. 2000. Climate extremes: Observations, modeling, and impacts. *Science* 289: 2068–2074.
- FORREST, J., D. W. INOUE, AND J. D. THOMSON. 2010. Flowering phenology in subalpine communities: Does climate variation reshuffle species assemblages? *Ecology* 91: 431–440.
- GORDO, O., AND J. J. SANZ. 2009. Long-term temporal changes of plant phenology in the Western Mediterranean. *Global Change Biology* 15: 1930–1948.
- INOUE, D. W. 2008. Effects of climate change on phenology, frost damage and floral abundance of montane wildflowers. *Ecology* 89: 353–362.
- INOUE, D. W., M. A. MORALES, AND G. J. DODGE. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): The roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* 130: 543–550.
- INOUE, D. W., F. SAAVEDRA, AND W. LEE-YANG. 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany* 90: 905–910.
- IPCC. 2007. Climate change 2007—Synthesis report. Contribution of working groups I, II, and III to the fourth assessment report of the Intergovernmental Panel on Climate Change, Cambridge, UK.
- KAUFMANN, R. K., AND D. I. STERN. 1997. Evidence for human influence on climate from hemispheric temperature relations. *Nature* 388: 39–44.
- LAMBERT, A., A. J. MILLER-RUSHING, AND D. W. INOUE. 2010. Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* Pursh (glacier lily, Liliaceae). *American Journal of Botany* 97: 1431–1437.
- MENZEL, A., T. H. SPARKS, N. ESTRELLA, E. KOCH, A. AASA, R. AHAS, K. ALM-KUBLER, ET AL. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1969–1976.
- MILLER-RUSHING, A., AND D. W. INOUE. 2009. Variation in the impact of climate change on flowering phenology and abundance: An examination of two pairs of closely related wildflower species. *American Journal of Botany* 96: 1821–1829.
- MILLER-RUSHING, A., AND R. PRIMACK. 2008. Global warming and flowering times in Thoreau's Concord: A community perspective. *Ecology* 89: 332–341.
- NICHOLLS, N. 1996. Climate change—An incriminating fingerprint. *Nature* 382: 27–28.
- OLESEN, J. M., J. BASCOMPTE, H. ELBERLING, AND P. JORDANO. 2008. Temporal dynamics in a pollination network. *Ecology* 89: 1573–1582.
- PEÑUELAS, J., I. FILELLA, AND P. COMAS. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8: 531–544.
- PRIMACK, R. B., H. HIGUCHI, AND A. J. MILLER-RUSHING. 2009. The impact of climate change on cherry trees and other species in Japan. *Biological Conservation* 142: 1943–1949.
- RATHCKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.
- ROOT, T. L., J. T. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROSENZWEIG, AND J. A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- SCHEIFINGER, H., A. MENZEL, E. KOCH, AND C. PETER. 2003. Trends of spring time frost events and phenological dates in Central Europe. *Theoretical and Applied Climatology* 74: 41–51.
- SCHEMSKE, D. W. 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution; International Journal of Organic Evolution* 38: 817–832.
- SCHWARTZ, M. 1994. Monitoring global change with phenology: The case of the spring green wave. *International Journal of Biometeorology* 38: 18–22.
- SCHWARTZ, M. D., A. AHAS, AND A. AASA. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* 12: 343–351.
- SHERRY, R., X. ZHOU, S. GU, J. ARNONE, D. SCHIMEL, P. VERBURG, L. WALLACE, AND Y. LUO. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences, USA* 104: 198–202.
- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: The principles and practice of statistics in biological research. W. H. Freeman Company, New York, New York, USA.
- SPARKS, T. H., AND P. D. CAREY. 1995. The responses of species to climate over two centuries: An analysis of the Marsham phenological record. *Journal of Ecology* 83: 321–329.
- STEVENS, O. A. 1917. Plants of Manhattan and Blue Rapids, Kansas with Dates of Flowering. I. *American Midland Naturalist* 5: 71–87.
- STEVENS, O. A. 1921. Plants of Fargo, North Dakota, with dates of flowering I. *American Midland Naturalist* 7: 54–62.
- STEVENS, O. A. 1961. Plants of Fargo, North Dakota. *American Midland Naturalist* 66: 171–177.
- TAYLOR, B., AND D. GARBARY. 2003. Late-flowering plants from northern Nova Scotia, Canada. *Rhodora* 105: 118–135.
- TRAVERS, S., AND K. DUNNELL. 2009. First-flowering dates of plants in the northern Great Plains. *Ecological Archives* 90: 2332.
- WALTHER, G.-R., E. POST, P. CONVEY, A. MENZEL, C. PARMESAN, T. J. C. BEEBEE, J.-M. FROMENTIN, ET AL. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- WASER, N. M. 1979. Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). *Oecologia* 39: 107–121.
- WIELGOLASKI, F. E., AND D. W. INOUE. 2003. High latitude climates. In M. D. Schwartz [ed.], *Phenology: An integrative environmental science*, 175–194. Kluwer Academic Publishing, Dordrecht, Netherlands.
- YU, H., E. LUEDELING, AND J. XU. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences, USA* 107: 22151–22156.
- ZAR, J. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.
- ZHENG, J. Y., Q. S. GE, Z. X. HAO, AND W. C. WANG. 2006. Spring phenophases in recent decades over eastern China and its possible link to climate changes. *Climatic Change* 77: 449–462.