



Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland

P. Lesica^{a,*}, P.M. Kittelson^b

^a Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

^b Department of Biology, Gustavus Adolphus College, St. Peter, MN 56082, USA

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ABSTRACT

Advances in spring blooming of wildflowers have been associated with climate change; however, the majority of long-term community-level studies have been conducted in humid-temperate regions. Less is known about phenological changes in herbaceous, semi-arid plant communities. We recorded first-bloom date of common spring wildflowers in a semi-arid grassland in the Rocky Mountains, USA from 1995 through 2008 and analyzed these data along with mean monthly temperature and precipitation. Advanced flowering predominated; 75% of the 32 species displayed a negative linear regression slope, and this trend was strong for nine species (slope < 1.0, $p < 0.10$). Only one species showed a strong trend for later flowering. Mean advance for all 32 species was 0.61 days/year and mean advance for the nine species displaying a strong tendency to flower earlier was 1.6 days/year. Species flowering early showed stronger trends toward advanced flowering than later species. Average March temperature and January plus December precipitation, falling mainly as snow, were explanatory variables in the best multiple linear regression model for mean first-flowering date of strongly advanced species. Our results suggest that flowering phenology may be changing faster and precipitation may play a more important role in semi-arid grasslands than in humid-temperate systems.

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1. Introduction

Climate change is predicted to have important effects on biological communities (Chapin et al., 2008; Hughes, 2000; IPCC, 2007a). Phenological changes, including changes in flowering dates, are some of the most obvious effects. Changes in the timing of important events such as flowering or fruiting could result in failure to produce offspring or have them adequately dispersed. For example, Inouye (2008) found that several montane plant species were more prone to frost damage of flowers and loss of fruits when they bloomed earlier. Bee-pollinated spring wildflowers of deciduous forests set fewer seeds during warm springs when flowering was advanced (Kudo et al., 2004; Motten, 1986). Published studies have begun to document phenological changes and their relationship to climate, although no vegetation-level studies that we are aware of have been conducted in arid or semi-arid systems.

Several trends have become apparent from these studies. At least some species were flowering earlier than in the past (Abu-Asab et al., 2001; Bradley et al., 1999; Beaubien and Freeland, 2000; Fitter et al.,

1995; Menzel and Fabian, 1999; Miller-Rushing and Primack, 2008; Sparks et al., 2000), and earlier-flowering species demonstrated the greatest advance in flowering date (Bradley et al., 1999; Fitter et al., 1995; Fitter and Fitter, 2002; Menzel and Fabian, 1999; Miller-Rushing and Primack, 2008; Post and Stenseth, 1999). Fitter et al. (1995) also found that earlier-flowering species in southern England were more phenologically variable than those flowering later. Life form has sometimes been shown to be correlated with this flowering response to climate. In one study from northeast North America, flowering date of annuals was found to be more variable than for perennial herbs or shrubs (Miller-Rushing and Primack, 2008), and annuals in England showed a stronger response than did perennials (Fitter and Fitter, 2002).

The trend toward earlier flowering has frequently been found to be associated with climate change (Menzel et al., 2006). It has most often been correlated with warmer temperatures in the 1–3 months prior to anthesis (Abu-Asab et al., 2001; Beaubien and Freeland, 2000; Fitter et al., 1995; Miller-Rushing and Primack, 2008; Sparks and Carey, 1995; Sparks et al., 2000; Thórhallsdóttir, 1998). Mean advances in flowering date ranged from 0.08 to 0.20 days/year for eastern USA and Europe (Abu-Asab et al., 2001; Bradley et al., 1999; Menzel and Fabian, 1999). Flowering dates of early-flowering species advanced by four days in England, more

* Corresponding author. Tel.: +1 406 243 5141; fax: +1 406 243 4184.

E-mail address: peter.lesica@mso.umt.edu (P. Lesica).

than three days in northeast North America and up to six days in Europe for each increase of 1 °C in spring temperatures (Fitter et al., 1995; Menzel and Fabian, 1999; Miller-Rushing and Primack, 2008). However, Fitter et al. (1995) found that flowering of late-summer and fall flowering species tended to be retarded by warmer temperatures. While temperature is important, few studies have examined the relationship between flowering date and precipitation among species in herbaceous communities, and none have found a significant association (Abu-Asab et al., 2001; Sparks and Carey, 1995; Þórhallsdóttir, 1998).

Associations between climate and flowering dates led biologists to predict large future changes in phenological relationships in biological communities that could cause a decoupling of ecological relationships (Hughes, 2000; Stenseth and Mysterud, 2005; Walther et al., 2002). Such changes are likely to be community-specific. For this reason it is important to know how climate and phenology are related under different climatic regimes. However, most published studies of shifts in plant community phenology have been from humid-temperate climates (i.e., western Europe, eastern North America; but see Peñuelas et al., 2004). The purpose of our study is to examine changes in wildflower phenology between 1995 and 2008 in the semi-arid climate of intermountain western North America. We intend to compare and contrast our study with those from more humid systems. Specifically, we recorded first-flowering dates along a single transect, and we ask whether there has been a trend toward earlier flowering and how these trends are associated with temperature and precipitation.

2. Study area

Mount Jumbo is the southernmost spur ridge of the Rattlesnake Mountains at the northeast edge of the city of Missoula, Montana, USA (46° 52.6'N, 113° 57.5'W). Elevations range from 1005 m at the base to 1385 m at the summit. Climate is semi-arid. In 1994–2007 winters were cold with mean temperatures of ca. –5 °C in December and January, and summers were moderate with mean temperatures of 19–20 °C occurring in July and August. Mean annual precipitation was 337 mm. Precipitation peaked in May and June with 56 mm per month, while other months received 27–36 mm (National Climatic Data Center Website accessed July 2008; www.ncdc.noaa.gov). In many ways Missoula's precipitation regime is similar to that found in a Mediterranean climate except that winter precipitation is mainly in the form of snow, which usually melts by early March.

Vegetation of Mount Jumbo is grassland dominated by the bunchgrasses bluebunch wheatgrass (*Agropyron spicatum*), Sandberg bluegrass (*Poa secunda*) and junegrass (*Koeleria macrantha*) on the warmer aspects with rough fescue (*Festuca scabrella*) and Idaho fescue (*Festuca idahoensis*) dominating in cooler or moister sites. Mueggler and Stewart (1980) describe these communities as the *A. spicatum*/*Poa sandbergii* and *F. scabrella*/*F. idahoensis* habitat types respectively. More than 50 species of broad-leaved plants, both native and introduced, occur in these grasslands. Most wildflowers bloom between April and June and become dormant during summer.

3. Materials and methods

3.1. Field methods

We collected first-flowering data for herbaceous broad-leaved species from 1995 through 2008 along an existing trail (the permanent transect) that went up the south face of Mount Jumbo to 1340 m and returned on the west face (Fig. 1). Individual species were recorded from approximately the same place along the



Fig. 1. Photograph of the Mount Jumbo, Missoula, Montana study site showing the permanent transect route.

transect each year. One of us (PL) walked this same transect every 2–5 days for three months starting in early March, recording the date on which we first observed at least one individual of a species flowering along the transect. Allowing up to five days between observations may result in an underestimate of advances in first-flowering date. Observation gaps were haphazard by year and so would not affect the associations with climatic factors across years. There was at least one period each year when closely spaced observations were not possible; we did not use data from the first recording day following an interval greater than five days. These gaps were at different times each year and affected different species each year. As a result, there are fewer than 14 first-flowering observations for most species (Table 1). We used only those 32 species for which we had observations for seven or more years. It is possible that reported phenological shifts would be quantitatively different if we had data from all 14 years, but we do not believe this has biased the data or would change our conclusions.

3.2. Data analysis

We used simple linear regression models to determine which species demonstrated a strong trend for earlier or later flowering over the study period. Species for which the absolute value of the slope was >1.0 and $p < 0.10$ for the model were considered to demonstrate a strong trend. We chose an alpha-level of 0.10 in order to compensate for the small sample sizes for many of the models. We tested for a trend toward earlier flowering using a one-sample t -test to compare the distribution of regression slopes to a distribution with a mean of zero. We asked whether species that flower earlier demonstrated a stronger tendency for advanced first flowering with time by regressing the regression-model slope on mean flowering date. We used t -tests to assess the effect of growth form (annual/biennial, perennial) and origin (native, exotic) on trend in flowering date (regression slope).

We assumed that the species showing a strong trend toward earlier or later flowering experienced an actual change in flowering phenology. We used the ten species (nine advanced and one delayed; see Results) to search for associated weather variables. For each of the two groups of plants we employed a backward stepwise linear regression analysis (with $p > 0.05$ as a criteria for removing potential independent variables; Sokal and Rohlf, 1981, p. 663) to examine the trend over our 14-year sampling period. The dependent variable for the advanced group was the mean of the first-flowering dates of all nine species while the dependent variable for the delayed species (*Hydrophyllum capitatum*) was the first-flowering date in each year. For each of the two models we

Table 1

Wildflower species and their family, growth form, origin, mean first-flowering date and standard deviation in days of this date at Mount Jumbo, Missoula, Montana. Results of linear regressions of flowering date across n years are provided in the last three columns. A negative slope indicates that flowering advanced over the course of the study. Species in bold showed a strong trend for changed first flowering (absolute value slope > 1.0 and $p < 0.10$).

Species	Family	Form	Origin	Flower date	SD	n	Slope	R^2	P
Ranunculus glaberrimus	Ranunculaceae	Perennial	Native	March 11	7.41	14	−1.105	0.39	0.017
Lomatium cous	Apiaceae	Perennial	Native	March 25	10.75	14	−1.774	0.477	0.006
<i>Lithophragma glabrum</i>	Saxifragaceae	Perennial	Native	March 30	8.01	14	−0.358	0.035	0.522
Draba verna	Brassicaceae	Annual	Native	March 30	9.79	12	−1.248	0.304	0.063
<i>Fritillaria pudica</i>	Liliaceae	Perennial	Native	April 1	7.49	14	−0.486	0.074	0.348
<i>Douglasia montana</i>	Primulaceae	Perennial	Native	April 5	11.20	12	0.916	0.119	0.273
Arabis holboellii	Brassicaceae	Perennial	Native	April 6	10.74	13	−1.896	0.573	0.003
Holosteum umbellatum	Caryophyllaceae	Annual	Exotic	April 7	8.17	13	−1.222	0.364	0.029
Lomatium ambiguum	Apiaceae	Perennial	Native	April 9	8.29	13	−1.026	0.249	0.083
Alyssum desertorum	Brassicaceae	Annual	Exotic	April 9	21.45	10	−3.020	0.451	0.030
<i>Lomatium macrocarpum</i>	Apiaceae	Perennial	Native	April 12	11.11	8	−1.040	0.095	0.459
<i>Lomatium triternatum</i>	Apiaceae	Perennial	Native	April 12	6.94	10	−0.247	0.025	0.663
<i>Besseyia wyomingensis</i>	Scrophulariaceae	Perennial	Native	April 12	7.67	11	0.571	0.094	0.359
<i>Dodecatheon conjugens</i>	Primulaceae	Perennial	Native	April 13	7.27	9	−0.574	0.104	0.398
<i>Antennaria dimorpha</i>	Asteraceae	Perennial	Native	April 14	8.95	11	−0.371	0.033	0.595
<i>Taraxacum laevigatum</i>	Asteraceae	Perennial	Exotic	April 15	10.90	9	−1.517	0.296	0.130
Lithospermum arvense	Boraginaceae	Annual	Exotic	April 17	10.67	7	−1.907	0.637	0.032
<i>Mertensia oblongifolia</i>	Boraginaceae	Perennial	Native	April 17	7.15	11	−0.251	0.025	0.641
<i>Delphinium bicolor</i>	Ranunculaceae	Perennial	Native	April 18	6.89	9	−0.352	0.058	0.533
<i>Microsteris gracilis</i>	Polemoniaceae	Annual	Native	April 18	9.54	7	0.623	0.096	0.499
<i>Astragalus cibarius</i>	Fabaceae	Perennial	Native	April 18	4.40	7	−0.593	0.399	0.128
<i>Arabis nuttallii</i>	Brassicaceae	Perennial	Native	April 18	6.69	7	0.055	0.001	0.938
Astragalus purshii	Fabaceae	Perennial	Native	April 20	8.63	7	−1.720	0.839	0.004
<i>Lomatium dissectum</i>	Apiaceae	Perennial	Native	April 20	7.57	10	−0.681	0.166	0.242
<i>Lithophragma parviflorum</i>	Saxifragaceae	Perennial	Native	April 20	6.33	8	−0.955	0.447	0.070
<i>Balsamorhiza sagittata</i>	Asteraceae	Perennial	Native	April 23	8.84	9	0.035	0	0.964
Hydrophyllum capitatum	Hydrophyllaceae	Perennial	Native	April 25	10.07	8	1.630	0.532	0.040
<i>Myosotis micrantha</i>	Boraginaceae	Annual	Exotic	April 26	3.02	8	−0.080	0.018	0.755
<i>Erigeron compositus</i>	Asteraceae	Perennial	Native	April 27	9.44	9	−0.580	0.051	0.558
<i>Veronica verna</i>	Scrophulariaceae	Annual	Exotic	April 29	9.28	9	−0.279	0.015	0.756
<i>Castilleja hispida</i>	Scrophulariaceae	Perennial	Native	May 7	8.06	10	0.551	0.06	0.494
<i>Erysimum asperum</i>	Brassicaceae	Annual	Native	May 10	9.24	8	0.804	0.175	0.302

regressed the dependent variable against all of the previous 12 months of precipitation and mean monthly temperatures that were strongly correlated with first-flowering date ($r > 0.35$). December and January precipitation were both strongly correlated so we combined these two months for the final model. We also assessed the effect of average heating degree days, but results were very similar to those yielded by our mean monthly temperature data (data not shown), so we did not attempt to use it as an explanatory variable. Weather data for Missoula, Montana were obtained from National Climatic Data Center Website accessed July 2008 (www.ncdc.noaa.gov). Some first-flowering-date data were missing for all but two of the species (Table 1), and missing years were different for different species. In order to use all 14 years of the study, we imputed missing data using a standard iterative expectation-maximization (EM) maximum likelihood method, which uses all the data to estimate the missing values (Little and Rubin, 1987). Seven of the nine advanced species had at least ten years ($>71\%$) of observations and 103 observations of these nine species over 14 years were used to determine the weather variables most likely to have influenced phenological shifts. We had data from only eight years for the delayed *H. capitatum*, and imputed six other observations. All computations were done using SYSTAT 10 (SPSS, 2000).

4. Results

4.1. Phenology trends

Mean first-flowering dates ranged from March 11 to May 10 (Table 1). Overall, species showed a strong tendency for earlier flowering during the 14-year study period (one-sample $t = 3.94$, $p < 0.001$). Twenty-four of the 32 species (75%) showed a trend toward earlier flowering (negative regression slope). This trend

was strong for nine of these species (absolute value slope > 1.0 , $p < 0.10$): *Alyssum desertorum*, *Arabis holboellii*, *Astragalus purshii*, *Draba verna*, *Holosteum umbellatum*, *Lithospermum arvense*, *Lomatium ambiguum*, *Lomatium cous* and *Ranunculus glaberrimus*. Mean slope for these nine species was -1.6 days/year, and mean slope for all 32 species was -0.61 days/year. Only one species, *H. capitatum*, showed a significant trend toward later flowering (Table 1).

Earlier-flowering species showed stronger trends toward earlier flowering than species that flowered later ($R^2 = 0.18$, $p = 0.014$). Seven of the nine species displaying a strong trend toward earlier flowering had a mean first-flowering date during the first half of our observation period (March 10–April 9), while only two flowered after that (April 10–May 10). There was no association between mean date of first flowering and the standard deviation of first-flowering date ($R^2 = 0.02$, $p = 0.40$). We found no evidence that trend in flowering date was different between annual and perennial herbs ($n = 7, 25$; $t = 0.07$, $p = 0.95$). However, mean slope for exotic species ($n = 6$, mean slope = -1.34) was more negative than for native species ($n = 28$, mean slope = -0.43 ; $t = 2.48$, $p = 0.019$).

4.2. Climate and phenology

Average March temperature and combined January plus December precipitation were explanatory variables in the best multiple regression model for mean first-flowering date for the nine species that demonstrated a strong advance of flowering ($R^2 = 0.65$, $p = 0.003$). Mean first-flowering date advanced with a decline in December plus January precipitation and an increase in March temperature. By itself January plus December precipitation explained 47% of the variation in mean first-flowering date with an

advance of 1.2 days for every 1 °C decline in precipitation ($p = 0.007$). March temperature by itself explained 37% of the variation with an advance of 1.5 days/1 °C increase ($p = 0.021$).

March, July and September precipitation were explanatory variables in the best model for *H. capitatum*, the only species that demonstrated a strong delay in flowering date ($R^2 = 0.98$, $p = 0.001$). First-flowering date tended to be later with increased March and September precipitation and decreased July precipitation. However, the results of this modeling should be viewed with caution since it is based on a single species with six missing flowering dates.

Over the 14-year sampling period, December plus January precipitation declined an average of 4.8 mm per year but the decline was not statistically significant ($R^2 = 0.20$; $p = 0.11$); however January precipitation by itself declined 2.3 mm ($R^2 = 0.34$; $p = 0.03$). Average March temperatures increased 0.2 °C per year, but this trend was not significant ($R^2 = 0.07$, $p = 0.37$).

5. Discussion and conclusions

There was a strong overall trend for spring wildflowers in semi-arid grasslands of western Montana to flower earlier. This trend was apparent even though our study spanned only 14 annual observations. The trend for earlier flowering averaged 0.6 days/year, which was nearly eight days over the course of the study. This was a more rapid advance than previously documented for species in the eastern (0.08 days/year over 30 years; Abu-Asab et al., 2001) or central USA (0.12 days/year over 61 years; Bradley et al., 1999). Our higher absolute rate of first-flowering advance could be due to an increased rate of climatic change since 1995 and/or an intrinsically higher rate of change associated with semi-arid compared to humid-temperate floras. It may also be because we studied only spring-flowering species which have a stronger tendency for advanced flowering (see below). Additional studies of herbaceous species in semi-arid or Mediterranean climates should help determine the importance of these non-mutually exclusive explanations. Only one species displayed a strong trend to flower later. We were unable to detect a strong advance or decline in first flowering for the remaining 22 (69%) of the species studied. Other long-term studies have also detected trends in only a minority of the species examined (Abu-Asab et al., 2001; Bradley et al., 1999; Fitter and Fitter, 2002). This may be because there were no trends or because the error variation was too large to allow detection of small trends.

Warmer March temperatures and lower winter precipitation were associated with advance of first flowering in our study. Earlier flowering has most often been correlated with warmer temperatures in the months prior to anthesis (Abu-Asab et al., 2001; Beaubien and Freeland, 2000; Fitter et al., 1995; Miller-Rushing and Primack, 2008; Sparks and Carey, 1995; Sparks et al., 2000; Thórhalldóttir, 1998). Our results show the same pattern with most of our study species flowering in April (Table 1). Our regression model suggests an advance in first flowering of 1.5 days/1 °C increase in March temperature. This is a smaller increase in flowering per 1 °C than reported for longer-term studies in England (4 days/1 °C, Fitter et al., 1995) and northeast North America (3.4 days/1 °C, Miller-Rushing and Primack, 2008) however.

The tendency for advanced first flowering was stronger in early compared to late spring species, and studies from England and eastern North America obtained similar results (Bradley et al., 1999; Fitter et al., 1995; Fitter and Fitter, 2002; Miller-Rushing and Primack, 2008). Fitter et al. (1995) also found that the species flowering earliest expressed the most variable first-flowering date at their English study site. However, Miller-Rushing and Primack (2008) found that eastern North American summer flowering perennials showed more inter-annual variability in flowering date

than spring species. We found no evidence that the earliest flowering species had the most variable first-flowering date. Both temperature and photoperiod are important cues for initiating flowering (Heide, 2006; Keller and Körner, 2003; Yanovsky and Kay, 2003). Data from these phenological studies suggest that the former cue may be more important early in the growing season (Fitter et al., 1995; Miller-Rushing and Primack, 2008). However, differences among our studies and the others suggest that several different cues are likely responsible for initiating flowering, and the variability of cues differs among sites.

The relationship between precipitation and flowering phenology at the community level has rarely been examined in the temperate zone, and it has been found to be insignificant (Abu-Asab et al., 2001; Sparks and Carey, 1995; Thórhalldóttir, 1998). However, our results suggest that winter precipitation, usually falling as snow, is at least as important as spring temperature to flowering of wildflowers of semi-arid grasslands in the Northern Rocky Mountains. One explanation for this association applies mainly to regions or habitats that receive significant snow during winter. The ground and the plants growing in it cannot be warmed much above 0 °C until snow melts. More snow can mean later snowmelt, later warming, and later flowering. This relationship has been demonstrated for mountain wildflowers; snow release date was the primary determinant of flowering time in *Delphinium barbeyi* and *Androsace septentrionalis* (Inouye et al., 2002, 2003). Moreover, the strong effect of winter precipitation on first-flowering date may also explain why species at our site have a higher absolute advanced rate of flowering relative to eastern and central USA species, but a slightly lower advanced rate when only expressed on a per 1 °C basis.

Precipitation patterns also strongly influence flowering time in Mediterranean shrubs (Peñuelas et al., 2004; Prieto et al., 2008), woody desert species (Friedel et al., 1993) and some tropical trees (Rathcke and Lacey, 1985). The intermontane grasslands of western Montana experience a precipitation regime similar to Mediterranean areas; most of the yearly 337 mm of precipitation occurs in winter and spring. Few community studies that examined flowering time have explored environmental factors other than temperature and photoperiod (but see Bowers and Dimmitt, 1994), and even fewer have attempted to explain mechanistically how environmental factors such as precipitation trigger earlier flowering. Precipitation may interact with edaphic factors, resulting in more optimal resource assimilation (McMillan and Pagel, 1958). A pulse of nutrients can occur with snowmelt, spring rain and warmer temperatures, and earlier flowering has been related to higher nutrient levels (Dahlgren et al., 2007; Wielgolaski, 2001). At the genetic level, Caicedo et al. (2005) found that proximate environmental cues such as January precipitation and vernalization time interact to trigger the *FRI* allele and the transcription factor *FLC*, which led to flowering in *Arabidopsis thaliana*.

Exotic species at our site demonstrated a stronger tendency for earlier flowering than natives. Five of the six exotics were annuals; however, we found no evidence that flowering dates of annuals were more variable than for perennials, although they were more variable in England (Fitter et al., 1995) and eastern North America (Miller-Rushing and Primack, 2008). Results of this analysis should be viewed with caution as sample sizes for both annuals and exotics were small.

We were unable to detect a strong trend for advanced or retarded flowering for 22 of the 32 species examined. In many cases the trend may be swamped by the variation in the data. However for some species, climatic factors may not directly trigger flowering; instead internal rhythms like flowering may be genetically constrained and more closely tied to day length (Keller and Körner, 2003; Yanovsky and Kay, 2003; Hamann, 2004). However, Van Dijk

and Hautekeete (2007) found significant genetic variability for photoperiod-induced flowering and predicted that selection toward an earlier photoperiod due to climatic shifts could be accomplished in nine generations.

Most other studies on changes in flowering phenology were conducted in relatively humid areas dominated by deciduous forest vegetation that receive an average of more than 750 mm of annual precipitation. Our results suggest that flowering phenology of semi-arid grasslands of western North America may be changing faster on an absolute scale than in more humid-temperate regions and that changes in precipitation may play a more important role in phenology than in these other regions. However, our results may have differed from other reports that covered a longer period of time and probably included periods of little change, while our study covered a time period of rapid warming (IPCC, 2007b).

Taken together our results indicate that flowering phenology of many spring wildflowers in semi-arid valleys of western North America is changing rapidly and is related to both temperature and precipitation. Early-flowering species can comprise the majority of dicotyledonous plants in summer-arid ecosystems (West, 1988). Earlier flowering in semi-arid grasslands could result in a loss of reproductive capacity due to increased frost damage (Inouye, 2008) or uncoupling plant–pollinator interactions (Kudo et al., 2004). Changes in plant phenology could also result in adverse effects on insect pollinators as well as herbivores that depend on these species for food (Saavedra et al., 2003; Stenseth and Mysterud, 2005). We cannot predict the exact results of climate change in semi-arid systems, but further studies may help determine the scope of changes to come.

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References

- Abu-Asab, M.S., Peterson, P.M., Shelter, S.G., Orli, S.S., 2001. Earlier plant flowering in spring as a response to global warming in the Washington D.C. area. *Biodiversity and Conservation* 10, 597–612.
- Beaubien, E.G., Freeland, H.J., 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. *International Journal of Biometeorology* 44, 53–59.
- Bowers, J.E., Dimmitt, M.A., 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. *Journal of the Torrey Botanical Society* 121, 215–229.
- Bradley, N.L., Leopold, A.C., Ross, J., Huffaker, W., 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America* 96, 9701–9704.
- Chapin, F.S., Randerson, J.T., McGuire, A.D., Foley, J.A., Field, C.B., 2008. Changing feedbacks in the climate–biosphere system. *Frontiers in Ecology and Environment* 6, 313–320.
- Caicedo, A.L., Stinchcombe, J.R., Olsen, K.M., Schmitt, J., Purugganan, M.D., 2005. Epistatic interaction between *Arabidopsis* FRI and FLC flowering time genes generates a latitudinal cline in a life history trait. *Proceedings of the National Academy of Sciences of the United States of America* 101, 15670–15675.
- Dahlgren, J.P., von Zeipel, H., Ehrlén, J., 2007. Variation in vegetative and flowering phenology in a forest herb caused by environmental heterogeneity. *American Journal of Botany* 94, 1570–1576.
- Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., Williamson, M.H., 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology* 9, 55–60.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689–1691.
- Friedel, M.H., Nelson, D.J., Sparrow, A.D., Kinloch, J.E., Maconochie, J.R., 1993. What induces central Australian arid zone trees and shrubs to flower and fruit? *Australian Journal of Botany* 41, 307–319.
- Hamann, A., 2004. Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes. *Journal of Ecology* 92, 24–31.
- Heide, O., 2006. Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiological Plantarum* 40, 21–26.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15, 56–61.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89, 353–362.
- Inouye, D.W., Morales, M.A., Dodge, G.J., 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.
- Inouye, D.W., Saavedra, F., Lee-Yang, W., 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany* 90, 905–910.
- Intergovernmental Panel on Climate Change, 2007a. Summary for policymakers. In: Metz, B., Davidson, O.R., Bosch, P.R., et al. (Eds.), *Climate Change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge, UK.
- Intergovernmental Panel on Climate Change, 2007b. Summary for policymakers. In: Solomon, S., Qin, D., Manning, M., et al. (Eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge, UK.
- Keller, F., Körner, C., 2003. The role of photoperiodism in alpine plant development. *Arctic Antarctic Alpine Research* 35, 361–368.
- Kudo, G., Nishikawa, Y., Kasagi, T., Kosuge, S., 2004. Does seed production of spring ephemerals decrease when spring comes early? *Ecological Research* 19, 255–259.
- Little, R.J.A., Rubin, D.R., 1987. *Statistical Analysis with Missing Data*. John Wiley & Sons, New York, USA.
- McMillan, C., Pagel, B.F., 1958. Phenological variation within a population of *Symphoricarpos occidentalis*. *Ecology* 39, 766–770.
- Menzel, A., Fabian, P., 1999. Growing season extended in Europe. *Nature* 397, 659.
- Menzel, A., Sparks, T.H., Estrella, N., et al., 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12, 1969–1976.
- Miller-Rushing, A.J., Primack, R.B., 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology* 89, 332–341.
- Motten, A.F., 1986. Pollination ecology of the spring wildflower communities of a temperate deciduous forest. *Ecological Monographs* 56, 21–42.
- Mueggler, W.F., Stewart, W.L., 1980. *Grassland and Shrubland Habitat Types of Western Montana*. USDA Forest Service General Technical Report INT-66, Ogden, Utah, USA.
- Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* 161, 837–846.
- Post, E., Stenseth, N.C., 1999. Climatic variability, plant phenology and northern ungulates. *Ecology* 80, 1322–1339.
- Prieto, P., Peñuelas, J., Ogaya, R., Estiarte, M., 2008. Precipitation-dependent flowering of *Globularia alypum* and *Erica multiflora* in Mediterranean shrubland under experimental drought and warming and its interannual variability. *Annals of Botany* 102, 275–285.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16, 179–214.
- Saavedra, F., Inouye, D.W., Price, M., Harte, J., 2003. Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. *Global Change Biology* 9, 885–894.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry. The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Company, San Francisco, California, USA.
- Sparks, T.H., Carey, P.D., 1995. The responses of species to climate over two centuries: an analysis of the Marsham phenological record. *Journal of Ecology* 83, 321–329.
- Sparks, T.H., Jeffree, E.P., Jeffree, C.E., 2000. An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology* 44, 82–87.
- SPSS, 2000. SYSTAT 10. SPSS Inc., Chicago, Illinois, USA.
- Stenseth, N.C., Mysterud, A., 2005. Climate, changing phenology and other life history traits: non-linearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America* 99, 13379–13381.
- Thórhallsdóttir, T.E., 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* 114, 43–49.
- Van Dijk, H., Hautekeete, N., 2007. Long day plants and the response to global warming: rapid evolutionary change in day length sensitivity is possible in wild beet. *Journal of Evolutionary Biology* 20, 349–357.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- West, N.E., 1988. Intermountain deserts, shrub steppes, and woodlands. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, New York, USA.
- Wielgolaski, F.E., 2001. Phenological modification in plants by various edaphic factors. *International Journal of Biometeorology* 45, 196–202.
- Yanovsky, M.J., Kay, S.A., 2003. Living by the calendar: how plants know when to flower. *Nature Reviews: Molecular Cell Biology* 4, 265–276.