

Phenological responses of prairie plants vary among species and year in a three-year experimental warming study

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Abstract. As temperature is a common regulator of temperate plant phenology, future increases in global temperatures are likely to cause shifts in the timing of plant phenophases such as flowering and senescence, with potential feedbacks on species interactions and carbon cycling. We used a 3-year field warming study in a temperate grassland to investigate the effects of two levels of warming ($+ \sim 1.5^{\circ}\text{C}$ and $+ \sim 3^{\circ}\text{C}$) on the phenology of budding, flowering onset, and peak flowering of ten perennial plant species at both individual and population scales. We also examined the effect of warming on green-up and senescence by measuring normalized difference vegetation index (NDVI) for one year. Populations and individuals of *Amorpha canescens*, *Dalea purpurea* (*Petalostemum purpureum*), and *Andropogon gerardii* flowered five to eight days earlier under high warming. For seven species, interannual variability in flowering time equaled or exceeded experimental warming treatment effects in any given year. Responses to warming were not consistent among years for several species, especially *Liatris aspera*. Warming led to higher NDVI values in the spring, indicating that warming accelerated spring biomass growth but did not significantly affect senescence. These results suggest that the community flowering profile may be altered under warming, potentially affecting pollinator, trophic and competitive interactions, and indicate that the timing to peak biomass may be accelerated, possibly affecting ecosystem carbon cycling.

Key words: climate change; flowering; grassland; NDVI; warming.

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INTRODUCTION

Global mean air temperatures have risen 0.65°C in the past 50 years and are predicted to rise another $1.8\text{--}4.0^{\circ}\text{C}$ by 2100 (IPCC 2007). Many plant phenological properties, defined as the timing of recurring life history events such as leaf emergence, flowering, and senescence, are partly controlled by temperature and may change with climate (Peñuelas and Filella 2001). Indeed, both observational studies (Fitter and Fitter 2002, Menzel et al. 2006, Miller-Rushing

and Primack 2008) and manipulative warming experiments (Dunne et al. 2003, Sherry et al. 2007, Jarrad et al. 2008, Liancourt et al. 2012) document shifts in plant phenology that have already occurred or are likely to occur in the near future. Phenological changes have significant implications for trophic interactions (Yang and Rudolf 2010), global carbon cycling (Richardson et al. 2010), and climate-vegetation feedbacks (Peñuelas et al. 2009). While studies that find changes in phenology with temperature change are accumulating, a comprehensive understand-

ing of which variables are most sensitive to temperature change and how US prairie species will respond has yet to emerge.

Most plant phenological investigations focus on either leaf phenology (i.e., emergence and senescence) or reproductive phenology. Shifts in emergence and senescence can alter the length of the growing season with implications for net primary productivity and thus global carbon cycling (Peñuelas et al. 2009, Polgar and Primack 2011). Some studies have shown earlier emergence or leaf out dates and delays in senescence when individual plants are monitored (Arft et al. 1999, Menzel et al. 2001). The response is species-specific, though, as some species display shifts at both ends of the season while others only shift at one end (Arft et al. 1999, Peñuelas et al. 2002). The lengthening of the growing season has also been observed with remotely sensed imagery (Myneni et al. 1997, Jeong et al. 2011). For North America, satellite data suggest that the lengthening of the growing season is due mostly to a delay in autumn senescence of approximately 9.4 days over the past thirty years (Jeong et al. 2011).

Shifts in the timing of reproduction (budding, flowering, seeding) may have consequences for plant-pollinator interactions, fitness, and competitive interactions (Visser and Both 2005, Parmesan 2007, Forrest et al. 2010, Wolkovich and Cleland 2011, CaraDonna et al. 2014). Collectively, studies have found that the effect of warming on flowering time is species-specific, with some species displaying a response while others are not affected (Bradley et al. 1999, Peñuelas et al. 2002, Hovenden et al. 2008, Bloor et al. 2010, Liancourt et al. 2012). This result is not surprising as some species are regulated by factors other than temperature (e.g., photoperiod; Rathcke and Lacey 1985, Tooke and Battey 2010). Most species exhibiting a shift in flowering with temperature show an advancement of flowering (Dunne et al. 2003, Cleland et al. 2006, Menzel et al. 2006, Miller-Rushing and Primack 2008) but a few show delayed flowering (Peñuelas et al. 2002, Sherry et al. 2007, Dunnell and Travers 2011). For example, one study examining 80 species of the US Northern Great Plains found that 35 showed advancement in flowering while only 3 showed delayed flowering in recent years compared to the first half of the twentieth century (Dunnell and Travers 2011). Within a species, the temper-

ature sensitivity of reproduction can differ depending on the specific phenophase observed (Sherry et al. 2007) or the measure used to observe a phase (e.g., first flowering vs. peak flowering dates; CaraDonna et al. 2014), often leading to changes in the duration of the reproductive phases. These inconsistent warming-induced shifts between and within species will alter the temporal flowering profile of the plant community (Sherry et al. 2007, Forrest et al. 2010, CaraDonna et al. 2014).

In an effort to enhance predictions of which plant species will respond to warming, researchers have tried to find patterns that correlate phenological responses to species' traits. One trait commonly considered is timing of flowering during the season, e.g., early vs. late flowering. Several studies focusing predominantly on temperate systems have reported a stronger response in early flowering species (Fitter and Fitter 2002, Menzel et al. 2006, Miller-Rushing and Primack 2008, Dunnell and Travers 2011, Wolkovich et al. 2012, Calinger et al. 2013) while others focusing on more arid systems found no correlation between the response and flowering seasonality (Peñuelas et al. 2002, Jarrad et al. 2008, Liancourt et al. 2012). Because increasing temperatures signal the start of the season in temperate systems, early flowering species in these communities may be more sensitive to temperature than early flowering species in arid systems where the start of the season may be signaled by other factors, such as precipitation or soil moisture (Crimmins et al. 2013). One study of temperate grassland species detected a relationship between the direction of the shift and timing of flowering (Sherry et al. 2007). In that study, early flowering species flowered earlier while later flowering species showed delayed flowering when plots of prairie vegetation were experimentally warmed for one year. A similar lack of consensus among studies exists when the dependence of phenology on taxonomy, growth form, or origin (native vs. non-native) are considered (Fitter and Fitter 2002, Peñuelas et al. 2002, Jarrad et al. 2008, Davis et al. 2010).

While the patterns of plant phenological responses to increasing temperatures are emerging (Ellwood et al. 2013), especially for regions such as Eastern deciduous forests, there are at least three gaps in understanding that climate

Table 1. Ambient annual and potential growing season (April through September) climate summaries (<http://cedarcreek.umn.edu/research/weather/>) and warming treatment effect, mean (SD), on surface soil temperature for the first 3 years of an experimental warming study at Cedar Creek Ecosystem Science Reserve, East Bethel, Minnesota, USA.

Variables	Annual			April–September		
	2009	2010	2011	2009	2010	2011
Mean temp (°C)	6.4	8.0	8.7	16.1	17.2	15.9
Mean min temp (°C)	0.01	1.9	2.4	8.7	10.7	9.9
Mean max temp (°C)	12.7	14.1	13.5	23.5	23.7	22.0
Cumulative precipitation (mm)	636	832	790	388	655	721
Increase in surface soil temperature in high warming treatment (°C)†						
4-species	2.4 (1.3)	1.9 (1.1)	1.6 (1.1)
16-species	1.6 (1.2)	1.3 (1.2)	1.2 (1.3)
32-species	2.6 (1.8)	1.5 (1.4)	1.0 (1.4)
Increase in surface soil temperature in low warming treatment (°C)†						
4-species	1.2 (0.8)	0.9 (0.6)	0.8 (0.7)
16-species	0.7 (0.9)	0.5 (0.7)	0.5 (0.7)
32-species	1.2 (0.8)	0.8 (0.8)	0.8 (0.8)

† Values are mean daily temperature differences averaged across nine 4-species, nine 16-species, and six 32-species plots for 95, 186, and 157 days in 2009, 2010, and 2011, respectively.

warming experiments can help address, particularly for prairie ecosystems, which are amenable to experimentation. (1) Which phenological variables are the most sensitive to temperature? (2) Do slight increases in temperature (e.g., 1.5°C) elicit phenological changes proportional to those from larger temperature increases? (3) What is the magnitude of inter-annual variation in these processes?

Here we used a manipulative field warming experiment to examine the impact of low (~1.5°C) and high (~3°C) warming on the phenology of perennial grassland plants at three scales: individual, population, and patch (i.e., groups of plants from different species) using the distinct but complementary methods of direct observations and reflectance spectrometry of communities. Our study is unusual in that most studies typically focus on either direct observations of marked plants or analysis of remotely sensed imagery. For three years, we monitored reproductive timing on tagged individuals and observed flowering in populations of ten species that vary in functional group (C_4 warm-season grasses, C_3 cool-season grasses, legumes, and non-leguminous forbs) and timing of flowering (Howe 1994, Pavlovic et al. 2011). To monitor green-up and senescence of the community, we measured canopy reflectance of small patches from which we calculated the normalized difference vegetation index (NDVI), a measure of greenness.

Since temperature is likely a limiting condition to flowering in our temperate ecosystem, especially at the start of the season, we predicted that our focal species would show advancement of flowering, with a larger response by early flowering species. We expected warmed communities to show accelerated green up and delayed senescence, but that the response of senescence would be more apparent than emergence because annual spring burning would disconnect emergence from temperature in our experimental prairie ecosystems. We further predicted that our low warming treatment would induce significant changes in phenology but at a smaller magnitude than those of high warming.

METHODS

Site description

This study was conducted in a manipulative field warming experiment at Cedar Creek Ecosystem Science Reserve in East Bethel, Minnesota, USA. The site occurs on a glacial outwash sand plain with sandy soils low in nitrogen (Tilman 1987). Ambient climatic data for the three years of our experiment appear in Table 1 (<http://cedarcreek.umn.edu/research/weather/>). The long-term mean annual temperature is 6.8°C, and mean annual precipitation is 799 mm, 12% of which typically falls as snow. For April through September, the long-term mean temperature is 16.4°C, and long-term mean precipitation is 583

mm. Over the five decades of climate observations for this area, the average maximum daily temperatures per year have ranged from 10.6 to 15.0°C with no directional change through time, while the average minimum daily temperatures have a range of −1.5 to 3.3°C and have been increasing since 1963 (<http://cedarcreek.umn.edu/research/weather/>).

Experimental design

The warming experiment was superimposed on an existing grassland biodiversity experiment over a decade old at the start of the warming treatments (Tilman et al. 2001). In 1994 and 1995, 9 × 9 m plots were sowed with seed mixtures containing 1, 4, 16, or 32 species of perennial grassland plants that vary in functional group (Tilman et al. 2001). In 2008, 38 of these plots (14 monocultures, nine 4-species, nine 16-species, and six 32-species plots) were chosen to be part of the warming experiment. Each plot was split into three 2.5 × 3 m subplots (minimum distance between subplots is 1 m), and overhead infrared heat lamps (Kalglo Electronics, Bethlehem, Pennsylvania, USA) were hung over two of these subplots (one lamp per subplot) to achieve two levels of warming: low and high. From March to November, lamps emitted a constant output of 600 and 1200 watts of radiation in low and high warming subplots, respectively. The height of lamps (1.8 m) and amount of radiation were chosen for their ability to warm bare ground surface soil by 3°C (high) and 1.5°C (low) warming. The presence of vegetation, though, attenuated soil warming (see below). Surface soil temperature was monitored hourly with three iButtons (Maxim, Sunnyvale, California, USA) buried ~1 cm deep in each subplot. Soil temperature data indicated that our warming treatments effectively warmed the surface soil (and by inference, also the air temperature), but that the magnitude of soil warming effects varied among diversity treatment and year (Table 1; Appendix: Figs. A1–3). On average, high and low warming increased surface soil temperature by 1.3°C and 0.7°C, respectively, over the growing season. Soil moisture data appear in the Appendix: Figs. A4–6.

Plots were burned on April 21, 2009, April 5, 2010, and April 12, 2011 as part of routine maintenance of these grassland communities.

Burning occurs in early spring before almost any aboveground living biomass has emerged, but the exact timing depends upon weather. Prescribed burning is a common method of grassland maintenance to prevent woody establishment (Adams et al. 1982). Fire has been found to advance or delay the timing of flowering for many plant species, with advancement reported more often (Wroblewski and Kauffman 2003, Jarrad et al. 2008, Pavlovic et al. 2011). However, since all plots in our experiment were burned, we are unable to measure the potential impact of fire on our results.

Phenological observations

We made phenological observations of flowering events at the individual scale (observations of single individuals over time) and the population scale (observations across all individuals of the species over time), as well as measured canopy reflectance at the patch scale (i.e., small areas that include many individuals of several species) because the footprint of the reflectance sensor is too large to isolate a single individual. Because, by design, not every species appears in the low diversity treatments (e.g., 1- and 4-species plots), we restricted our phenological observations of flowering to nine of the 16-species and two of the 32-species plots, where there was greater representation of our target species (Table 2). The two 32-species plots were added in an attempt to increase the sample sizes of certain species. The target species are all native, perennial prairie plants that were seeded in when the original biodiversity experiment was established. These species represent three families (Asteraceae, Fabaceae, and Poaceae) and have been placed previously into the following functional groups: C₃ (cool season) grasses, C₄ (warm season) grasses, legumes, and non-legume forbs. These species display a range of typical flowering times from May to September (Table 2). We grouped these species into three general flowering times (early, mid, and late flowering species) by splitting the growing season into three relatively equal lengths and using the mean flowering time in ambient plots to place each species.

Individual-scale measurements were made on tagged individuals of the target species, allowing us to follow the same plant over time and revealing the average response of individuals of

Table 2. Species characteristics and sample sizes of species monitored for flowering phenology.

Species	Family	Functional group	Flowering time	No. individuals tagged and percentage of those that flowered		
				2009	2010	2011
<i>Amorpha canescens</i>	Fabaceae	Legume	Middle	61, 62%	47, 79%	53, 74%
<i>Andropogon gerardii</i>	Poaceae	C4 grass	Middle	98, 24%	102, 62%	108, 55%
<i>Koeleria macrantha</i>	Poaceae	C3 grass	Early	32, 63%	39, 36%	43, 47%
<i>Lespedeza capitata</i>	Fabaceae	Legume	Middle	98, 65%	90, 70%	99, 72%
<i>Liatris aspera</i>	Asteraceae	Forb	Late	67, 28%	43, 53%	60, 42%
<i>Lupinus perennis</i>	Fabaceae	Legume	Early	100, 83%	102, 60%	108, 58%
<i>Dalea purpurea</i>	Fabaceae	Legume	Middle	77, 74%	73, 46%	80, 78%
<i>Poa pratensis</i>	Poaceae	C3 grass	Early	106, 14%	105, 19%	107, 15%
<i>Schizachyrium scoparium</i>	Poaceae	C4 grass	Late	100, 64%	96, 81%	103, 67%
<i>Solidago rigida</i> †	Asteraceae	Forb	Late	53, 8%	49, 31%	62, 53%

† Also referred to as *Oligoneuron rigidum* var. *rigidum*.

that species. At the start of each growing season from 2009 to 2011, up to three individuals of each species were tagged in each subplot of eleven of the plots planted with 16 or 32 species. We restricted our observations to a marked 40 cm × 2.5 m strip along the center of each subplot, below and parallel to the heat lamp, to ensure that the plants would not be disturbed by other measurements occurring in the plots. Tagged individuals were not always the first individuals to emerge, and when more than three individuals were present, we choose three growing in different locations along the strip. Once a week the reproductive stage, i.e., whether the plant was budding or flowering, was recorded. A single open flower was considered to be the start of flowering for that individual. For grasses, an open flower was defined as the presence of exposed stamens or stigmas, and an open flower was defined for forbs as the presence of exposed petals. The number of individuals tagged and the number of those that flowered are noted in Table 2. From these individual scale observations we calculated date of budding, date of flowering onset, and duration of flowering.

In addition to tracking individuals, we also monitored population-level flowering phenology in each subplot because measurements on a few individuals do not necessarily reveal whole population responses, such as first flowering date (FFD) and peak flowering (Forrest and Miller-Rushing 2010). For each species, the percentage of individuals flowering in the marked strip in each subplot was estimated to the nearest 10% each week. From these population scale observations, we calculated FFD, date

of peak flowering, and length of flowering season. First flowering date is the first date that the percentage of individuals flowering was greater than zero for a species. Peak flowering was the date with the highest proportion of individuals flowering for that species. Length of the flowering season is the number of weeks between FFD and when percentage of flowering individuals was zero for at least two weeks.

In 2011, we measured canopy reflectance spectra of subplots in all 4-, 16-, and 32-species plots throughout the growing season, starting in May 3 weeks and 2 days after plots were burned and ending in early November when the majority of plants had senesced. We measured canopy reflectance with a UniSpec single channel spectrometer (PP Systems International, Amesbury, Massachusetts, USA) equipped with a straight fiberoptic cable, which quantifies canopy reflectance at 3 nm wavelength intervals from 400 nm to 1000 nm. An L-shaped scaffold was used to hold the sensor 150 cm over the plots during measurement. We placed the scaffold in the same location to ensure that the same 36 cm diameter “patch” was measured each time. These patches were adjacent to the center strip where we monitored flowering phenology and generally contained an estimated 4–15 individuals depending on plot and diversity level. At each time point, we measured the reflectance spectra of two patches for each subplot. All readings were taken within two hours of solar noon and frequently referenced to a white standard.

We used these spectra to calculate the normalized difference vegetation index (NDVI) using the equation $(R_{800} - R_{660}) / (R_{800} + R_{660})^{-1}$, where R

is the reflectance at the indicated wavelength. The NDVI is used extensively in image analysis from both remote sensing and ground-based sensors as an index of 'greenness' that ranges from -1 to 1 , with higher values indicating more green biomass (Pettoirelli et al. 2005). Our NDVI values are useful for testing relative treatment effects, but it may not be appropriate to compare the absolute values of our data to values measured elsewhere because certain wavelengths saturated at high values.

Statistical analysis

The effects of species, year, and warming treatment on the calculated individual and population-level phenology variables were analyzed with analysis of variance using JMP 9 (SAS Institute, Cary, North Carolina, USA). To account for the multi-year split-plot design, the ANOVA models included plot, subplot (warming treatment) nested within plot, and year nested within subplot nested within plot as random factors in addition to the fixed main and interactive effects of species, year, and warming treatment. As it was not our intention to examine the effect of diversity on flowering and the majority of our measurements were at one diversity level (16-species plots), we did not include a diversity term in the analyses. The few plants in the 32-species plots might have experienced slightly different soil temperature changes in response to the treatments (Table 1), but we would lose degrees of freedom if we included diversity as a factor. Thus, we made the assumption that diversity differences between 16- and 32-species plots do not play a significant role in the flowering response to warming. Consistent with this assumption, Lemmens et al. (2008) detected neither an effect of species richness on the phenological response of perennial grassland plants to warming, nor an effect of species richness on the timing of flowering.

At the population scale, the ability to detect phenological extremes (first and last dates) or a species may depend on the abundance of that species in the plots (Miller-Rushing et al. 2008). To account for this potential bias when analyzing the population-level variables, we added unpublished data on species biomass (a proxy for abundance) as a covariate in the model. For each year, aboveground biomass was collected in 0.1

m wide strips in each subplot. For each species in each subplot, the biomass over the three years was summed and used as a proxy for relative abundance. These biomass data are significantly correlated with stem density measured in small areas (0.8 m^2) in 2011 (Pearson's correlation coefficient 0.67 , $P < 0.001$). When the number of individuals flowering was less than three for any warming treatment in any year, that species was removed from the analysis. For this reason, *S. rigida* was excluded from all ANOVA analyses, *L. capitata* was excluded from the duration of flowering analysis, and *A. gerardii* and *S. scoparium* were excluded from the budding analysis. When the three-way interaction was not near significance (P value > 0.3), it was removed from the model. Comparisons between treatment levels were analyzed either with Tukey HSD post-hoc tests or with pair-wise least square differences, using the Bonferroni adjustment to correct for multiple comparisons. Performing the above analyses without abundance as a covariate yielded very similar results.

We compared the size of the warming effect to the magnitude of interannual variation observed for each flowering variable across species. For each variable, we calculated the difference observed between years for each species in each subplot and then averaged across years and subplots to find the mean interannual variation for each species in each plot. To calculate the size of the warming effect, we found the differences between high warming and ambient values observed in the same plot and year for each species and then averaged across years. Using paired t-tests in R (R Core Team 2013), we compared the mean warming effect and mean interannual variation for each species in each plot.

Patch-level NDVI of 4- and 16-species plots was analyzed with a repeated measures ANOVA using PROC MIXED in SAS 9.2 (SAS Institute, Cary, North Carolina, USA) with diversity, warming treatment, and measurement date as fixed factors. Plot, its interaction with warming treatment, and patch were added as random factors. NDVI was arcsine square root transformed to improve normality. Significant differences between means were determined using post-hoc Tukey's HSD tests. The 32-species plots were analyzed in a separate repeated measures

Table 3. *F* ratios (with degrees of freedom in parentheses) from ANOVAs on each reproductive variable. For population level variables, biomass (a proxy of abundance) was also included as a covariate in the models.

Source of variation	Population level ($n = 3-11$) [‡]			Individual level ($n = 3-27$) [‡]		
	First flowering date (FFD)	Length of flowering season [§]	Peak flowering date	Bud date	Flowering onset date	Flowering duration [§]
S	3146 (8,557)*	49.0 (8,583)*	2990 (8,584)*	882.2 (6,704)*	1976.2 (8,995)*	32.7 (7,600)*
W	18.9 (2,25)*	4.1 (2,24)*	23.5 (2,21)*	5.7 (2,30)*	14.2 (2,30)*	8.1 (2,28)*
Y	90.1 (2,69)*	2.5 (2,69)†	65.4 (2,70)*	115.6 (2,94)*	29.4 (2,88)*	0.04 (2,87)
S × W	2.7 (16,559)*	0.9 (16,583)	2.4 (16,584)*	1.8 (12,689)*	1.6 (16,977)†	1.6 (14,620)†
S × Y	16.3 (14,561)*	18.6 (16,586)*	14.1 (16,584)*	39.7 (12,708)*	9.0 (16,1005)*	9.4 (14,714)*
W × Y	3.7 (4,68)*	2.0 (4,59)	0.8 (4,60)	1.8 (4,56)	1.0 (4,56)	2.7 (4,51)*
S × W × Y	1.4 (32,562)†

Notes: S, species; W, warming; Y, year. † and * indicate $P < 0.10$ and 0.05 , respectively. The first degrees of freedom (df) value is numerator df and second value is denominator df.

[‡] Sample sizes (n , the number of data points for each species in each warming treatment in each year) varied among species and years due to differences in abundances.

[§] The duration of flowering indicates the length of time a single individual flowers. The length of flowering season represents the period when any individual of that species is flowering.

ANOVA with the same model structure (but excluding the diversity factor), because they were planted with species drawn from a different species pool and so cannot be included as another diversity level in the above analysis where diversity is examined as a factor.

RESULTS

Warming effects on flowering phenology

Warming significantly affected all reproductive variables, generally leading to earlier flowering at both the population and individual scales, with the largest response seen under high warming. Budding for *A. canescens* and *D. purpurea* tagged individuals was 7 days earlier and flowering onset occurred 7–8 days earlier under high warming compared to ambient (Table 3, species × warming; Figs. 1 and 2; Appendix: Fig. A7). High warming also accelerated FFD and peak flowering by 7–9 and 5–7 days, respectively, for *A. canescens* and *D. purpurea* (Table 3, species × warming; Figs. 1 and 2). *A. gerardii* and *S. scoparium* reached peak flowering 6 days earlier under high warming (Table 3, species × warming; Figs. 1 and 2). Tagged individuals of *A. gerardii* flowered 7 days earlier in both the low and high warming treatments. (Table 3, species × warming; Fig. 1). Effects of warming on flowering variables were not statistically significant for *K. macrantha*, *L. capitata*, and *P. pratensis*.

Across all species and years, the length of the flowering season was 9% longer under high warming compared to ambient (Table 3, warm-

ing effect; Appendix: Fig. A8), and the duration of flowering for tagged individuals in 2010 was 16% longer under high warming than ambient (Table 3, warming × year; Appendix: Fig. A9). The low warming treatment was not significantly different from high warming or ambient for these two variables.

Interannual variability in flowering phenology

Across all species, FFD and peak flowering date were 8 days earlier in 2010 and 1–2 days earlier in 2011 compared to 2009 (Table 3, year effect). Compared to 2009, flowering onset occurred 6 days earlier in 2010 and 3 days earlier in 2011, while budding occurred 16 days earlier in 2010 and 6 days earlier in 2011 (Table 3, year effect). All species displayed significant interannual variation in at least one of the flowering variables, with four species (*A. gerardii*, *L. capitata*, *L. aspera*, *L. perennis*) showing yearly variation in at least five variables (Table 3, species × year; Appendix: Tables A1–2).

Averaged across species, the magnitude of interannual variation in budding date was twice (8 days) the magnitude of the warming response ($t_{54} = -5.9$, $P < 0.001$; Fig. 3). Interannual variation was 60% (3.3 days) and 44% (2.5 days) larger than the effect of warming for FFD and peak flowering, respectively, while there was no detectable difference between interannual variation and warming response for flowering date of tagged individuals (FFD $t_{88} = -4.6$, $P < 0.001$, peak flowering $t_{88} = -3.4$, $P = 0.0011$, flowering of tagged individuals $t_{68} = -0.7$, $P = 0.49$; Fig. 3).

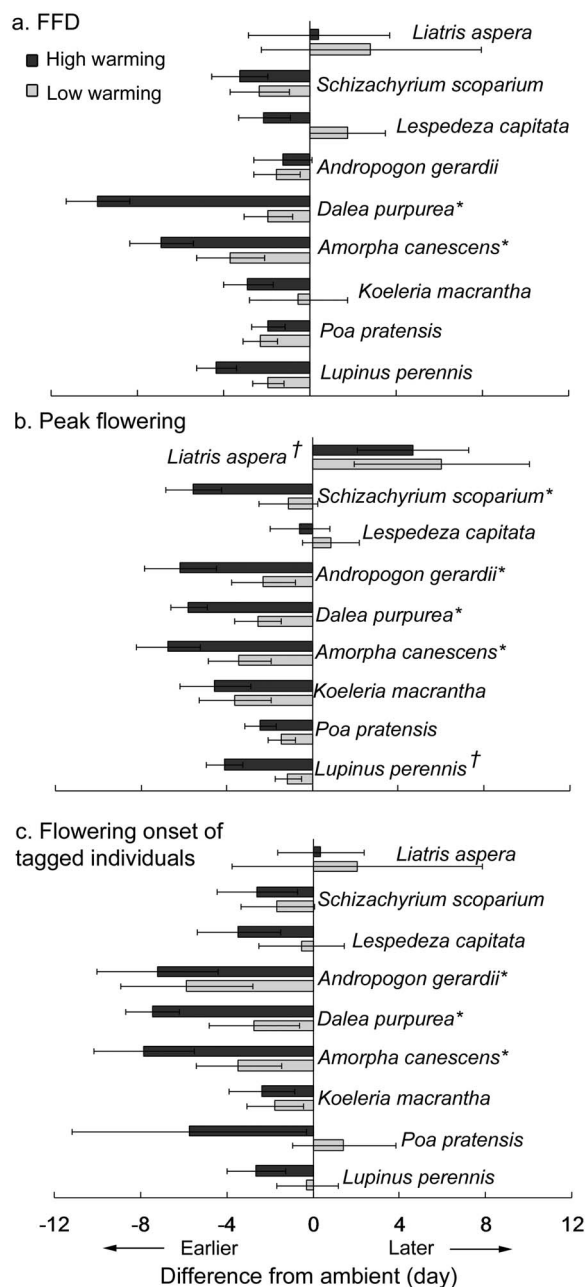


Fig. 1. Difference in (a) first flowering date (FFD) at population level, (b) peak flowering date at population level, and (c) flowering date of tagged individuals in warmed subplots compared to ambient subplots for each species. Black bars denote difference in high warming subplots and light gray bars denote difference in low warming subplots. *Koeleria macrantha*, *Solidago rigida*, and *Sorghastrum nutans* were excluded from the analysis. * indicates significant difference ($P < 0.006$ (Bonferroni adjusted), least square differences

For length of flowering season, interannual variation was 2.6 (37%) days larger than that caused by warming treatment ($t_{88} = -4.0$, $P < 0.001$), while duration of flowering for individuals showed similar interannual variation and warming response ($t_{66} = -1.7$, $P = 0.10$; Fig. 3).

Patch-level NDVI

For 4- and 16-species plots, warming treatment only significantly affected NDVI early in the 2011 growing season, on 17-May and 23-May (warming \times date, $F_{30,1450} = 2.6$, $P < 0.0001$), though high warming subplots tended to have higher NDVI throughout the growing season, especially in the 4-species plots (Fig. 4). High warming subplots displayed 68% and 24% higher NDVI than ambient subplots on 17-May and 23-May, respectively. There was no significant diversity by treatment interaction.

For the 32-species plots, NDVI (averaged over the season) was 8% higher under high warming than under ambient (warming, $F_{2,96} = 4.0$, $P = 0.02$) (data not shown). NDVI was significantly higher in the high warming treatment compared to the ambient treatment only on 17-May, when it was 40% higher.

DISCUSSION

Our field warming experiment showed a clear signal of flowering advancement in response to warming across species. Observational flowering responses to warming were generally consistent between individual and population scales. Our 1-year of patch-level spectral NDVI data indicated that the warming treatment accelerated spring green-up but did not significantly affect senescence. As predicted, we found stronger responses under high warming than low warming. Although other studies have examined phenology in relation to changing temperature, our combination of experimental warming treatments conducted over three years allows us to compare

(continuation of Fig. 1 legend)
after ANOVA) between high warming treatment and ambient controls. † indicates trend ($P < 0.01$, Bonferroni adjusted) that at least one warming treatment was different from ambient. Error bars show SE of the mean difference.

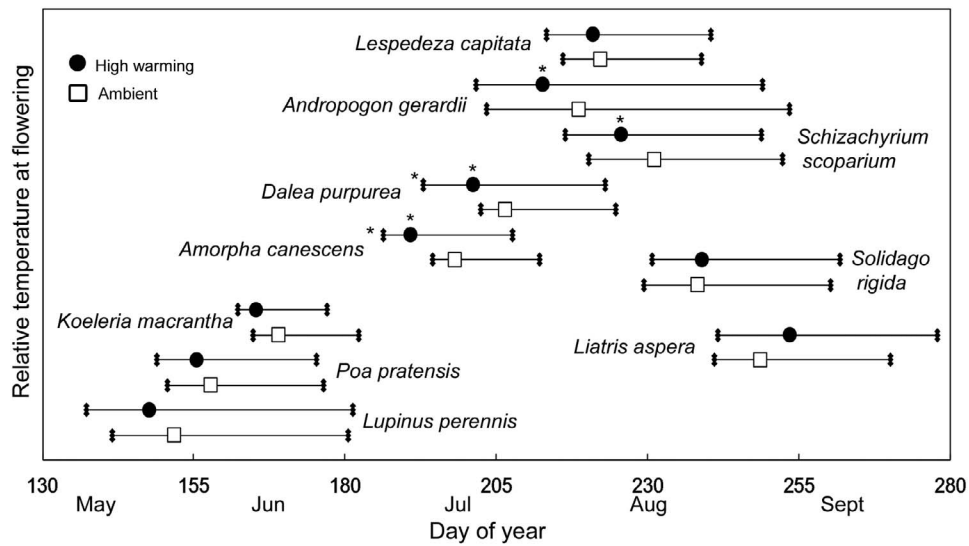


Fig. 2. Length of flowering at the population level for 10 species under high warming compared to ambient controls, averaged across three years. Open squares represent the mean date of peak flowering in ambient plots and closed circles denote mean date of peak flowering in the high warming treatment. Bars to the left start at the mean first flowering date (FFD) and bars to the right stop at the mean end date of flowering. Species are arranged on the *y*-axis based on their rank determined by the average ambient temperature at which each species flowers. * denotes significant difference ($P < 0.006$ (Bonferroni adjusted), least square differences after ANOVA) between warming treatments for either FFD or peak flowering date. Low warming data not shown as they are not significantly different from ambient.

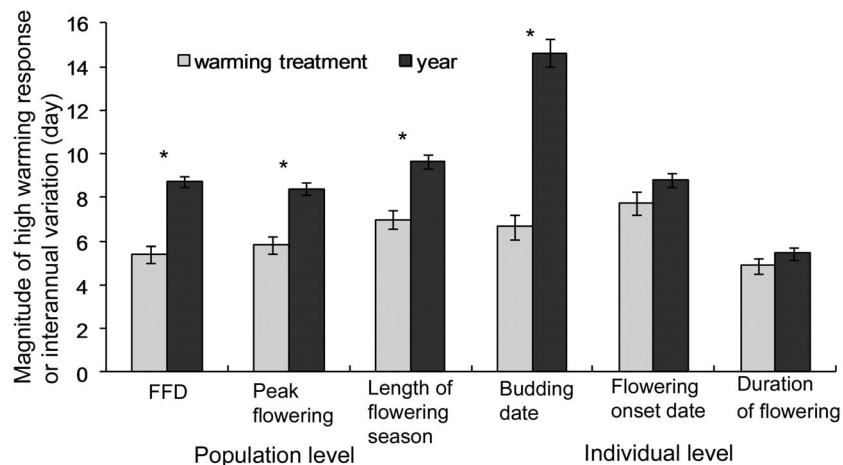


Fig. 3. Mean high warming response (warming – ambient) (light bars) compared to mean difference among years (dark bars) for all six flowering variables. Differences between warming treatments or between years were averaged across species. * indicates significant difference ($P < 0.05$, paired *t* test) between warming response and interannual variation). Error bars denote \pm SE.

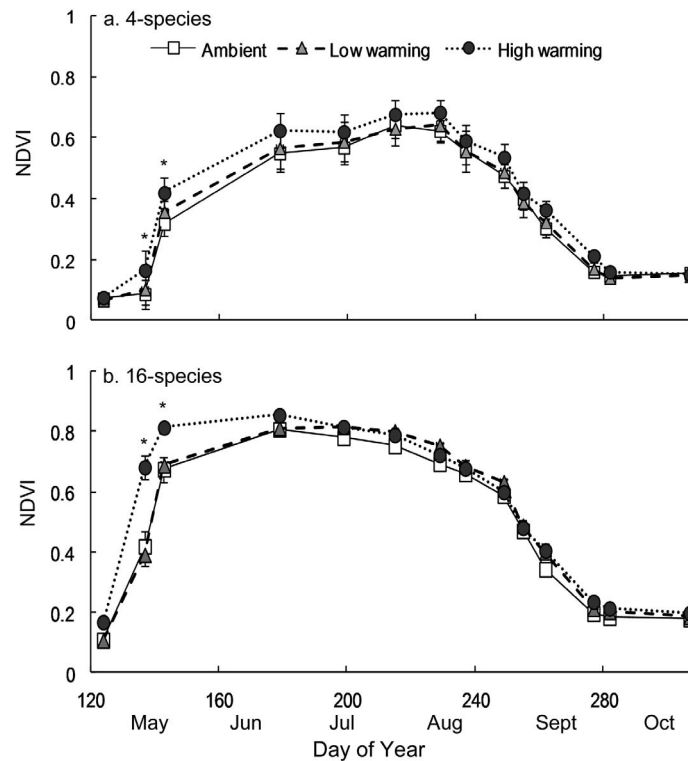


Fig. 4. Normalized difference vegetation index (NDVI) values over the 2011 growing season for 4-species (a) and 16-species (b) plots. Month names placed at middle of the month. * indicates high warming NDVI was significantly ($P < 0.05$ post-hoc Tukey's HSD test) different from ambient.

the magnitude of treatment effects to interannual variation (itself a reflection of climate) for ten prairie species.

Significant shifts in flowering phenology have already occurred in recent years for many prairie plant species in the United States (Dunnell and Travers 2011). When comparing flowering times for Northern Great Plains species in recent years (2007–2010) to flowering times in the first half of the last century (1910–1961), Dunnell and Travers (2011) observed shifts of 5–38 days in first flowering dates. In our warming study, we found shifts in flowering of 4 to 9 days. Without air temperature data, we cannot determine if this warming-induced shift is proportional to the long-term trends already seen, but our results do suggest that some species will continue to shift flowering phenology as temperatures rise. A comparison of experimental warming results and those from long-term observational studies indicated that phenological advances seen under experimental warming are smaller than those

already occurring in nature (Wolkovich et al. 2012). If this is true, the species in this study may be even more sensitive to warming than our results suggest.

As seen in numerous warming studies (Sherry et al. 2007, Hovenden et al. 2008, Liancourt et al. 2012), our warming treatment affected the timing of flowering in a species-specific manner. *A. canescens*, *A. gerardii*, and *D. purpurea* showed acceleration of at least two flowering variables under high warming. These species did not show significant advancement of budding under warming, suggesting that warming may have shortened the duration of budding. In a 1-year Oklahoma warming study, warming delayed flowering in *A. gerardii* and *S. scoparium* but accelerated budding in *A. gerardii* (Sherry et al. 2007). By contrast, we observed that warming accelerated flowering for these species but did not affect budding. There are a number of possible explanations for these discrepancies including the short duration (1 year) of the

Oklahoma study. The response to warming may differ between years, as we found for several variables and as seen in 2-year warming studies in an Australian grassland (Hovenden et al. 2008) and on the Mongolian steppe (Liancourt et al. 2012). These discrepancies could also arise if a species' response to warming depends on its location and the ambient climate. In the warmer climate of Oklahoma, warming that caused a 3°C increase in soil temperature (Sherry et al. 2008) may have exceeded a threshold and caused more stress on these species when compared to warming that caused a ~1.5°C increase in soil temperature in the cooler climate of Minnesota. Different ecotypes of the same species may respond differently, as well, due to adaptation to local climate or light regimes. The inconsistent results could also be due to different effects of warming on other variables, such as soil moisture, between the two studies. We also found evidence that *L. aspera* delayed flowering under warming. However, *L. aspera* was observed to have an accelerated FFD in recent years compared to historical data (Dunnell and Travers 2011). This discrepancy could be due to the different flowering response variables, as we found a significant effect on peak flowering date not FFD. The discrepancy could also be due to additional effects of warming on the environment, such as soil moisture, in our study.

Interspecific variation in the response to warming has the potential to alter the community flowering profile. While most species in our study show trends for earlier flowering under warming, variations in the magnitude of the shifts were observed (Figs. 1 and 2) and may lead to increased or decreased concurrent flowering among species. Most noticeable, the acceleration of flowering seen in *A. canescens* and *D. purpurea* decreases their overlap with *A. gerardii* (Fig. 2). Temporal changes to the flowering profile of a community have consequences for trophic and competitive interactions between species and individuals, and these interactions may feedback to influence community structure (Voigt et al. 2003, Elzinga et al. 2007, Memmott et al. 2007, Miller-Rushing et al. 2010, Yang and Rudolf 2010).

Contrary to our expectations and previous observational and warming studies (Bradley et al. 1999, Dunne et al. 2003, Miller-Rushing and

Primack 2008, Calinger et al. 2013, CaraDonna et al. 2014), early flowering species did not show the strongest shift in flowering in response to warming. Indeed, three of the four species that showed statistically significant shifts in flowering are species that flower in the middle of the growing season. Sherry et al. (2007) also observed that the largest warming induced shifts of flowering occurred in two species that flower in the middle of the growing season. Our warming treatments started in March, but winter temperatures can influence flowering time of spring flowering species in forests (Miller-Rushing and Primack 2008). The absence of winter warming could have caused our lack of a detectable response in our early flowering species. However, Dunnell and Travers (2011) found that April and May temperatures were the top predictors of first flowering dates for >100 US prairie species. Additionally, Wolkovich et al. (2012) saw no difference in the sensitivity of flowering to temperature when comparing experiments that elevated temperature year round with those that elevated temperature only during the growing season. They did find, however, that other experimental warming studies often did not show the larger phenological sensitivity to warming of early flowering species that is commonly seen in observational studies (Wolkovich et al. 2012); indeed, in our data, interannual variation typically exceeded treatment effects. It is also possible that the annual spring burns our plots experienced may have prevented or reduced the warming effect on early-flowering species, although Jarrad et al. (2008) observed a stronger phenological response to warming in two Australian subalpine plant species found in plots that had experienced burning the past year. Since all our plots experienced spring burning, we are unable to ascertain the potential effects of fire on our results.

There was good agreement among population and individual level variables in their response to warming overall, with a few small discrepancies. *Andropogon gerardii*, *L. perennis* and *S. scoparium* displayed trends for advances in peak flowering but no statistically significant effect of warming was detected for FFD (Fig. 1). If this result is not an artifact of the limitations of our observational methods but reflects a true biological response, it indicates that warming may not affect the start of

flowering for these species but increases the rate of flowering once it has started. Possibly, these species are responding to multiple drivers of flowering, and something other than temperature controls the onset of flowering (Heide 1994, Hovenden et al. 2008). Once that requirement is met, the species can respond to temperature. *Liatris aspera* displayed a trend for delayed peak flowering under warming but no statistically significant effect was found on FFD (Fig. 1). Possibly, warming delayed flowering in some, but not all, individuals. Last, one would expect similar results for peak flowering and flowering of tagged individuals, since tagged individuals should represent the average for the species. However, *L. aspera*, *L. perennis*, and *S. scoparium* displayed significant or near significant effects of warming on peak flowering in the population-level observations that were not detected on the tagged individuals (Fig. 1). This discrepancy is most likely due to larger variation among a few individuals than when observing an aggregate of individuals, making it more difficult to statistically detect a response.

Many species exhibited significant interannual variation in several flowering variables, with most species flowering earliest in the warmest year, 2010. As stated above, the effect of year accounted for more variation in all flowering variables than did warming treatment. Differences in the flowering times between two years were often similar or larger in magnitude than the differences observed between warmed and unwarmed treatments within a year (Fig. 3). Some species, such as *A. gerardii*, *L. aspera*, and *L. perennis*, showed interannual variability in the timing of all six flowering variables. *D. purpurea* and *A. canescens*, however, exhibited significant interannual variation in three or fewer variables (budding, length of flowering season and duration of flowering). The reduced interannual variation in these two species was unexpected and seems to contradict the results of the warming treatment, as their significant response to warming suggests that they are responsive to temperature. Several experimental warming studies have also observed that interannual variation in flowering phenology can be just as large or larger than the variation induced by warming treatment (Dunne et al. 2003, Jarrad et al. 2008, Liancourt et al. 2012).

While yearly variations in temperature probably played a role in causing interannual variation in flowering time, yearly variation in other factors such as precipitation and the timing of spring burning likely also contributed to interannual variation in these variables (Henebry 2003, Peñuelas et al. 2004, Liancourt et al. 2012). During the study period, plots were burned in April (within a 3-week period) each year. The exact timing of burning in our plots is often correlated with spring weather, making it difficult to disentangle these potential drivers of phenology. While the order of flowering among years corresponds to the timing of burning (e.g., earliest flowering seen in 2010, the year of the earliest burn), the time from burn to flowering was not consistent among years, suggesting that other factors, in addition to burn time, may have played a role in interannual variability of flowering.

In 2011, we observed statistically significant warming treatment effects on NDVI only in the spring, contrary to our prediction that senescence would show a stronger response. Instead of disconnecting emergence and temperature, spring burning, through clearing litter and ground cover, may have allowed the warming treatments to have a larger effect on soil and air temperature. Our results are consistent with a temperate grassland warming study that observed no effect of warming on senescence (Hutchison and Henry 2010), but differ from another grassland study that found warming to accelerate early spring leaf phenology and delay senescence (Lemmens et al. 2008). The higher NDVI in warmed plots during May could have been caused by earlier emergence of plants, faster growth, or both. Unfortunately, our measurements do not allow us to distinguish between these possibilities. The lack of a detectable warming treatment effect on senescence may have been due, at least in part, to the lack of precipitation during this period that may have overridden any effect of warming. The fall of 2011 was very dry, with virtually no precipitation (only ~4 mm) in September through October. It is also possible that emergence is more strongly tied to temperature than senescence, which may have other regulating factor such as photoperiod (Arft et al. 1999). While our results predict a longer growing season and/or shorter time

period to peak biomass, one year of data cannot establish if this trend will persist over time.

At all our measurement scales we generally found larger responses under high warming than low, and were often unable to detect a statistically significant response under low warming. However, we do not believe this necessarily indicates that the plants are not responding to the lower warming treatment. Several long-term observational studies have shown that plant species have shifted phenology in response to the natural $\sim 1.5^{\circ}\text{C}$ increase in air temperature that has occurred in the last 50–100 years (Peñuelas et al. 2002). The magnitude of the trends observed in our study is within the range seen in these observational studies. We were unable to statistically determine if responses seen in the low warming treatments were proportional to those seen in the high warming treatments (results not shown). Shifts in the timing of leaf unfolding in several oak species were found not to be linear with increases in temperature (Morin et al. 2010) while male flowering in a walnut cultivar was found to be linear with increasing temperature (Pope et al. 2013). Recent shifts in flowering of several Wisconsin and Massachusetts spring flowering species have been linear with temperature (Ellwood et al. 2013). However, it is not known if this trend is the same for species that flower later in the season or if the shifts will continue to be linear as temperatures rise.

Overall, our results show that elevated temperature can shift flowering phenology and accelerate spring vegetative growth of many common prairie perennials. Warming also accelerated spring green-up but affected the timing and rate of senescence less, if at all. Most variables showed the strongest response under high warming, but the direction of response was generally similar under high and low warming. We also found that the magnitude of interannual variation was similar to or larger than the effect of warming. Longer-term studies are needed to determine if the changes in phenology that we observed are cumulative and if they can influence community composition and carbon cycling.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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