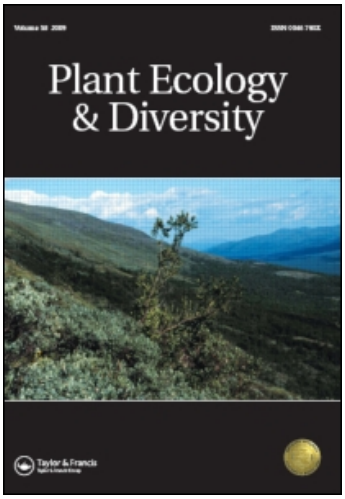

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Changes in duration of reproductive phases and lagged phenological response to experimental climate warming

Rebecca A. Sherry[a]; Xuhui Zhou[a]; Shiliang Gu[ab]; John A. Arnone III[c]; Dale W. Johnson[d]; David S. Schimel[e]; Paul S. J. Verburg[c]; Linda L. Wallace[a]; Yiqi Luo[a]
[a] Department of Botany and Microbiology, University of Oklahoma, Norman, USA [b] Department of Agronomy, Yangzhou University, Yangshou, P.R. China [c] Division of Earth and Ecosystem Sciences, Desert Research Institute, Reno, USA [d] Department of Natural Resources and Environmental Science, University of Nevada, Reno, USA [e] National Center for Atmospheric Research, Boulder, USA

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Changes in duration of reproductive phases and lagged phenological response to experimental climate warming

Rebecca A. Sherry[a]*, Xuhui Zhou[a], Shiliang Gu[a,b], John A. Arnone III[c], Dale W. Johnson[d], David S. Schimel[e], Paul S.J. Verburg[c], Linda L. Wallace[a] and Yiqi Luo[a]

[a]*Department of Botany and Microbiology, University of Oklahoma, Norman, USA;* [b]*Department of Agronomy, Yangzhou University, Yangshou, P.R. China;* [c]*Division of Earth and Ecosystem Sciences, Desert Research Institute, Reno, USA;* [d]*Department of Natural Resources and Environmental Science, University of Nevada, Reno, USA;* [e]*National Center for Atmospheric Research, Boulder, USA*

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Background: Climate manipulation experiments have found lagged responses in biomass and community composition.
Aims: To look for lagged responses of flowering phenology and effects on duration of reproductive phases.
Methods: Treatment and post-treatment year phenological data from 12 species in a 1-year step warming and double precipitation experiment was examined.
Results: Changes in phenology due to the previous year's warming were in the opposite direction to those observed during the treatment year. Six species responded to warming in 2004, delaying flowering 6.2 days and fruiting 7.9 days. Unlike 2003, no species advanced flowering phenology in 2004. Delays resulted from a soil moisture deficit in formerly warmed plots that lasted 3 months or more after warming ended. Increased precipitation altered phenology in one species but did not affect duration of reproductive phases. While 10 of 11 responsive species entered bud phase earlier under warming than in controls in 2003, in only two species showed a phenological delay at the beginning of the bud phase in 2004. Warming tended to shorten flowering and fruiting stages and total duration in spring annuals.
Conclusions: Together, these results suggest that climate anomalies can influence phenology in the following year, here due to a lag in soil moisture recharge.

Keywords: climate change; climate warming; flowering duration; flowering phenology; increased precipitation; lagged effects; lagged response

Introduction

Interest in phenology, the timing of annual life-cycle events in plants and animals, has risen in the past decade because of global climate change (Schwartz et al. 2006; Cleland et al. 2007). Spring flowering phenology has been proposed as an accurate indicator of climate change because of its sensitive dependence on temperature in many species (Menzel et al. 2006). Averaged measurements of spring events for over 1000 plant and animal species indicated that spring had been advancing 2.3 days per decade (Parmesan and Yohe 2003). Climate warming experiments have reported similar responses of flowering to warming (Wookey et al. 1993; Arft et al. 1999; Dunne et al. 2003; Sherry et al. 2007; Hovenden et al. 2008). Other changes in climate, such as change in the amount of precipitation, do not have such clear effects on flowering time over entire plant communities (Post 2003), except in deserts (Bowers 2005). Changing leaf colour in the autumn has also been delayed by climate warming by 0.3–1.6 days per decade in Europe (Walther et al. 2002). There have been few studies on the phenology of other autumn events, such as fruit set, and those gave conflicting (or species-specific) reports of both advances and delays due to increasing temperature (Menzel et al. 2003).

When smaller increments of time (other than yearly temperature means) are examined, spring flowering phenology is often found to depend most closely on temperatures in the preceding autumn or winter (Grainger 1939; Fitter et al. 1995). This is especially the case in species that preform spring flower buds in the late summer or autumn of the preceding year (such as high alpine or arctic tundra plants or early spring flowering trees). However, such a lag effect has not yet been observed in climate warming manipulation experiments. Most climate warming experiments have been carried out in high alpine and arctic habitats, where the date of snow-melt can have even a more direct effect on plant emergence and flowering than temperature itself (Henry and Molau 1997; Walker et al. 1999; Dunne et al. 2003).

The duration of the flowering period is much more rarely examined than the date of flowering itself. The duration of flowering determines the time available for pollination, important for both plant and pollinator fitness. A lengthened flowering stage may indicate good resource availability (Burkle and Irwin 2009) or a dearth of pollinators (Rathcke 2003). The duration of the budding and fruiting stages can affect the amount of resources devoted to the developing ovaries, pollen or seeds (Galen and Stanton

*Corresponding author. Email: rsherry@ou.edu

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1991). A lengthened bud stage may also be due to dormancy, which may or may not be caused by a lack of resources (Bernier et al. 1981). The duration of flowering, as well as the duration of other stages within the reproductive cycle of plants, such as the length of the bud stage, length of flowering, and length of fruit development, can also be expected to show significant impacts from temperature and precipitation. High temperatures may speed plant growth through all stages of development, shortening such stages (Bernier et al. 1981; Halevy 1985; Kinet et al. 1985). Limited soil moisture, whether due to low precipitation or drying from high temperatures, may slow development during bud and fruit development stages, lengthening those stages, and shorten the period when flowers are open and losing water through transpiration (Galen et al. 1999). To explore the effect of an extreme climate year on all aspects of the ecosystem, we applied a + 4 °C increase in temperature and doubled precipitation to an old-field tallgrass prairie for 1 year, taking measurements before, during and after the treatment year. The immediate effect on flowering phenology during the treatment year was previously reported for 12 species (Sherry et al. 2007). Flowering was advanced in the first nine species to flower (before the peak of summer heat), but delayed in the last three species to flower. Here, we report on flowering phenology during the year following treatment. We also examine the duration of three phases of the plant reproductive cycle (bud stage, flower stage and fruiting stage) during and after the experimental year.

Materials and methods

Study site and species

The experimental site (34° 58′ 54″ N, 97° 31′ W) is an old-field tallgrass prairie in McClain County, Oklahoma, USA, on the Central Redbed Plains (Tarr et al. 1980; Zhou et al. 2006; Sherry et al. 2007; Sherry et al. 2008). It was abandoned from agriculture in 1974 and lightly grazed until 2002 when large herbivores were excluded. The soil is a silt loam with 36% sand, 55% silt and 10% clay in the top 15 cm (A. Subedar and Y. Luo, unpublished data). Mean annual temperature at the site is 16.3 °C, with monthly mean air temperature ranging from 3.3 °C in January to 28.1 °C in July. Mean annual precipitation is 967 mm (averaged from 1948 to 1999, Oklahoma Climatological Survey). Precipitation is usually highest in May and June (240 mm), followed by September and October (192 mm), and lowest in January and February (82 mm) and July and August (125 mm).

We have identified over 70 angiosperm species within the plots used in this experiment (R. Sherry, unpublished data). In spring, the site is dominated by the C_3 winter annual grass *Bromus arvensis*, and in summer by the perennial C_4 grasses *Andropogon gerardii*, *Panicum virgatum*, and *Schizachyrium scoparium,* and the C_3 forb *Ambrosia psilostachya.* At the time of peak biomass (August), the three C_4 grasses represented almost three-quarters of the biomass in each plot (Y. Luo et al., unpublished data). Plant nomenclature follows the USDA PLANTS Database (USDA NRCS 2008).

Experimental design

We used a randomised block design with two levels of temperature (ambient and + 4 °C) and two levels of precipitation (ambient and doubled). Twenty 3 × 2 m plots were placed 1.5 m apart in two rows 3 m apart. A slight difference in plant composition between the two rows and a larger difference from one end of the rows to the other were used to orient the five blocks. Warmed plots had two 165 × 15 cm radiant infrared heaters suspended above them at a height of 1.4 m (Kalglo Electronics Inc., Bethlehem, Pennsylvania, USA). Previous experimentation determined that, at this height, two heaters, each with a radiation output of 100 watt/m^2 would warm the soil surface approximately 4 °C (Wan et al. 2002). Rigorous testing has shown that the infrared radiation from the heater does not generate any visible light affecting photosynthesis (Kimball 2005). The remaining 10 plots each had two 'dummy' heaters, the same size and shape as the infrared heaters, constructed of metal flashing, suspended over the plots at the same height and position as in the warmed plots.

Ten plots had attached 'water catchments,' an angled sheet of corrugated plastic the same size as the plots. During a rainfall, these catchments directed precipitation onto the plots via three PVC pipes. Non-watered plots were also fitted with the PVC pipes. During natural rainfall events, this design supplied extra precipitation approximately equal to the natural rain event. Heaters, dummy heaters, water catchments, and PVC pipes were in place and functional for 1 year, from 20 February 2003, when the earliest winter annuals emerged, to 20 February 2004, well after all species had senesced. This period is referred to as the 'treatment year.'

Each plot was divided into four equal quadrants. Scientific instruments were located in the north-east and south-west quadrants. Air temperature at 15 cm above the soil surface and soil temperature at five depths below the surface were continuously recorded, along with soil moisture at five depths. Plant root simulator (PRS^{TM}) probes (Western Ag Innovations Inc., Saskatoon, Canada) monitored available soil NH_4^- and NO_3^+ for a period of 1 month four times per year (Hangs et al. 2004). The PRS probes consist of anion or cation exchange membranes imbedded in plastic stakes. After exposure to the soil, the PRS probes were sent to Western Ag Innovations, Saskatoon, Canada for extraction. At Western Ag, the probes were extracted with 17.5 ml of 0.5 N HCl for 1 h in a zip lock bag, and the extractant was analysed for NH_4^+ and NO_3^- colorimetrically using a Technicon Autoanlyzer II.

Treatment effects on air and soil temperature, soil moisture, and available NH_4^+ and NO_3^- (henceforth referred to as available N), reported in full in Sherry et al. 2008,

are summarised here. During 2003, relative to the temperature in control plots, the air temperature at 15 cm above the soil surface decreased by 0.4 °C in the double precipitation plots, increased by 4.2 °C in the warmed plots, and by 4.8 °C in the warming plus doubled precipitation treatment during the treatment period (type T thermocouples, Campbell Scientific, Logan, UT, USA). Average soil moisture (± SE) from 0–120 cm was 27.50 ± 0.18, 28.10 ± 0.19, 21.54 ± 0.20, and 25.28 ± 0.19% vol., in control, double precipitation, warmed, and both warmed plus double precipitation treatments, respectively, during the treatment year (MP-917 Instrument with PRB-A profiling probes, ESI Environmental Sensors, Inc., Sidney, BC, Canada; Figure 1). After treatments ended in the spring of 2004, soil moisture in the previously warmed plus doubled precipitation plots rapidly reached levels identical to those in the control and double precipitation plots, but average soil moisture in the formerly warmed plots did not reach the level of the control plots until 4 months later (Sherry et al. 2008; Figure 1). Total annual precipitation at the site for the years 2002, 2003 and 2004 was 854, 622, and 965 mm, respectively, 2003 being especially droughty during the summer and autumn (Oklahoma Climatological Survey). Levels of available N did not differ between treatments in the spring of 2003, but were higher in double precipitation plots than in other treatments during the summer and winter of 2003. Levels of available N did not correlate with biomass (Sherry et al. 2008).

Phenological measurements

Species and techniques used were the same as reported in Sherry et al. 2007, except that data for *Bromus arvensis* was not available for 2004. Twelve study species were chosen as they were the only species that occurred in almost every plot. They consisted of five winter annual species (four forbs and one C_3 grass – *Bromus arvensis*, *Cerastium glomeratum*, *Plantago virginica*, *Veronica arvensis*, *Viola bicolor*), one biennial forb (*Erigeron strigosus)*, and six perennials, two of which were forbs (*Achillea millefolium*, *Ambrosia psilostachya*), one a C_3 grass (*Dichanthelium oligosanthes*), and three C_4 grasses, (*Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*). These 12 species represented 17% of the species in the plots and made up an average of 79% of the relative cover in the spring, and about 70% in the late summer.

For *Plantago*, *Veronica*, *Viola*, and *Dichanthelium*, phenology data were collected from the south-east and north-west quarters of each plot (lacking equipment). For the relatively more numerous *Bromus and Cerastium*, data were collected from a 400 cm^2 and a 100 cm^2 quadrat, respectively, placed in the same position within the south-east and north-west quarters of the plot at each observation time. For the large, less numerous perennials, *Achillea*, *Ambrosia*, *Andropogon*, *Erigeron*, *Panicum*, and *Schizachyrium*, the entire plot was used.

As soon as buds were noticed on the study species, the collection of flowering phenology data for that species

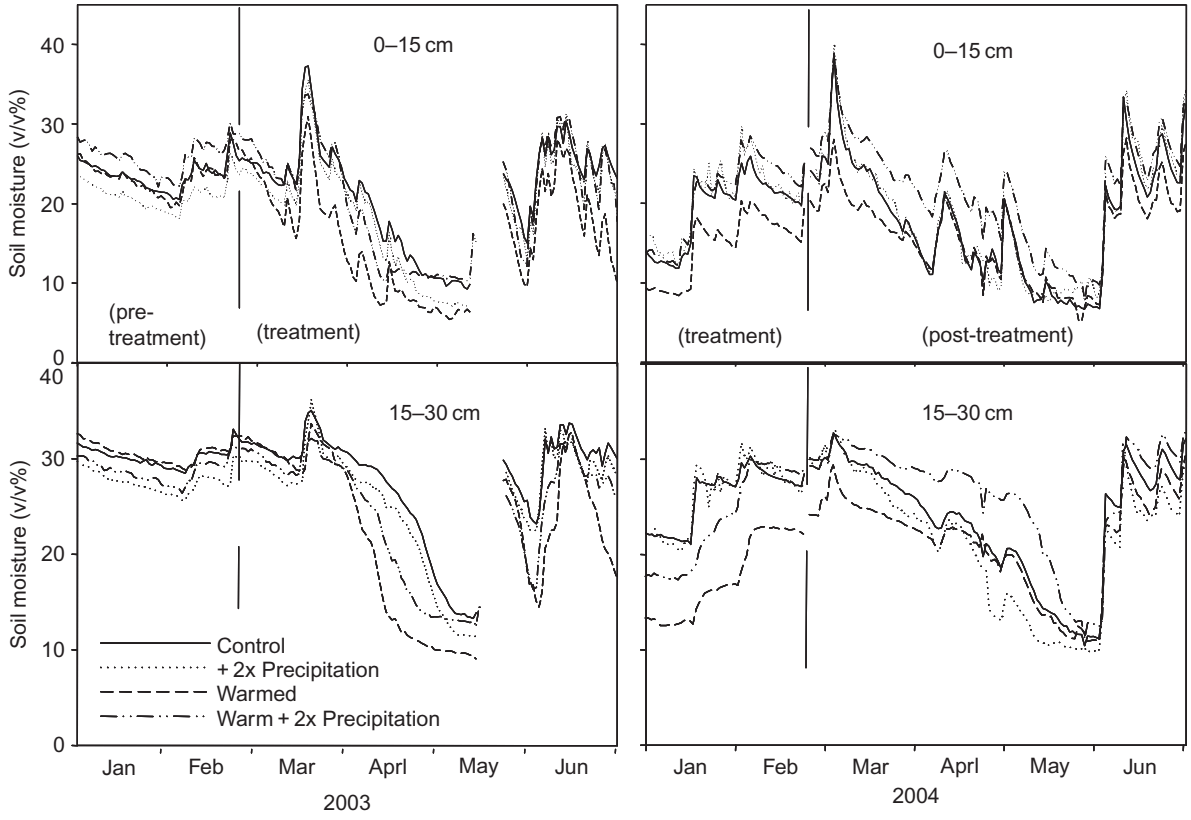

Figure 1. Soil moisture at two depths in all four treatments during the treatment year (2003) and the post-treatment year (2004).

began. Data collection for the first species to flower, *Viola bicolor*, began 7 March 2003. Plants were scored every 5–10 days. Phenological scoring was modified slightly from Price and Waser (1998) and Dunne et al. (2003). For forbs, vegetative plants were given a score of 0, unopened buds a score of 1, open flowers a score of 2, old flowers (post anthesis) a score of 3, visible initiated fruit a score of 4, expanding fruit a score of 5, and dehisced fruit a score of 6. (On very small flowers, when initiated and expanded fruit were difficult to distinguish, a score of 4.5 was assigned.) For grasses, plants with flower stalks (in boot) were given a score of 0, spikelets present (out of boot) a score of 1, exerted anthers or styles a score of 2, past the presence of anthers and styles (developing fruit, separated glume tips) a score of 3, and disarticulating florets a score of 4.

For the first six species to flower in the spring (in order: *Viola*, *Veronica*, *Cerastium*, *Plantago*, *Dichanthelium*, and *Bromus*), which were also the smallest plants, every plant with buds or older was counted and given a phenological score based on the phenological stage of the oldest flower position on the plant. The scores of plants in an individual quarter of a plot were averaged to yield two phenological scores (pseudo-replicates, one for each quarter), which were then averaged to yield the average phenological score of the plot per observation day. The number of vegetative plants up to the date of peak flowering was inferred by subtracting the number of plants scored on that observation day from the number of plants scored on the day of peak flowering (i.e. the maximum number of plants counted in one day). For the early summer-flowering species, *Achillea millefolium and Erigeron strigosus*, each flowering stage present on every plant in each plot was noted and an unweighted average calculated for each plant on each observation day. For the summer-flowering perennial species, *Panicum virgatum*, *Andropogon gerardii*, *Schizachyrium scoparium* and *Ambrosia psilostachya,* 10 stems (if available) in each plot were tagged at the beginning of the season so individual plants could be followed throughout the summer. For each observation day, each phenological stage present on each tagged plant was noted and an unweighted average calculated for each plant. If a tagged plant died or was grazed during observations, another nearby stem was tagged to replace it, when available. Mortality was large enough in these summer-blooming species that several plots had less than 10 tagged stems of each species by the end of the season.

Data collection ended when all plants of a species had reached a phenological stage of 6 for forbs or 4 in grasses. (Phenological stages will hereafter be referred to as F1–F6 for forbs and G1–G4 for grasses.) One exception occurred in *Ambrosia*, where plants were clipped at ground level in 2003 at the first sign of seed dehiscence to measure seed set and above-ground biomass (results discussed elsewhere).

Analysis

When phenological stage was plotted vs. time, the data took on an obvious S-shape. These curves were fitted to the Richard's growth equation:

$$Y = K/(1 + a^{*}\exp(-b^{*}X))^{m}$$

where K is the maximal growth (here the last phenological stage, F6 or G4); a is an initial parameter whose value is related to the first observation date; b is growth rate over time X; and m is a variable curve shape parameter. In order to estimate the four parameters precisely, the contraction–expansion algorithm developed by Gu et al. (1998) was used. With minimal residual sum of squares as the objective, the algorithm searches for optimal parameters by contracting and expanding search space alternatively. Parameter estimations were conducted separately for the two quarters of each plot (for the six earliest blooming species), for each plot (for *Erigeron* and *Achillea*), or for each plant (for the last four species to bloom).

After generating the four parameters of the Richard's equation for each quarter, plot, or plant, the resulting regression equation was then used to calculate the time at stages F1, F2, F3.5, and F5 (or G1, G2, G2.5 and G3, or buds present, petals open, fruit initiated, and expanding fruit). Duration was calculated as the number of days between F1 and F5, following Price and Waser (1998) and Dunne et al. (2003). While the first visible flower or inflorescence buds is an adequate indicator of the onset of the reproductive phases for the forbs studied here, in grasses, inflorescence and flower buds are formed long before the buds become visible (Rice 1950). In grasses, new buds are protected by several layers of sheathing leaf bases for most of their development, when they are said to be 'in boot.' To partially reflect those early bud stages and more closely correspond with the bud stage reflected by F1 in forbs, the beginning of the reproductive phase in grasses was taken to be the date when the most culms in boot were visible per plot and called G0.5. So, duration in grasses was calculated as G3–G0.5. G0.5 was the only parameter not calculated from the fitted equations, but was taken directly from field counts of culms. Finally, the entire reproductive phase was divided into three developmental stages: a bud stage, F1–F2 or G0.5–G2; a flowering stage, F2–F3.5 or G2–G2.5; and a fruiting stage, F3.5–F5.5 or G2.5–G3.5. Effect size of warming on duration and stage lengths was calculated as the difference from the mean divided by the standard deviation (Hedges 1985).

A separate multivariate analysis of variance (MANOVA) for each species was used to test for differences between treatments in F1, F2, and F3.5 (or G1, G2, and G2.5), Duration, and the three phases of reproductive development. When MANOVA results found significant differences between treatments, univariate

(ANOVA) analyses were consulted to determine which of these parameters differed due to which factors. When ANOVA indicated significant differences, pair-wise Tukey's tests were used to determine which treatments differed significantly from the control.

For the five responsive species, multiple linear regression was used to determine which of the measured environmental variables correlated most closely with flowering phenology. Flowering (F2 or G2) was used as the dependent variable and predictor variables were: average air temperature at 15 cm above the soil surface in winter and spring; average soil moisture at 15–30 cm below the soil surface in winter and spring; and total available N during the months of February and May. For this purpose winter was the three months January, February and March, and spring was April, May and June. All statistics were performed in SAS 9.1 (SAS Institute 2004).

Results

Flowering phenology in 2004

In 2004, after the warming and double precipitation treatments had stopped, six of the species followed in 2003 still had altered phenology at some point during reproduction (Table 1, Figure 2). All of these species bloom in the spring; four are winter annuals, and two are biennial. In formerly warmed plots, these six species delayed flowering or fruiting compared with the control. Averaged over the six species, flowering was delayed by 7.7 ± 3.6 days (± SE) in warmed plots in comparison with control plots, and fruiting was delayed by 8.9 ± 2.4 days. The preceding year's double precipitation treatment significantly delayed flowering in one species, *Cerastium*. In 2003, double precipitation had no effect (Sherry et al. 2007). In *Achillea*, *Cerastium*, *Veronica*, and *Viola* warming delayed reproductive phenology at all stages tested. *Plantago* differed only during the stages of fruit development and dehiscence, while *Erigeron*, which had not varied significantly in phenology between treatments in 2003, differed at only one of the tested stages, F3.5, approximate fruit initiation. *Dichanthelium*, a C_3 grass, and the last four of the species to bloom in 2004, did not differ significantly among treatments (Figure 2).

Comparing phenology of 2003 and 2004

During the treatment year of 2003, the phenology of reproductive stages was advanced by an average of 7.6 days by warming in the first nine species to bloom and delayed by an average of 5.1 days in the last three species to bloom (Sherry et al. 2007). In general, the difference in phenology due to warming was slightly longer in 2004 than in 2003 (as well as in a different direction), averaging a delay of 8.3 days for flowering and 8.2 days for fruiting.

The difference in the onset of flowering between 2003 and 2004 could be large, but there was no consistent direction among species. Averaging over all treatments, *Schizachyrium* flowered 26 days earlier in 2004 than it had in 2003, while *Panicum* flowered 31 days later in 2004 compared with 2003. When considering only the warmed treatment, the difference could be even larger. *Andropogon* flowered 27 days earlier in warmed plots in 2004 than it had in 2003, while warmed *Panicum* flowered 39 days later in 2004 compared with 2003. On average, the difference between flowering in 2003 and 2004 in the first seven species to flower was much smaller (5.6 days) than that difference in the last four species to flower (24.4 days). The last three species to flower, which had all been delayed by warming in 2003, all flowered 20 or more days earlier in 2004 than in the dry 2003.

Likewise, differences in the duration of the entire reproductive period between 2003 and 2004 could also be large (Tables 2 and 3). In control plots, the duration of the reproductive period in *Panicum* was 35 days longer in

Table 1. *F*-values and associated probabilities (Wilks' lambda) for a MANOVA on stages F2, F3.5, F4, (or G2, G2.5, G3) in 2004. Species are listed in the order of flowering.

	F			*n*
Species	W	+2×Precip	W*+2×P	C,W, 2×P, W* 2×P
Viola bicolor	**10.3****	1.73	0.61	5, 5, 4, 5 (plots)
Veronica arvensis	**31.04*****	0.68	0.10	5, 5, 5, 5 (plots)
Cerastium glomeratum	**19.96*****	**3.61***	1.65	5, 4, 5, 4 (plots)
Plantago virginica	2.38	0.08	0.08	5, 4, 4, 5 (plots)
Dichanthelium oligosanthes	0.11	0.65	0.30	5, 5, 4, 5 (plots)
Achillea millefolium	3.28	1.92	1.74	5, 5, 5, 5 (plots)
Erigeron strigosus	2.27	0.14	0.25	5, 5, 4, 5 (plots)
Panicum virgatum	0.06	0.48	1.68	37, 35, 53, 38 (tillers)
Andropogon gerardii	0.15	1.93	1.90	45, 48, 47, 42 (tillers)
Schizachyrium scoparium	0.32	0.39	0.32	50, 50, 50, 50 (tillers)
Ambrosia psilostachya	0.30	0.63	0.52	42, 33, 22, 36 (stems)

C, control; W, warming by ca. 4 °C; +2×P, double precipitation; W*+2×P, warming with double precipitation; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

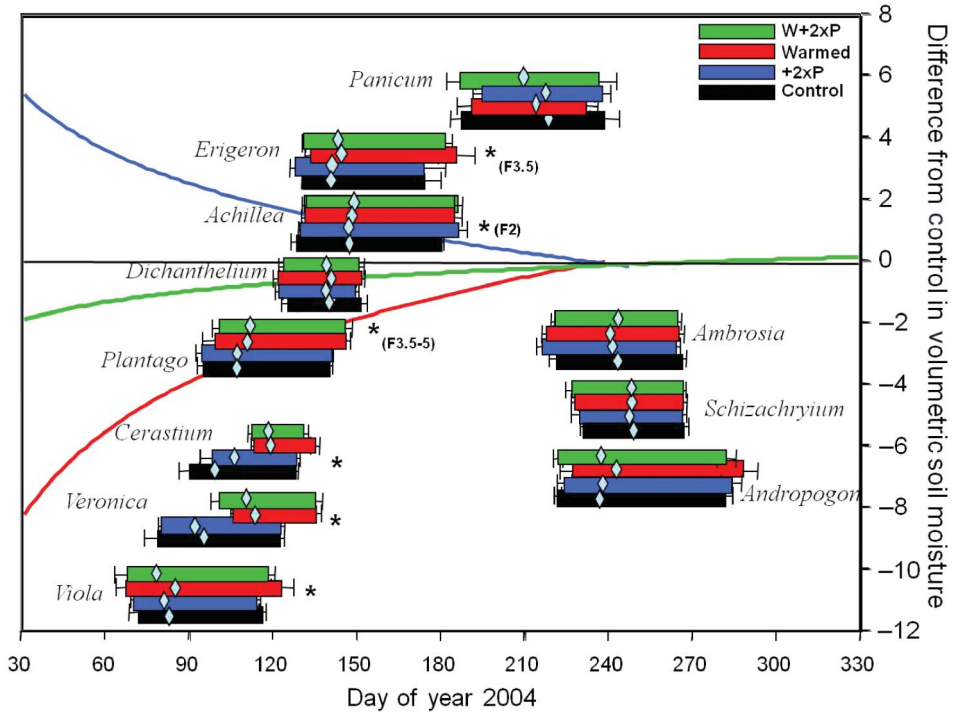

Figure 2. Duration of the reproductive cycle for the 11 species in 2004 (the post-treatment year). ♦ indicates flowering, stage F2 (G2), petals open. Three species (*) differed significantly from control at all stages; two species differed only at particular stages. Doubled precipitation (+2xP) significantly altered flowering phenology only in *Cerastium*. Coloured lines represent average difference in soil moisture from control (black) for the warmed (red), double precipitation (blue) and combined treatments (green).

2004 than in 2003, while in *Andropogon* it was 18 days shorter. When comparing only the warmed treatment, *Viola* duration increased by 30 days from 2003 to 2004, while *Andropogon* duration decreased by 37 days. In contrast to timing, there was some pattern to how duration changed between 2003 and 2004. The first four species to flower in the spring all increased in duration between 2003 and 2004 in both the control and the warmed plots, while the last three species to bloom at the end of the year all significantly shortened duration. With the exception of *Panicum*, the four species flowering closer to the middle of the season had very small changes in duration.

The duration of the entire reproductive period is the only phenological parameter examined so far to show an effect of the double precipitation treatment. In 2003, duration of *Viola* was lengthened by 3 days by the extra precipitation, but in *Andropogon* and *Schizachyrium* duration was shortened by extra precipitation by 11 and 15 days, respectively (Table 2). However, double precipitation in 2003 had little effect on duration in 2004 (Table 2 and 3).

Length of the bud, flowering, and fruiting stages

There was no obvious pattern to how treatments changed the lengths of bud, flowering and fruiting stages across years and species (Tables 2 and 3), except that the direction of change of in reproductive stage length caused by warming and extra precipitation was often the same within a species. To see if any other generalisations were possible, examining the effect size of warming on duration showed that the bud stage was lengthened in 2003, while flowering, fruiting and total duration were shortened (Figures 3 and 4). No trends were apparent for 2004. When the first five species to flower in 2003 (all annuals) were analysed separately from the other species, another trend appeared. Flowering, fruiting and duration were shortened in the annuals in 2003, but not in other species (Figure 4). Too few species responded to warming in 2004 to allow the same analysis.

Effect of soil moisture, temperature and nitrogen on phenology

In 2003, day of flowering correlated negatively with temperatures in all seven spring-blooming species but had no correlation with soil moisture (Figures 4 and 5). In 2004, only one species had any correlation between flowering time and temperature, *Plantago*, but this correlation was mainly due to a single outlier (Figure 6, top left). However, in four of the seven species (*Achillea*, *Cerastium*, *Veronica*, and *Viola*) flowering correlated positively with soil moisture in 2004 (Figures 4 and 5). Total available N in May accounted for some variation in flowering time in three species, with slight positive correlations in *Plantago* and *Erigeron* in 2003, and a negative correlation in *Achillea* in 2004 (Figure 6).

Table 2. Length in days of duration of entire reproductive phase, bud phase, flowering phase, and fruiting phase for each species in each treatment in 2004 (least-square means ± standard error). Species are listed in the order of flowering. Values in bold with shading are significantly different from the control in both the MANOVA and univariate analyses ($P < 0.05$). Only those species with significant differences in phenology at some stage were examined.

Species	Control	+2×Precip	Warming	Warm*+2×Precip
Length of the Bud Phase (days)				
Viola bicolor	10.8 ± 1.5	11.1 ± 1.5	**17.0 ± 1.5**	**15.5 ± 1.5**
Veronica arvensis	10.2 ± 1	11.1 ± 1	7.1 ± 1	9.0 ± 1
Cerastium glomeratum	9.3 ± 1	7.8 ± 1	**5.3 ± 1**	6.0 ± 1
Plantago virginica	11.7 ± 1.5	12.5 ± 1.5	11.3 ± 1.5	10.8 ± 1.5
Achillea millefolium	18.5 ± 1.5	17.4 ± 1.5	16.5 ± 1.5	17.5 ± 1.5
Erigeron strigosus	9.8 ± 1.5	12.8 ± 1.5	11.0 ± 1.5	12.0 ± 1.5
Length of the Flower Phase (days)				
Viola bicolor	13.2 ± 1.5	16.6 ± 1.5	16.5 ± 1.5	**20.4 ± 1.5**
Veronica arvensis	11.1 ± 1.5	13.9 ± 1.5	8.3 ± 1.5	11.6 ± 1.5
Cerastium glomeratum	12.8 ± 1	9.8 ± 1	**8.2 ± 1**	**8.5 ± 1**
Plantago virginica	16.3 ± 1.5	16.1 ± 1.5	16.3 ± 1.5	16.9 ± 1.5
Achillea millefolium	17.1 ± 1.5	22.8 ± 1.5	16.3 ± 1.5	16.9 ± 1.5
Erigeron strigosus	16.0 ± 2.5	14.8 ± 2.5	23.0 ± 2.5	18.0 ± 2.5
Length of the Fruiting Phase (days)				
Viola bicolor	28.3 ± 1.5	28.4 ± 1.5	30.8 ± 1.5	30.2 ± 1.5
Veronica arvensis	21.8 ± 2	22.1 ± 2	17.4 ± 2	18.4 ± 2
Cerastium glomeratum	22.8 ± 2	18.0 ± 2	**12.0 ± 2**	**11.3 ± 2**
Plantago virginica	25.4 ± 2	27.0 ± 2	23.8 ± 2	21.2 ± 2
Achillea millefolium	22.0 ± 1.5	22.4 ± 1.5	24.2 ± 1.5	23.6 ± 1.5
Erigeron strigosus	25.8 ± 3.5	24.3 ± 3.5	23.0 ± 3.5	29.5 ± 3.5
Total Duration of the Reproductive Phase (days)				
Viola bicolor	44.0 ± 2	43.8 ± 2	**55.5 ± 2**	**55.3 ± 2**
Veronica arvensis	37.2 ± 3	41.6 ± 3	29.4 ± 3	33.6 ± 3
Cerastium glomeratum	37.8 ± 2	29.8 ± 2	**21.3 ± 2**	**22.0 ± 2**
Plantago virginica	45.1 ± 3	46.2 ± 3	46.2 ± 3	44.9 ± 3
Achillea millefolium	51.6 ± 3	57.0 ± 3	53.4 ± 3	55.2 ± 3
Erigeron strigosus	43.3 ± 5.5	45.3 ± 5.5	52.0 ± 5.5	50.5 ± 5.5

Table 3. *F*-values and associated probabilities (Roy's Greatest Root) for a MANOVA on duration, length of bud phase, length of flower phase, and length of fruiting phase in 2004. Species are listed in the order of flowering. Only species with significant treatment effects on phenology were analysed.

	F			*n*
Species	W	+2×Precip	W*+2×P	C,W, 2×P, W* 2×P
Viola bicolor	**1.93***	0.43	0.07	5, 5, 4, 5 (plots)
Veronica arvensis	0.50	0.35	0.21	5, 5, 5, 5 (plots)
Cerastium glomeratum	**3.42***	0.24	0.47	5, 4, 5, 4 (plots)
Plantago virginica	0.63	0.01	0.12	5, 4, 4, 5 (plots)
Achillea millefolium	0.14	0.63	0.61	5, 5, 5, 5 (plots)
Erigeron strigosus	0.34	0.38	0.81	5, 5, 4, 5 (plots)

C, control; W, warming by ca. 4 °C; +2×P, double precipitation; W*+2×P, warming with double precipitation; *, $P < 0.01$.

Discussion

Lagged effect of warming on phenology

At least one flowering stage was significantly delayed in the post-treatment year in six of the seven earliest blooming species in 2004. While flowering in 2003 was significantly negatively correlated with spring temperatures in all of these species, in 2004 flowering correlated with spring temperature in only one species, and that correlation was positive. Flowering had no relation to soil moisture in 2003, but in 2004, when soil moisture was extremely low in the formerly warmed plots, five of the seven earliest blooming species showed some correlation between flowering and soil moisture. Available soil N did correlate with flowering in three species in one year or the other, a much less pronounced pattern than for temperature and soil moisture. Therefore, the soil moisture deficit was likely the major cause of the delay in flowering phenology in formerly warmed plots in the spring of 2004, the post-treatment year.

While climate change analyses tend to focus on the advance of flowering by warming, several agricultural species are known to delay flowering in high heat, for

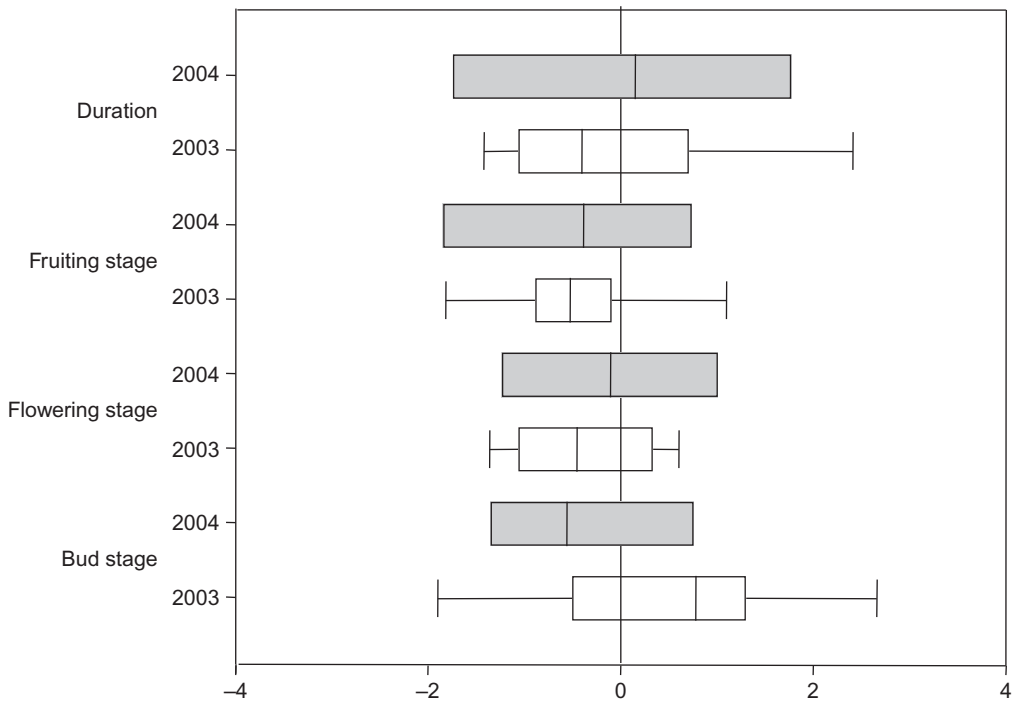

Figure 3. Effect size of warming on bud, flowering, fruiting stage length, and total duration. Open boxes are 2003; shaded boxes 2004. Ends of the boxes represent 75% confidence intervals and whiskers 95% confidence intervals. The number of species that responded to warming in 2004 did not allow calculation of 95% confidence intervals.

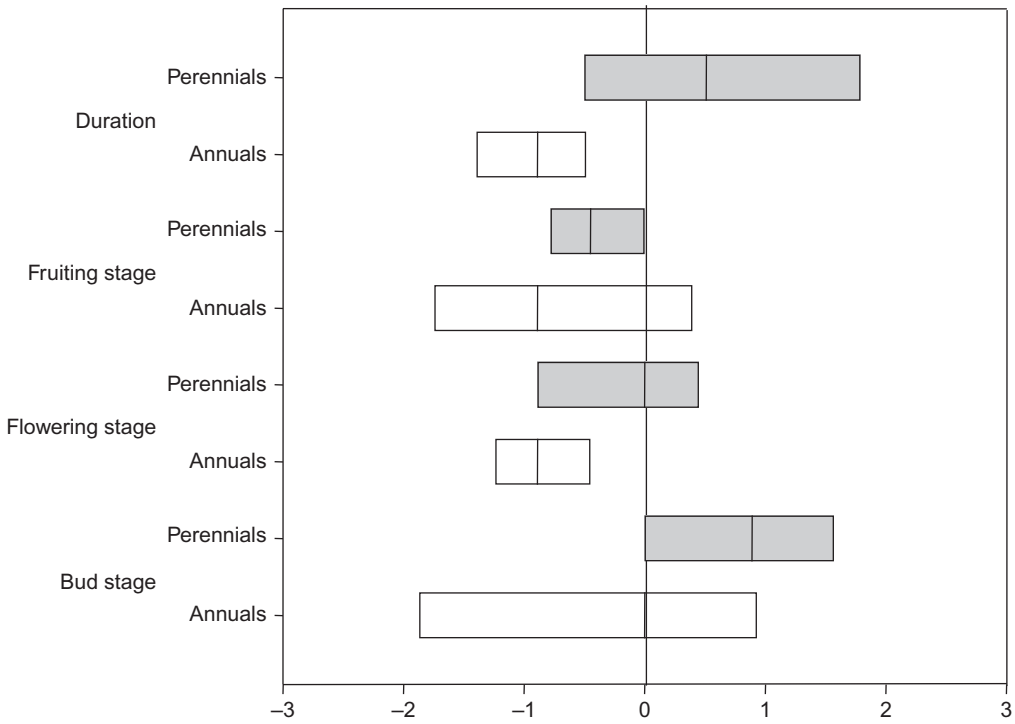

Figure 4. Effect size of warming on bud, flowering, fruiting stage length, and total duration on spring annuals and other species in 2003. Open boxes are annuals; shaded boxes perennials. Ends of the boxes represent 75% confidence intervals. The number of species was too small to allow calculation of 95% confidence intervals.

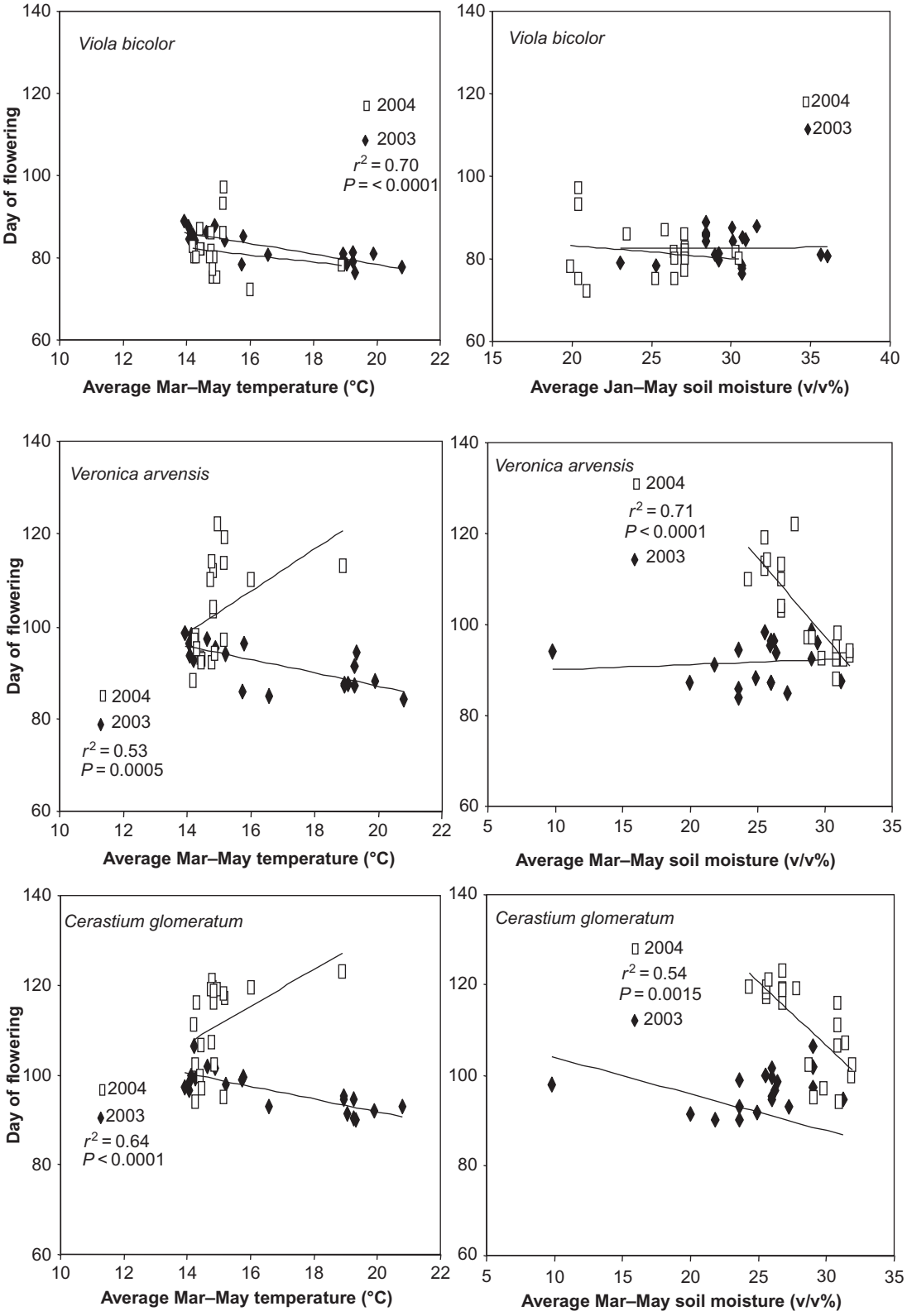

Figure 5. Relationship between flowering time (F2 or G2) and temperature (left column) and soil moisture (right column) for the first three species to flower in 2003 (♦) and 2004 (□).

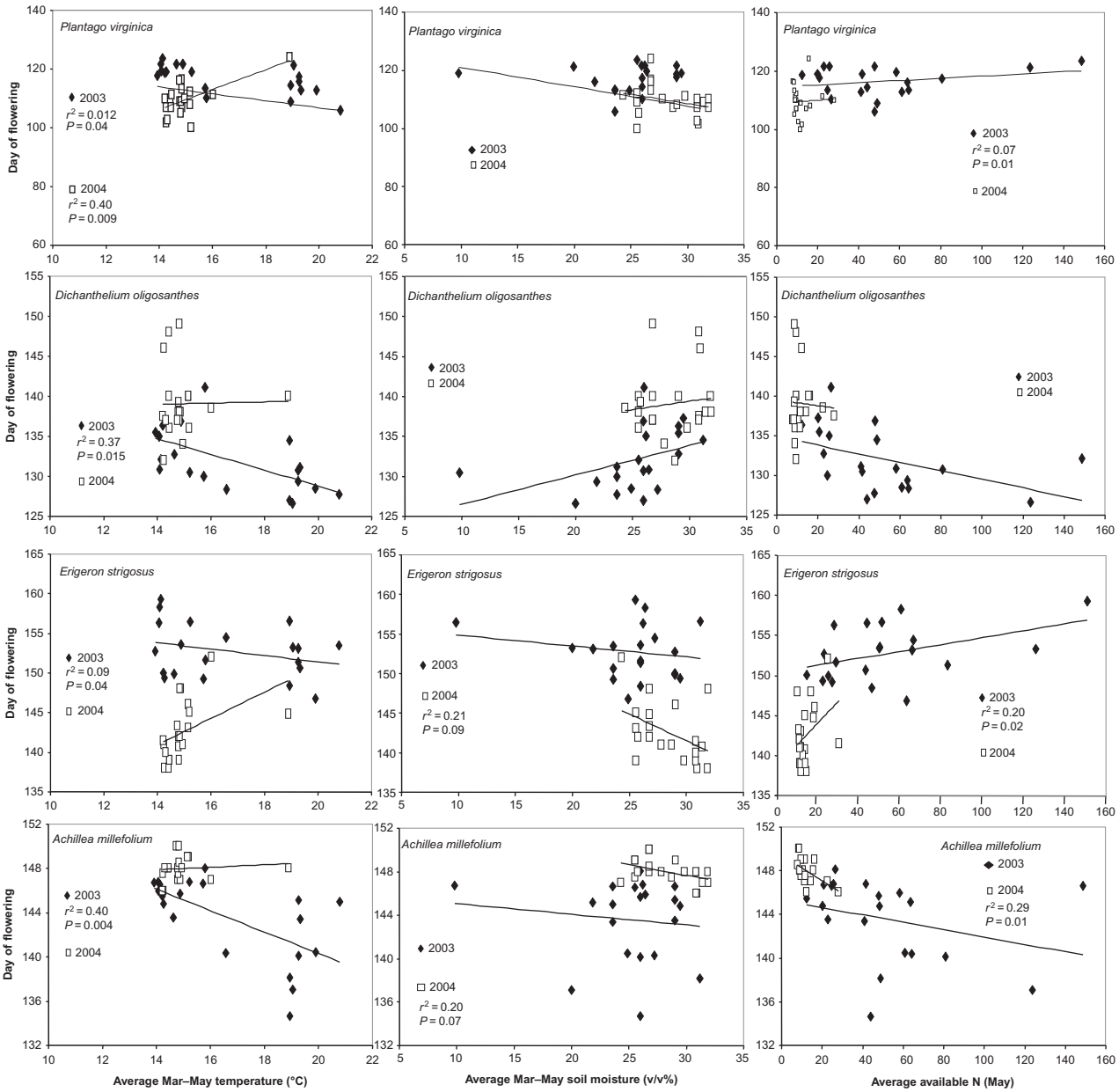

Figure 6. Relationship between flowering time (F2 or G2) and temperature (left column), soil moisture (centre column), and May available nitrogen (right column) for the second four species to flower in 2003 (⧫) and 2004 (□).

example, spinach, beets, soybeans and rice (Garner and Allard 1920; Steinberg and Garner 1936; Knott 1939; Baker et al. 1992). The same could be expected of many non-agricultural species, especially cool-season plants, as all species are expected to have an optimal temperature range for flower development beyond which flowering is delayed (Roberts and Struckmeyer 1938; Loomis and Connor 1992; Amthor and Loomis 1996; Heide 1996). There are a few evident reasons why the data on altered phenology due to changing soil moisture have been few and contradictory. First, the levels of soil moisture may need to fall outside of certain thresholds before an effect is seen. In other words, only relatively extreme levels of soil moisture may affect flowering phenology. The ambient background level of soil moisture at the time of the experiment can determine whether a precipitation treatment is 'relatively extreme' or not. Furthermore, these thresholds may differ from species to species. To use an obvious example, mesophytes, xerophytes and hydrophytes likely differ in their optimal ranges of soil moisture for growth (Raven et al. 2004). Finally, the direct effect of warming and its indirect drying effect can be confounded in some experiments (Niu et al. 2008).

The data presented here are phenological averages for populations, not individuals. However, the data still illustrate a few possible different developmental pathways for achieving altered phenology. Where phenology differed in the species observed here, most of those species entered

the bud phase at different times in control and warmed plots. These plants may have germinated or emerged earlier with warming and then proceeded through their life cycle at the normal rate. A few species entered the bud stage at the same time in both warmed and control plots. These plants may have germinated or emerged at approximately the same time in control and warmed plots, and warmed plants may have then grown and developed at a faster rate throughout the season, or their rate of development could have progressively sped up during the season. These pathways could have different consequences for mortality in a warming climate. Plants that germinate or emerge earlier may be at greater danger from late frosts (Inouye 2008), while plants emerging at the normal time would have less risk in comparison and still have some of the advantages of flowering, such as a longer season for fruit and seed growth (Galen and Stanton 1991).

Effect of treatments on the duration of reproductive stages

Different species showed their largest differences between treatments at different times within their reproductive cycle (Figures 1, 2, 4 and 5), indicating that the treatments did not affect the rate of development equally over the whole reproductive period. This may be a response to the immediate temperature and soil moisture status, which changes along with ambient conditions, or may be a result of different species-specific rates of development at various points in the reproductive cycle. Different species have different optimal temperatures for growth that change during the various stages of development (Parker and Borthwick 1939; Went 1957; Went and Overland 1969; Heide 1996). Generally, warmer temperatures are optimal for germination and early growth, while later growth has a lower optimal temperature, but flowering and fruiting stages can have their own temperature optima, and winter and spring annuals have lower optimal germination temperatures than other plants (Went 1957; Went and Overland 1969). Often, these optimal temperatures are not reached in spring in temperate regions, one cause of the positive effects of warming on plant development and phenology.

Warming shortened the flowering and fruiting stages and total duration for annuals in the spring of 2003 (Figure 3). That this effect was not seen later in 2003 may be due to the different life history of perennials, or to simply to different ambient background conditions later in the year. Warming can speed development directly by increasing the rate at which metabolic reactions occur, or may decrease water availability, slowing growth and expansion. The length of time a flower could be open may be limited by the amount of water lost through transpiration (Galen et al. 1999). Fruit expansion and drying may be hastened by low water conditions. The direction in which phases were altered by warming tended to be the same for all phases within a species.

In 2004, warming significantly affected duration in only two species, lengthening the flowering period of *Viola*, and shortening that of *Cerastium*. Other researchers have also examined the effects of warming on total duration of the flowering period. While Post and Forchhammer (2008) found significant shortening of total duration with warming in seven of eight species examined, Price and Waser (1998) and Dunne et al. (2003) found lengthening of total duration in one of 10 and two of eight species, respectively. Generalisations about the effect of warming on flowering duration cannot yet be made and may be species specific. Duration of flowering is likely to also depend on water and pollination status.

Effects of soil moisture on flowering phenology

Water stress in mesophytes often delays flowering, although a few species need decreasing water to flower and excess water can inhibit flowering (Bernier et al. 1981; Kinet et al. 1985). Exceptions are likely due to different physiological tolerances. Extremes of precipitation can be expected to have different effects on mesophytes, xerophytes and hydrophytes (Halevy 1985; Knapp et al. 2008). The delaying effects of warming on phenology seen here, in the autumn of 2003 and the spring of 2004, are likely indirect, actually due to lower soil moisture in warmed and formerly warmed plots at those times.

Several ecological studies have demonstrated that drought often shortens the duration of flowering in both annual and perennial mesophytes (Dickinson and Dodd 1976; Steyn et al. 1996; Peñuelas et al. 2004; Giménez-Benavides et al. 2007; Alizoti et al. 2010). Here, duration was shortened significantly by the double precipitation treatment in *Andropogon* and *Schizachyrium* in the treatment year, but there were no statistically significant effects of the previous year's extra precipitation in 2004. That so few significant effects of the doubled precipitation treatment were seen in our experiment may be due to our method of increasing precipitation, which only increased rain during natural rain events. In a dry year, such as 2003, this meant that the increased precipitation plots had only slightly more soil moisture than the control plots, while the warmed plots were severely dried by the 4 °C increase in temperature. The precipitation treatment was, however, significant enough to increase total biomass (Sherry et al. 2008).

Conclusions

During the treatment year, warming advanced reproductive phenology in nine spring-flowering species. The following year, after treatments had been discontinued, the opposite was seen. Flowering was delayed in six of the spring-flowering species due to low soil moisture that resulted from soil drying by the earlier increased temperatures, a lagged effect of warming. Warming shortened flowering and fruiting stages and total duration of the reproductive period in spring annuals. The direction of change in reproductive stage length caused by

warming and extra precipitation was often the same within a species.

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Notes on contributors

Rebecca A. Sherry is a Research Assistant Professor of plant ecology at The University of Oklahoma interested in plant community responses to climate change.

Xuhui Zhou is a Research Assistant Professor of ecosystem ecology at The University of Oklahoma particularly interested in changes in soil respiration and the C-cycle with climate change.

Shiliang Gu is a Professor from Yangzhou University interested in mathematical biology.

John A. Arnone III is a Research Professor at the Desert Research Institute in Reno, Nevada, interested in the C-cycle and interannual variability.

Dale W. Johnson is a Professor of Natural Resources and Environmental Sciences at the University of Nevada, Reno, interested in soil chemistry and biogeochemical cycling.

David S. Schimel is CEO at NEON Inc in Boulder, Colorado. He is interested in terrestrial interactions with the atmosphere and shared the 2007 Nobel Peace Prize with other contributors to the Intergovernmental Panel on Climate Change's reports.

Paul S.J. Verburg is an Associate Research Professor at the Desert Research Institute in Reno, Nevada. He is interested in the impact of environmental change on carbon and nutrient cycling in soils.

Linda L. Wallace (1951–2009) was a popular teacher and a Presidential Professor of ecology at The University of Oklahoma and was especially known for her research on the effects of bison grazing on grassland ecosystems in Yellowstone National Park.

Yiqi Luo is a Professor of ecosystem ecology at The University of Oklahoma who studies responses of terrestrial carbon and nitrogen cycles to global change using both experimental and modeling approaches.

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