LETTER

doi:10.1038/nature13207

Elevated CO_2 further lengthens growing season under warming conditions

Melissa Reyes-Fox[1]*, Heidi Steltzer[2]*, M. J. Trlica[3], Gregory S. McMaster[4], Allan A. Andales[5], Dan R. LeCain[6] & Jack A. Morgan[6]

Observations of a longer growing season through earlier plant growth in temperate to polar regions have been thought to be a response to climate warming[1–5]. However, data from experimental warming studies indicate that many species that initiate leaf growth and flowering earlier also reach seed maturation and senesce earlier, shortening their active and reproductive periods[6–10]. A conceptual model to explain this apparent contradiction[11], and an analysis of the effect of elevated CO_2—which can delay annual life cycle events[12–14]—on changing season length, have not been tested. Here we show that experimental warming in a temperate grassland led to a longer growing season through earlier leaf emergence by the first species to leaf, often a grass, and constant or delayed senescence by other species that were the last to senesce, supporting the conceptual model. Elevated CO_2 further extended growing, but not reproductive, season length in the warmed grassland by conserving water, which enabled most species to remain active longer. Our results suggest that a longer growing season, especially in years or biomes where water is a limiting factor, is not due to warming alone, but also to higher atmospheric CO_2 concentrations that extend the active period of plant annual life cycles.

Climate varied considerably between the years studied in this experiment, most notably through a cool spring in 2009, greater precipitation than usual in 2009 and 2011, and low autumn soil water content in 2010 (Fig. 1 and Extended Data Figs 1, 2). Nonetheless, in all but one year, climate warming conditions (*cT*, where *c* is a condition of relatively low CO_2 and *T* is relatively high temperature) changed the timing of species' annual life cycles, increasing the length of the growing season and the reproductive season relative to control conditions (*ct*, where *t* is relatively low temperature) (Fig. 2). Warming led to earlier timing of events by the first species to leaf or flower in most years, but species' sensitivity to warming varied among species and among years (Fig. 3 and Extended Data Table 1). Often, a cool-season grass, *Koeleria macrantha*, was the first species to leaf and the first species to flower in control (*ct*) and warmed (*cT*) plots. In most years, warming advanced leaf emergence and flowering of *K. macrantha* (Fig. 3; see Supplementary Information for timing of annual life cycle events for all species in all treatments in all years), yet, in 2009, a year characterized by a cool spring (Fig. 1), warming delayed leaf emergence of *K. macrantha* by 9 days. Warming delays leafing and flowering for some species[7,15], although the mechanism behind this is not clear.

Contrasting species' responses to warming between years limits interpretation of 5-year means; thus we present data yearly. Additionally, yearly data illustrate that the first and last species to complete annual life cycle events that determine the start and end of the growing or reproductive seasons shifted between treatments and between years (Fig. 3). These shifts indicate complementarity among species in response to interannual climate variation and warming, countering the tendency of warming to shorten the growing season. For example, in 2009, when warming (*cT*) delayed leaf emergence of *K. macrantha*, leaf emergence of *Artemisia frigida*, a sub-shrub, was not affected, leading to a shift in which species was the first to leaf and no change in timing for the start of the growing season relative to the control (*ct*) (Fig. 3).

Warming (*cT*) led to earlier leaf emergence and flowering, but also to earlier seed maturation and canopy senescence for some species, especially *K. macrantha*, relative to the control (*ct*) (Fig. 3). Seed maturation by *A. frigida*, consistently the last species to complete this event, was not affected by warming. Therefore, a longer reproductive season in response to warming primarily resulted from earlier flowering by *K. macrantha*. The mean active period for *K. macrantha* shortened (Fig. 4 and Extended Data Table 2), but longer growing seasons resulted, because *A. frigida* and *Hesperostipa comata* did not change or delayed the timing of canopy senesce (Fig. 3). Warming extended the duration of the mean reproductive period over the 5 years for three of the six species, including *K. macrantha* (Fig. 4 and Extended Data Table 2), primarily through lengthening the reproductive period in 2011, the year with the most precipitation (Fig. 1 and Supplementary Information). Delayed canopy senescence due to warming and a later end of the growing season also only occurred in 2011 (Figs 2 and 3).

Variation in plant life history traits within the grassland, such as early season growth versus late season tissue maintenance, led to differences in species' responses to warming, supporting a conceptual model of how individual species' responses determine growing season length[11]. However, in contrast to the model's prediction, divergence in species' active periods was small. Several species, including *H. comata*, lengthened their

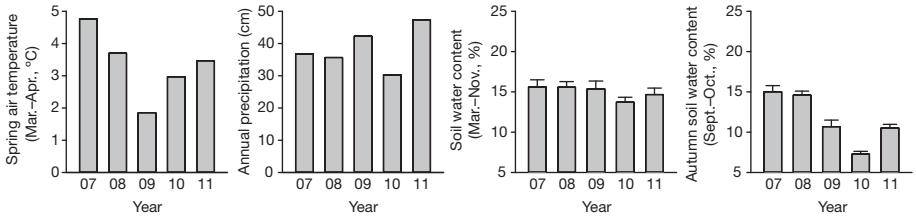


Figure 1 | Interannual variation in climate and microclimate (2007–2011). Values are mean spring air temperature for day of year (DOY) 60–120 and annual precipitation for the study site, and mean growing season (DOY 60–334) and autumn (DOY 244–304) soil water content for the control plots (means ± 1 standard error of the mean (s.e.m.), $n = 5$ plots). Spring air temperature and autumn soil water content correspond with timing of leaf emergence and canopy senescence, respectively.

[1]USDA-ARS, Soil Plant Nutrient Research Unit and Northern Plains Area, Fort Collins, Colorado 80526, USA. [2]Department of Biology, Fort Lewis College, Durango, Colorado 81301, USA. [3]Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado 80523, USA. [4]USDA-ARS, Agricultural Systems Research Unit and Northern Plains Area, Fort Collins, Colorado 80526, USA. [5]Department of Soil and Crop Sciences, Colorado State University, Fort Collins, Colorado 80523, USA. [6]USDA-ARS, Rangeland Resources Research Unit, Fort Collins, Colorado 80526, USA.
*These authors contributed equally to this work.

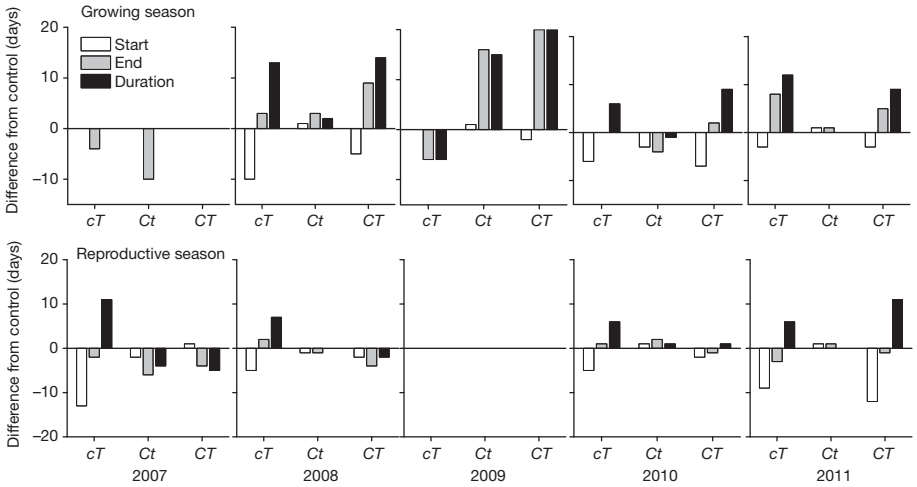


Figure 2 | Effect of warming and elevated CO_2 on growing and reproductive season length (2007–2011). Values are the mean number of days difference between treatment and control conditions for start, end and duration; see Fig. 3 for corresponding s.e.m. and significant effects ($n = 5$ plots). Negative values indicate earlier onset of events or shortening of growing or reproductive season length. See Methods for explanation of missing data.

active period in response to warming (Fig. 4), maintaining continuity of seasonal growth by the plant community. Similarly, for several species reproductive periods lengthened under warming (Fig. 4), limiting divergence within the reproductive season. Thus, our results contrast with other studies in which experimental warming led to divergent flowering responses between species[9] and mid-season, low floral abundance as the climate warmed[16]. Longer active and reproductive periods by at least some species would reduce the adverse effects of warming on trophic interactions and ecosystem function[17,18].

In conditions of elevated CO_2 (*CT*, where *C* is relatively high CO_2), growing season duration was further lengthened relative to warming alone (*cT*) through the delay of canopy senescence (Figs 2, 3 and Extended Data Table 1). In 2009, when spring was cool and annual precipitation was high, elevated CO_2 extended the growing season by delaying senescence of *A. frigida* by 29 days in the warmed ecosystem. Although the magnitude of the response was less, the growing season was also significantly increased in 2008, when under conditions of elevated CO_2 senescence occurred 6 days later in the warmed ecosystem. On average during our

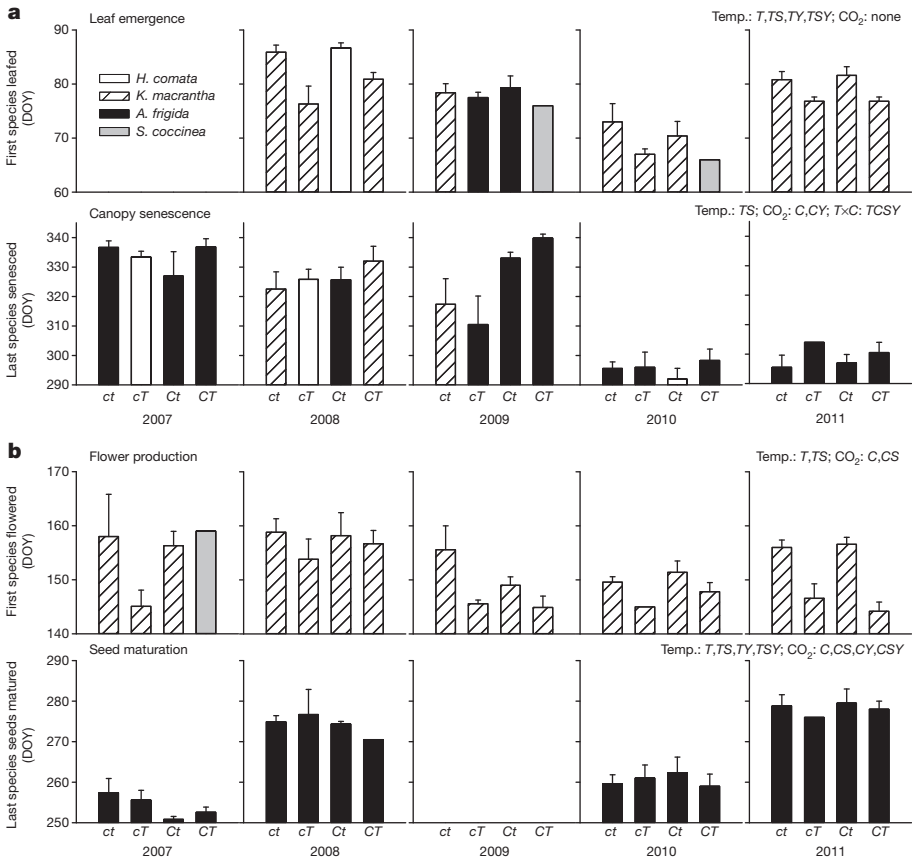


Figure 3 | Effect of warming and elevated CO_2 on timing of annual life cycle events (2007–2011). **a**, **b**, Values are day of year (DOY) for start and end of growing (**a**) and reproductive seasons (**b**) (means ± 1 s.e.m., $n = 5$ plots). Significant effects ($P < 0.05$, two-sided) from a four-way ANOVA testing temperature (Temp.; *T*), elevated CO_2 (*C*), species (*S*), year (*Y*) and all interactions are reported at the top of each row of panels. Species, year and their interactions were highly significant for all events ($P < 0.001$) and are not listed. See Extended Data Table 1 for complete ANOVA results.

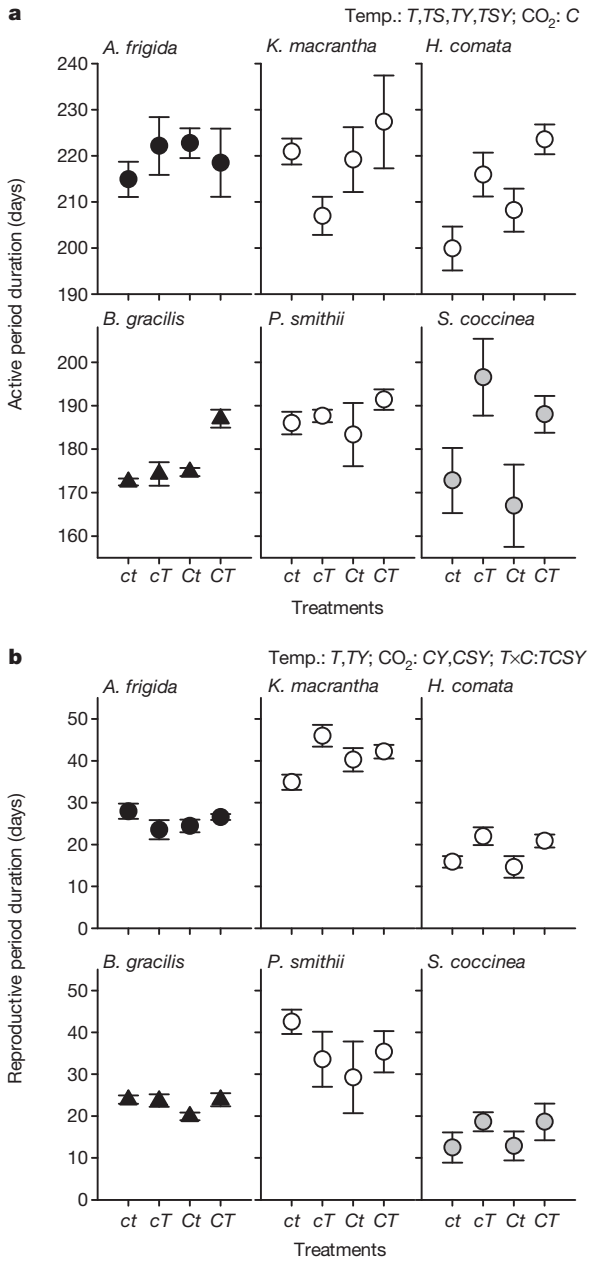


Figure 4 | Effect of warming and elevated CO_2 on the duration of species' active and reproductive periods. **a**, **b**, Values are means across years (2007–2011) for species' active period duration (**a**) and reproductive period duration (**b**) (means ± 1 s.e.m., $n = 5$ plots). Sub-shrub is indicated by filled black circles, cool-season grasses by open circles, warm-season grass by filled triangles, forb by filled grey circles. Significant effects ($P < 0.05$, two-sided) are reported as in Fig. 3 at the top of each group of panels. See Extended Data Table 2 for complete ANOVA results.

5-year study, the growing season ended 7.6 days later due to warming and elevated CO_2 (*CT*) relative to warming alone (*cT*), and was 14.2 days longer. Owing to warming alone (*cT* versus *ct*), the growing season began 4.7 days earlier and was 6.2 days longer on average. The effect of warming alone probably cannot account for the observed change in growing season length of ~2 to 5 days per decade during the mid- to late twentieth century[1–5].

Our results demonstrate that the effects of warming and elevated CO_2 (*CT*) on annual life cycle events that determine growing and reproductive season lengths depend on climate, varying in the magnitude and even direction of response between years (Figs 2, 3 and Extended Data Table 1). For example, in 2010, a year with low late summer and autumn precipitation and low autumn soil water content (Fig. 1), elevated CO_2 (*Ct* and *CT*) did not affect canopy senescence (Fig. 3). Although elevated CO_2 (*Ct* and *CT*) led to greater autumn soil water content in all years (Fig. 5 and Extended Data Table 3), in 2010 the water savings may not have been sufficient to increase water availability above a threshold (~10%) that corresponds to the permanent wilting point (11%) (ref. 19). In the warmed ecosystem, elevated CO_2 (*CT*) led to the greatest increase in autumn soil water content in 2008 and 2009 (Fig. 5), the years in which the greatest delays in canopy senescence due to elevated CO_2 (*CT*) occurred (Fig. 3).

Increasing the CO_2 concentration in the warmed ecosystem (*CT* versus *cT*) lengthened the active period of all grass species (Fig. 4 and Extended Data Table 2). Even the early growing grass *K. macrantha*, which senesced early due to warming alone (*cT*), showed delayed senescence under elevated CO_2 and warming conditions (*CT*). Warming and elevated CO_2 (*CT*) led to a shorter reproductive season in 3 of 4 years relative to warming alone (*cT*) by decreasing the advance in flowering date and earlier seed maturation by *A. frigida* in 2007 and 2008 (Figs 2 and 3). Elevated CO_2 tended to decrease or have no effect on species' reproductive period (Fig. 4 and Extended Data Table 2). Thus, in the warmed ecosystem, elevated CO_2 (*CT* versus *cT*) caused species to remain active longer after seed maturation, which would not benefit fitness in the year in question but may affect it in consequent years.

Altered flowering times and species' reproductive periods may have long-term consequences for plants and other trophic levels. Other studies have also found that elevated CO_2 has a greater effect on flowering times under warming conditions, as well as a greater effect on late-flowering species[14,20]. Our data indicate that higher atmospheric CO_2 concentrations may be contributing to observed changes over time in flowering patterns, such as a shorter reproductive season and greater asynchrony with pollinators, which have previously been attributed to warming[16,17].

Furthermore, the dominant hypothesis among global change ecologists is that Earth's longer growing seasons are due to climate warming alone. Our results suggest that this hypothesis needs modification to incorporate the effects of elevated CO_2. We provide evidence in multiple years and of a mean effect over the 5-year study that elevated CO_2 further increases growing season length in a warmed, temperate plant community. In many ecosystems, sufficient water availability is needed to sustain plant tissues from summer into autumn. Dry conditions during warm years have led to early senescence and even the death of long-lived plants[21,22]. Elevated CO_2 counteracts the negative effect of warming on water availability[19,23] (Fig. 5), often delaying the timing of plant life cycle events[12,13] (Fig. 3). The effects of

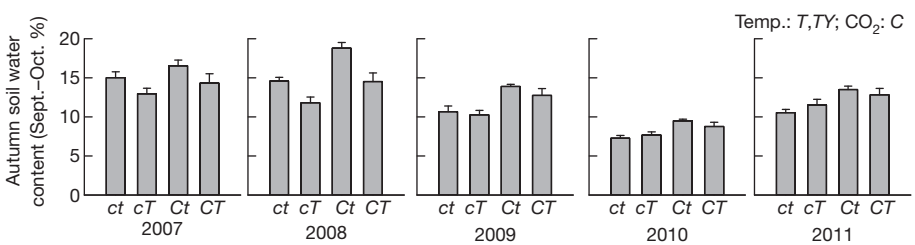


Figure 5 | Effect of warming and elevated CO_2 on autumn soil water content (5–25 cm, September–October, 2007–2011). Values are means for soil water content corresponding with the timing of canopy senescence (means ± 1 s.e.m., $n = 5$ plots). Significant effects ($P < 0.05$, two-sided) are reported as in Fig. 3. See Extended Data Table 3 for complete ANOVA results.

warming and elevated CO_2 vary across species, events and years. At the community level, the different responses lead to a longer growing season in most years, because only one species within the plant community needs to leaf earlier for spring to begin earlier and a different species can senesce later to extend autumn[11]. We demonstrate that warming fairly consistently leads to earlier growth in spring and elevated CO_2 to later senescence in autumn, with both mechanisms leading to a longer growing season.

The stature of grasslands and their ability to encompass thousands of individual plants, many species, and different growth forms within a relatively small area make them ideal ecosystems in which to conduct global change experiments[9,12,23]. For example, in our experiment, the varied responses of the three cool-season grasses, *K. macrantha*, *H. comata* and *Pascopyrum smithii*, a species that did not affect growing or reproductive season length in any year, suggest that different species, even within a growth form, respond in unique ways to warming and elevated CO_2 (Figs 3 and 4). As a result, plant community response did not depend on a specific species or growth form, and we expect that responses would be similar in other temperate to polar plant communities, especially in years or biomes where water is a limiting factor.

Although considerably less than the ~200 p.p.m. of CO_2 enrichment that occurred in our experiment, the ~60 p.p.m. increase in global atmospheric CO_2 concentrations since the 1970s is probably sufficient to elicit significant stomatal closure[24,25], resulting in some water savings and an effect on phenology, as in our experiment. Certainly the ~115 p.p.m. increase in global atmospheric CO_2 concentrations since industrialization has been more than enough to elicit considerable CO_2-induced water savings[23] and affect growing season length, although data on growing season length are available primarily from the mid-twentieth century[1–5]. Ongoing increases in ambient CO_2 are expected to continue to shift the timing of species' reproductive periods and senescence, and thus the duration of the growing and reproductive seasons.

METHODS SUMMARY

The experiment, initiated in 2006, is located in temperate grassland in Wyoming, United States (41° 11′ N, 104° 54′ W). It includes two levels of temperature (ambient and warmed, 1.5 or 3.0 °C warmer during the day and night, respectively) and two levels of atmospheric CO_2 concentrations (ambient and elevated, 385 p.p.m.v. and 600 p.p.m.v. CO_2, respectively) in a factorial combination with five replicate plots per treatment. T-FACE technology was used for increasing the temperature[26]. Free air CO_2 enrichment (FACE) technology was used for elevating CO_2 (ref. 27). Further description of the experiment can be found elsewhere[19].

The timing of the four annual life cycle events that determine the start and end of species' active and reproductive periods (leaf emergence, flower production, seed maturation and canopy senescence) was observed weekly for six common species. The most abundant species in each growth form were chosen. From 2007 to 2009, individual plants were marked upon emergence and monitored for the duration of the growing season. The timing of each event was characterized by the mean value for the marked individuals of each species. In 2010 and 2011, the timing of each event was characterized by the median value, the point at which an event was completed by half the typical number of marked individuals for each species within a plot. Further description is included in the Methods.

We analysed the data across the years through an analysis of variance (ANOVA) for each life cycle event, duration of active and reproductive periods, and autumn soil water content, using Proc Mixed to test the main effects of temperature, elevated CO_2, species (if applicable) and year, and all their interactions (SAS version 9.2). Soil type was included as a random effect and was not significant. Mixed model ANOVA allows for unequal variances and data were near a normal distribution. Analyses were done on untransformed data.

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 4 November 2013; accepted 5 March 2014.
Published online 23 April 2014.

1. Kim, Y., Kimball, J. S., Zhang, K. & McDonald, K. C. Satellite detection of increasing Northern Hemisphere non-frozen seasons from 1979 to 2008: implications for regional vegetation growth. *Remote Sens. Environ.* **121,** 472–487 (2012).
2. Menzel, A. *et al.* European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12,** 1969–1976 (2006).
3. Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. Increased plant growth in the northern latitudes from 1981 to 1991. *Nature* **386,** 698–702 (1997).
4. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42 (2003).
5. Schwartz, M. D., Ahas, R. & Aasa, A. Onset of spring starting earlier across the Northern Hemisphere. *Glob. Change Biol.* **12,** 343–351 (2006).
6. Hoffmann, A. A. *et al.* Phenological changes in six Australian subalpine plants in response to experimental warming and year-to-year variation. *J. Ecol.* **98,** 927–937 (2010).
7. Hollister, R. D., Webber, P. J. & Bay, C. Plant response to temperature in northern Alaska: implications for predicting vegetation change. *Ecology* **86,** 1562–1570 (2005).
8. Post, E. S., Pedersen, C., Wilmers, C. C. & Forchammer, M. C. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* **89,** 363–370 (2008).
9. Sherry, R. A. *et al.* Divergence of reproductive phenology under climate warming. *Proc. Natl Acad. Sci. USA* **104,** 198–202 (2007).
10. Zavaleta, E. S. *et al.* Plants reverse warming effect on ecosystem water balance. *Proc. Natl Acad. Sci. USA* **100,** 9892–9893 (2003).
11. Steltzer, H. & Post, E. Seasons and life cycles. *Science* **324,** 886–887 (2009).
12. Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A. & Field, C. B. Diverse responses of phenology to global changes in a grassland ecosystem. *Proc. Natl Acad. Sci. USA* **103,** 13740–13744 (2006).
13. Körner, C. Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytol.* **172,** 393–411 (2006).
14. Springer, C. J. & Ward, J. K. Flowering time and elevated atmospheric CO_2. *New Phytol.* **176,** 243–255 (2007).
15. Fitter, A. H. & Fitter, R. S. R. Rapid changes in flowering time in British plants. *Science* **296,** 1689–1691 (2002).
16. Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A. & Miller-Rushing, A. J. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *J. Ecol.* **99,** 905–913 (2011).
17. Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K. & Forchhammer, M. C. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change* **3,** 759–763 (2013).
18. Richardson, A. D. *et al.* Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agric. For. Meteorol.* **169,** 156–173 (2013).
19. Morgan, J. A. *et al.* C_4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* **476,** 202–205 (2011).
20. Hovenden, M. J., Wills, K. E., Vander Schoor, J. K., Williams, A. L. & Newton, P. C. D. Flowering phenology in a species-rich temperate grassland is sensitive to warming but not elevated CO_2. *New Phytol.* **178,** 815–822 (2008).
21. Breshears, D. D. *et al.* Regional vegetation die-off in response to global-change-type drought. *Proc. Natl Acad. Sci. USA* **102,** 15144–15148 (2005).
22. van Mantgem, P. J. *et al.* Widespread increase of tree mortality rates in the western United States. *Science* **323,** 521–524 (2009).
23. Fay, P. A. *et al.* Soil-mediated effects of subambient to increased carbon dioxide on grassland productivity. *Nature Climate Change* **2,** 742–746 (2012).
24. Ainsworth, E. A. & Rogers, A. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant Cell Environ.* **30,** 258–270 (2007).
25. Ball, J. T., Woodrow, I. E. & Berry, J. A. in *Progress in Photosynthesis Research* (ed. Biggens, J.) 221–224 (Martinus-Nijhoff, 1987).
26. Kimball, B. A. *et al.* Infrared heater arrays for warming ecosystem field plots. *Glob. Change Biol.* **14,** 309–320 (2008).
27. Miglietta, F. *et al.* Free-air CO_2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. *New Phytol.* **150,** 465–476 (2001).

Supplementary Information is available in the online version of the paper.

Acknowledgements The following individuals contributed to the installation and maintenance of the Prairie Heating and CO_2 Enrichment (PHACE) project: D. Smith, D. Blumenthal, E. Pendall, E. Hardy, L. Griffith, A. Hansen, K. Corp, V. Banuelos, G. Tinnin, M. West, C. Brooks, M. Busick, D. Milchunas, G. Dunn and L. Ahuja. Funding for this work was supported by the US Department of Agriculture Agricultural Research Center (USDA-ARS) Climate Change, Soils & Emissions Program, by the US Department of Energy's Office of Science through the Terrestrial Ecosystem Science Program, by the National Science Foundation (DEB no. 1021559) and by Colorado State University. D. Inouye provided comments that improved the manuscript.

Author Contributions M.R.-F., M.J.T., A.A.A., G.S.M. and J.A.M. designed the research. M.R.-F. and D.R.L. conducted the observations. J.A.M. oversaw the PHACE experiment. H.S. and M.R-F. analysed the data and wrote the manuscript. All authors contributed to revision of the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to H.S. (steltzer_h@fortlewis.edu) or M.R.-F. (Melissa.reyes@ars.usda.gov).

METHODS

Site description. The Prairie Heating and Carbon Dioxide Enrichment (PHACE) experiment, initiated in 2006, is located west of Cheyenne, Wyoming, United States at the USDA-ARS High Plains Grasslands Research Station in the US Great Plains (41° 11′ N, 104° 54′ W, elevation 1,930 m). This is a Northern mixed-grass prairie ecosystem, with a plant community composed of 55% cool-season grasses, 25% warm-season grasses, and 20% sedges, forbs and small shrubs. Total annual precipitation averages 38.5 cm and mean daily air temperatures range from −2.5 °C in January to 17.5 °C in July. The average wind speed is 6 m s^{-1} with gusts up to 35 m s^{-1}. The site comprises two distinct soil types: an Ascalon variant loam (fine loamy, mixed mesic) at the north end of the field and an Altvan loam (fine loamy over sandy, mixed mesic) on the south end. The site has a history of moderate grazing from 1928 until the PHACE project began in 2006.

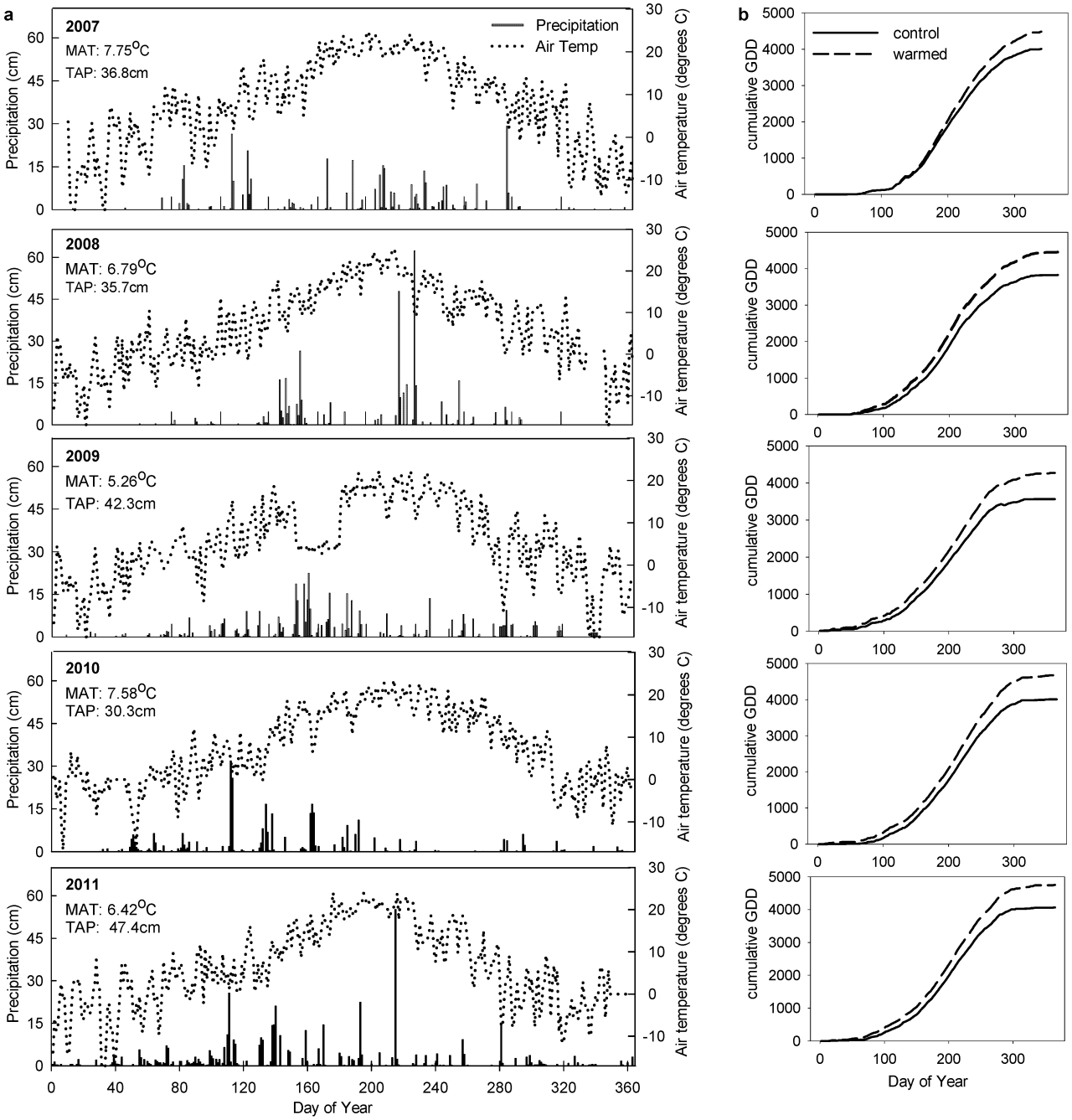
Experimental design. The experiment includes two levels of temperature (ambient and warmed, 1.5 and 3.0 °C warmer during the day and night, treatments *t* and *T*, respectively) and two levels of atmospheric CO_2 concentrations (ambient 385 p.p.m.v. and elevated 600 p.p.m.v. CO_2, treatments *c* and *C*, respectively) in a factorial combination with five replicate plots per treatment (*ct*, *cT*, *Ct* and *CT*) for a total of 20 plots. Warming and elevated CO_2 treatments were randomly assigned to the 3.3 m diameter circular plots. T-FACE technology for increasing temperature was implemented on 10 April 2007, after leaf emergence by cool-season grasses and shrubs, and warmed plots year round for the duration of the experiment[26]. As warming began after the first species leafed in 2007, leaf emergence data were omitted for all species in 2007 and growing season length was not calculated. Dummy heaters were installed in non-heated plots to eliminate response differences that may result from shading or other influences caused by the heating apparatuses. Free air CO_2 enrichment (FACE) technology was used for elevating CO_2 and began in 2006 (ref. 27). The CO_2 fumigation system ran continuously during the growing season. The warming treatment effectively accelerated the accumulation of growing degree days in all years (Extended Data Fig. 1). When placed in the historical context of the last century, below average precipitation fell in 2007, 2008 and 2010 with above average precipitation falling in 2009 and 2011. Further description of the experiment, including the instrumentation used for monitoring climate and microclimate, is available elsewhere[19].

Phenology observations. The timing of four life cycle events that determine the start and end of species' active and reproductive periods (leaf emergence, flower production, seed maturation and canopy senescence) was observed weekly for six common species. The most abundant species in each growth form were chosen, including the one sub-shrub (*A. frigida*, *L.*), a warm-season grass (*Bouteloua gracilis*, *Lag. ex Griffiths*), three cool-season grasses (*H. comata (Elias) Barkworth*; *K. macrantha (Ledeb.) Schult*; and *P. smithii (Rydb.) Á. Löve*), and a widespread forb (*Sphaeralcea coccinea (Nutt.) Rydb.*). Leaf emergence was characterized by the first new, green leaf to appear on a shoot. The first open flower (forb and sub-shrub) or inflorescence to emerge from the leaf sheath (grasses) determined the timing of flower production. Flower desiccation (forb and sub-shrub) and seed head colour and release (grasses) identified the timing of seed maturation. And the timing of canopy senescence was characterized by the first sign of full canopy leaf death or loss.

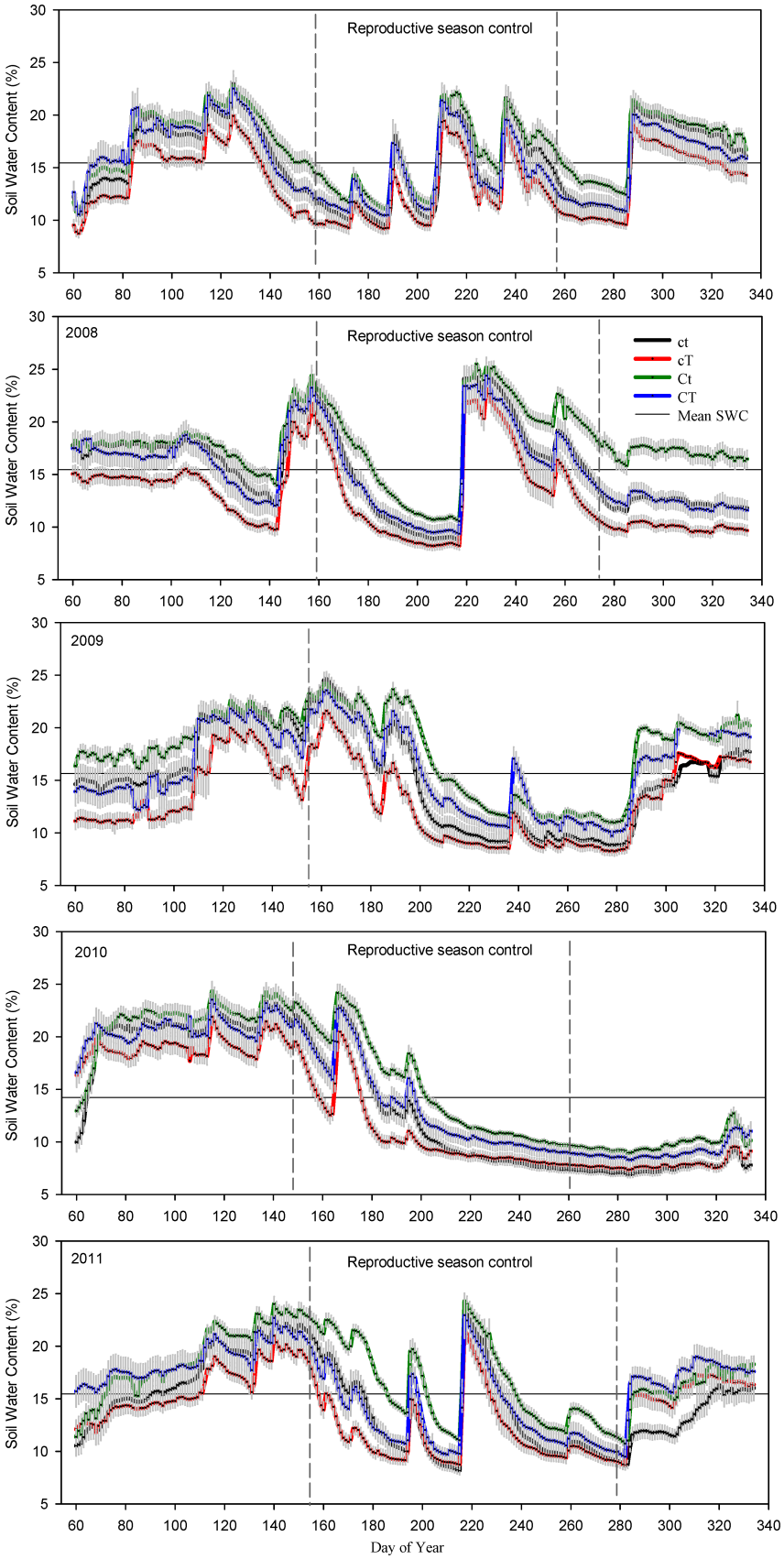
From 2007 to 2009, individual plants of each species were marked upon emergence (typically 12) and monitored for the duration of the growing season. The timing of an event was characterized by the mean value (day of year (DOY)) for the marked individuals of each species. Some species did not flower in all years. In 2009, incomplete data were collected on reproductive life cycle events, so reproductive season length was not determined. In 2010 and 2011, the timing of an event was characterized as the point at which a minimum number of individuals (typically 6) for each species within a plot had completed an event, representing the median value. Both approaches characterize central tendency for event timing across multiple individuals per plot. We used these data to determine changes in growing and reproductive season length, presenting data annually, and across years for the duration of species' active and reproductive periods. The start and end of the growing season were characterized by the mean across replicate plots for leaf emergence by the first species to leaf and for canopy senescence by the last species, respectively. Similarly, the start and end of the reproductive season were characterized by the date on which the first species flowered and seed maturation by the last species, respectively.

Climate and microclimate. Mean daily and mean annual temperature (MAT) and mean daily and total annual precipitation (TAP) were calculated on the basis of half hourly data from a meteorological station (HOBO, Onset, Inc.) at the field site (Extended Data Fig. 1). Growing degree day calculations were completed using data from infrared radiometers located within the experimental plots and a base temperature of 0 °C. In each plot, the volumetric soil water content (SWC) was measured hourly at 10, 20, 40, 60 and 80 cm depth (EnviroSMART probe; Sentek Sensor Technologies). Daily means were calculated for SWC at the primary rooting depth (5–25 cm) by averaging the values for the sensors at 10 and 20 cm depth (Extended Data Fig. 2). We present data on mean spring air temperature across DOY 60–120, annual precipitation for the study site, and mean growing season (DOY 60–334) and autumn (DOY 244–304) SWC for the control plots (Fig. 1). Mean autumn SWC is also presented for experimental plots (Fig. 5).

Data analysis. We analysed the data across years through ANOVA for each life cycle event, duration of active and reproductive periods, and autumn SWC, using Proc Mixed to test the main effects of temperature, elevated CO_2, species (if applicable) and year, and all their interactions (SAS version 9.2). For all ANOVAs, soil block based on the two soil types at the site was included as a random effect in the analyses and was not significant. Mixed model ANOVA allows for unequal variances and data were near a normal distribution. Analyses were done on untransformed data. Significant main effects and interactions ($P < 0.05$) are reported on figures with complete ANOVA results reported in Extended Data Tables 1–3.



Extended Data Figure 1 | Climate and warming effect for 2007–2011. **a**, **b**, Seasonal variation in precipitation and air temperature for the study site (**a**) and cumulative growing degree days (GDD) in control and warmed plots, averaged across CO_2 levels (**b**) (means, $n = 10$ plots). Mean annual temperature (MAT) and total annual precipitation (TAP) are listed each year.



Extended Data Figure 2 | Seasonal variation in soil water content for 2007–2011. Values are means ± 1 s.e.m. for soil depth 5–25 cm ($n = 5$ plots). Mean annual soil water content (SWC) for control is represented by the horizontal grey line; vertical dashed lines show reproductive season timing for control.

Extended Data Table 1 | ANOVA results for the timing of annual life cycle events 2007–2011

Years 2007-2011	Leaf emergence		Flower production		Seed maturation		Canopy senescence	
Main effects	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Temp	**143.7***	**<0.001**	**42.0**	**<0.001**	**12.5**	**<0.001**	0.4	0.503
CO_2	0.3	0.594	**7.5**	**0.007**	**17.7**	**<0.001**	**9.5**	**0.002**
Species	**136.1**	**<0.001**	**1639.5**	**<0.001**	**1557.8**	**<0.001**	**74.0**	**<0.001**
Year	**50.3**	**<0.001**	**42.2**	**<0.001**	**9.7**	**<0.001**	**118.8**	**<0.001**
Temp x CO_2	1.0	0.325	0.1	0.793	0.0	0.998	2.5	0.117
Temp x species	**5.1**	**<0.001**	**5.1**	**<0.001**	**3.4**	**0.006**	**3.6**	**0.003**
CO_2 x species	1.0	0.419	**3.4**	**0.005**	**4.0**	**0.002**	1.9	0.094
Temp x year	**28.0**	**<0.001**	0.8	0.529	**6.0**	**<0.001**	1.4	0.224
CO_2 x year	0.1	0.956	0.7	0.605	**6.1**	**<0.001**	**5.8**	**<0.001**
Species x year	**10.3**	**<0.001**	**27.1**	**<0.001**	**94.9**	**<0.001**	**12.1**	**<0.001**
Temp x CO_2 x species	0.4	0.859	2.2	0.060	0.3	0.928	1.5	0.191
Temp x CO_2 x year	0.2	0.905	1.1	0.342	0.8	0.556	0.6	0.685
Temp x species x year	**1.8**	**0.043**	1.5	0.106	**2.3**	**0.002**	1.3	0.154
CO_2 x species x year	0.7	0.824	1.6	0.054	**5.2**	**<0.001**	1.5	0.072
Temp x CO_2 x species x year	1.1	0.377	1.7	0.053	1.1	0.381	**1.6**	**0.048**

* Significant effects and interactions are in bold.

Extended Data Table 2 | ANOVA results for the duration of species' active and reproductive periods

Years 2007-2011	Active period duration		Reproductive period duration	
Main effects	***F***	***P***	***F***	***P***
Temp	**20.1***	**<0.001**	**10.0**	**0.002**
CO_2	**4.2**	**0.04**	0.3	0.59
Species	**103.9**	**<0.001**	**84.6**	**<0.001**
Year	**34.0**	**<0.001**	**42.1**	**<0.001**
Temp x CO_2	0.1	0.72	0.0	0.98
Temp x species	**6.1**	**<0.001**	1.3	0.28
CO_2 x species	0.9	0.48	0.3	0.91
Temp x year	**7.7**	**<0.001**	**3.3**	**0.01**
CO_2 x year	2.3	0.08	**2.6**	**0.04**
Species x year	**10.3**	**<0.001**	**36.2**	**<0.001**
Temp x CO_2 x species	1.3	0.28	1.5	0.18
Temp x CO_2 x year	2.0	0.12	1.6	0.17
Temp x species x year	**2.7**	**0.001**	1.5	0.09
CO_2 x species x year	1.4	0.14	**2.4**	**0.002**
Temp x CO_2 x species x year	1.4	0.14	**2.4**	**0.005**

* Significant effects and interactions are in bold.

Extended Data Table 3 | ANOVA results for autumn soil water content

Years 2007-2011	Autumn soil water content	
Main effects	***F***	***P***
Temp	**17.6***	**<0.001**
CO_2	**57.5**	**<0.001**
Year	**62.2**	**<0.001**
Temp x CO_2	2.9	0.09
Temp x year	**5.0**	**0.001**
CO_2 x year	1.5	0.21
Temp x CO_2 x year	0.2	0.94

* Significant effects and interactions are in bold.