

# Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology

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**Abstract.** The semiarid, northern Mongolian steppe, which still supports pastoral nomads who have used the steppe for millennia, has experienced an average 1.7°C temperature rise over the past 40 years. Continuing climate change is likely to affect flowering phenology and flower numbers with potentially important consequences for plant community composition, ecosystem services, and herder livelihoods. Over the growing seasons of 2009 and 2010, we examined flowering responses to climate manipulation using open-top passive warming chambers (OTCs) at two locations on a south-facing slope: one on the moister, cooler lower slope and the other on the drier, warmer upper slope, where a watering treatment was added in a factorial design with warming. Canonical analysis of principal coordinates (CAP) revealed that OTCs reduced flower production and delayed peak flowering in graminoids as a whole but only affected forbs on the upper slope, where peak flowering was also delayed. OTCs affected flowering phenology in seven of eight species, which were examined individually, either by altering the time of peak flowering and/or the onset and/or cessation of flowering, as revealed by survival analysis. In 2010, which was the drier year, OTCs reduced flower production in two grasses but increased production in an annual forb found only on the upper slope. The particular effects of OTCs on phenology, and whether they caused an extension or contraction of the flowering season, differed among species, and often depended on year, or slope, or watering treatment; however, a relatively strong pattern emerged for 2010 when four species showed a contraction of the flowering season in OTCs. Watering increased flower production in two species in 2010, but slope location more often affected flowering phenology than did watering. Our results show the importance of taking landscape-scale variation into account in climate change studies and also contrasted with those of several studies set in cold, but wetter systems, where warming often causes greater or accelerated flower production. In cold, water-limited systems like the Mongolian steppe, warming may reduce flower numbers or the length of the flowering season by adding to water stress more than it relieves cold stress.

**Key words:** climate manipulation; flowering phenology; Mongolia; nomadic pastoralism; plant community; reproduction; semiarid steppe grassland; warming.

## INTRODUCTION

Shifts in phenology, the seasonal timing of biological events, have occurred worldwide, providing compelling evidence for response to recent climate change (Walther et al. 2002, Cleland et al. 2007). Changes in flowering phenology could be far-reaching, as they may cause temporal mismatch with pollinator activity (Mommott et al. 2007, Hegland et al. 2009) and modify gene flow among populations (Hall and Willis 2006, Forrest and Miller-Rushing 2010). Warming can also alter flower quantity (Arft et al. 1999, Hollister and Webber 2000, Aerts et al. 2004), thereby affecting the resources supplied to pollinators and, potentially, seed produc-

tion. Therefore, flowering responses to climate change have the potential to profoundly affect plant community composition and ecosystem services.

Data on how global climate change affects flowering come from both observational studies that track the timing of flowering over decades or longer (e.g., Fitter et al. 1995, Miller-Rushing et al. 2008, Hulme 2011) and climate manipulation experiments (e.g., Arft et al. 1999). Both often show flowering starting earlier and/or ending later with increased temperatures (Hülber et al. 2010, Ibáñez et al. 2010, McEwan et al. 2011). The extent of phenological changes, however, varies with geographic location (Peñuelas et al. 2004, Primack et al. 2009, Ibáñez et al. 2010) and among species (Arft et al. 1999, Hollister and Webber 2000, Dunne et al. 2003, Kudo and Suzuki 2003, Primack et al. 2009). The quantity of flowers produced also appears to either increase or remain constant with warming (e.g., Hollister and Webber 2000, Aerts et al. 2004).

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While studies of flowering phenology in relation to increased temperatures have been conducted in cold climate ecosystems (e.g., Arft et al. 1999, Hollister and Webber 2000, Aerts et al. 2004), none, to our knowledge, have taken place in systems that are also water-limited. Warming may alleviate cold stress, but it may also exacerbate the stress of low water as seen in a Mediterranean habitat (Peñuelas et al. 2004). Thus, the effect of warming on flower number and phenology is difficult to predict for systems with co-limiting factors.

We conducted a two-year climate warming and water manipulation experiment in the mountain-steppe in northern Mongolia, a cold and water-limited ecosystem, in which plant communities have coevolved with the activity of nomadic livestock herds for millennia. Regional temperature increases (+1.7°C) and altered precipitation patterns have occurred over the past 40 years (Namkhajantsan 2006). Climate change may significantly affect steppe plant communities and ecosystem functioning with possible repercussions for the livelihood of nomadic pastoralists that still make up 50% of the Mongolian population (Batima et al. 2008). We examined responses in flower production and flowering phenology for the community as a whole and also for eight specific target species at two locations along a topographic gradient on a valley slope. We predicted: (1) flower production would decrease with the warming treatment due to increased evaporation and reduced water availability, (2) the greatest effect would be seen on the upper, drier, slope and the addition of water will reduce the effect of warming on the upper slope, and (3) warming would advance flowering time, with the greatest effect seen on the colder, mesic lower slope. We tested whether observed responses are consistent within two functional groupings, such as reported in other studies: grouped by the seasonal timing of flowering (Fitter et al. 1995, Sherry et al. 2007) and also by graminoids vs. forbs (Iversen et al. 2009, Tooke and Battey 2010).

## METHODS

### Study site

The study was conducted from June to August, 2009 and 2010, on a south-facing slope in the Dalbay River Valley in northern Mongolia (51°01.405' N, 100°45.600' E; 1670 to 1800 m a.s.l., above sea level; see Plate 1). The average annual air temperature is -4.5°C (Nandintsetseg et al. 2007), with average monthly temperatures ranging from -21°C (January) to 12°C (July). Regionally, average annual precipitation over the last 40 years was 265 mm (Namkhajantsan 2006). An on-site meteorological station recorded annual precipitation of 270 mm (2009) and 246 mm (2010), and summer rainfall (June–August) of 201 mm (2009) and 178 mm (2010). Summer rainfall was less evenly distributed in 2010, with most falling between 11 and 17 August. There was no snow cover when the experiment was set up either year. The bedrock consists of Cenozoic volcanic deposits, and the

soil is sandy loam, of alluvial origin, and classified as a non-carbonated Dark Kastanozem (Aridic Boroll or Typic Ustolls; Batkhishig 2006). The steppe vegetation is a mixture of sedges (e.g., *Carex pediformis*, *Carex dichroa*), grasses (e.g., *Festuca lenensis*, *Koeleria macrantha*, *Helictotrichon schellianum*, *Stipa krylovii*), and short forbs (e.g., *Aster alpinus*, *Potentilla acaulis*, *Artemisia commutata*, *Thymus gobicus*) (see Appendix: Fig. A1 for a complete list of species and their relative abundances). In 2009, vascular plant cover of the lower and upper slope was 78% and 64%, respectively, with the lower slope dominated by *Carex pediformis*, and *Potentilla acaulis* the most abundant species on the upper slope.

### Experimental design

The experiment was set up at two positions on the topographic gradient of the south-facing slope of the valley (Casper et al., *in press*). Eight 9 × 9 m experimental blocks, fenced to exclude livestock, were located on the lower slope (elevation ~1670 m a.s.l. with a flat to gentle incline), and seven blocks on the upper slope (elevation ~1800 m a.s.l.; incline ~20°). Each block included a plot in which climate was manipulated with an open-top, passive warming chamber (OTC), and a control plot without an OTC. On the upper slope only, an additional OTC and control plot per block were given supplemental water. The hexagonal OTCs were 1.0 m wide at the top and 1.5 m at the bottom, 40 cm tall, and made of Sun-Lite HP fiberglass glazing mounted on a clear Lexan frame (Marion et al. 1997). Control plots had the same footprint and dimensions as OTCs. Among a large variety of methods available for experiment warming (Aronson and McNulty 2009) we chose this passive warming device due to the absence of electricity at this remote study site. Temperature was measured in four of the paired OTC and control plots using HOBO dataloggers (Pro v2; Onset Computers, Bourne, Massachusetts, USA), and was elevated in OTC plots relative to the control by an average of 1.5°C in the day and depressed by -0.2°C at night (Appendix: Fig. A2). The OTC also decreased soil moisture, on average, by ~30% (Liancourt et al., *in press*). The supplemental water treatment added 10 L weekly from June to August, which mimics an extra 4.5 mm rainfall event per week, resulting in ~20% more summer precipitation. OTCs were removed during the winter but were placed in the same locations both summers, as were the control plots.

### Measurement of flowering phenology and production

Flowering phenology and total flower production were assessed weekly by counting the number of flowers or inflorescences in a 50 × 100 cm quadrat centered in each plot. For forbs, only fully opened flowers or inflorescences with fully open flowers were counted (see Appendix: Table A1). For graminoids, inflorescences were counted as “flowering” from the beginning of the



PLATE 1. Dalbay Valley, in northern Mongolia, with the climate manipulation experiment on the upper and lower slope at the end of July 2009. Photo credit: P. Liancourt.

transition to reproductive stage (i.e., bolting stage) to the anthesis stage, but not after anthesis. Cover for each species in each quadrat was also calculated in mid-July, using a grid of  $10 \times 10$  cm cells. The percentage cover per species per cell was estimated to the nearest 10% and cover in all 50 cells averaged to estimate percent cover per plot, which was used to weight flower number per plot. Flower counts and percent cover of the three co-occurring *Carex* spp. were combined due to difficulty in distinguishing between them when not in flower.

#### Statistical analyses

The effects of topography, chamber treatment (OTC vs. control), and watering treatment on patterns of flowering time and flower production were examined at the community and species level. For all analyses, watering and slope location were combined to give three levels of a single treatment called slope–watering (lower–no watering, upper–no watering, and upper–watering), because watering and elevation were not fully crossed. The chamber treatment was fully crossed with the slope–watering treatment.

For each species within each plot, we calculated peak flowering date and number of flowers produced at peak (flower production hereafter). Peak flowering date was calculated as  $\sum_j F_{ij}T_j / \sum_j F_{ij}$  where  $F_{ij}$  is the number of flowers produced by species  $i$  on a given plot in week  $j$ , and  $T_j$  is the Julian day (day 1 is 1 January) on which the count of week  $j$  was performed. Flower production was calculated as  $\sum_j (F_{ij}/P_i)$  where  $P_i$  is the percentage cover by species  $i$  in a given plot; the summation included the week of peak flowering and one week before and after the peak.

Community-level responses were analyzed using canonical analysis of principal coordinates (CAP; see Anderson and Willis 2003) to examine the effect of our treatments and their interactions separately for graminoids (11 species) and forbs (31 species). Data matrices contained 88 objects (44 plots  $\times$  2 years) by species. Distances were calculated using Gower's dissimilarity, which can handle the inclusion of plots in which some species were not present or present without flowering. For the forb analyses, two objects were dropped because only one species flowered in those plots. Effects of year, chamber, slope–watering, and all interactions were analyzed using permutation ANOVAs. The three-way interaction was not significant and therefore not included in the reduced model presented. Analyses were done in R (R Development Core Team 2008) with the packages FD (Laliberté and Legendre 2010) and Vegan (Oksanen et al. 2011).

Eight common (Appendix: Fig. A1) species with the largest correlations on the first two CAP axes and contributing most to differences identified in CAP analyses were selected for separate analyses using ANOVA. There were four graminoids, *Carex* spp., *Festuca lenensis*, *Koeleria macrantha*, and *Poa attenuata*; and four forbs, *Artemisia commutata*, *Dontostemon integrifolius* (upper slope only), *Potentilla sericea*, and *Thymus gobicus*. All are perennial except the annual *D. integrifolius*. *Carex* spp., *F. lenensis*, and *P. sericea* flower early in the season; *A. commutata*, *K. macrantha*, and *P. attenuata* flower mid-season; and *D. integrifolius* and *T. gobicus* flower late season (Appendix: Fig. A3). If the effect of the slope–watering treatment was significant, differences between the upper and lower slope and

TABLE 1. *P* values from permutation tests for the community-level CAP (canonical analysis of principal coordinates) analysis and for graminoids and forbs in northern Mongolia.

Treatment	Flower production		Date of peak flowering	
	Graminoids (17.6%)	Forbs (9.7%)	Graminoids (25.8%)	Forbs (19.3%)
Chamber	<b>0.030</b>	0.490	<b>0.030</b>	0.091
Year	<b>0.010</b>	<b>0.010</b>	<b>&lt;0.001</b>	<b>0.001</b>
Slope–watering (SW)	<b>0.010</b>	<b>0.020</b>	<b>&lt;0.001</b>	<b>0.002</b>
Chamber $\times$ year	<b>0.030</b>	0.750	0.103	0.528
Chamber $\times$ SW	0.610	0.610	0.397	<b>0.020</b>
Year $\times$ SW	<b>0.010</b>	0.090	$\sim 1$	0.408

Notes: Significant *P* values are shown in bold. Values in parentheses in the graminoid and forb column headings are the percentage of total variance explained by the four axes.

between watering and no watering were tested using Tukey HSD tests. All ANOVAs were done in JMP 8.0 (SAS Institute 2008).

The effects of the chamber and slope–watering treatments and year on the onset and cessation of flowering in individual species were analyzed using accelerated failure time models based on the Weibull distribution. Data were the first observed flowering (i.e., onset) and disappearance (cessation) of flowering per species per plot. Data were left-, right-, and interval-censored, which allowed the inclusion of species that started flowering before the first sampling date (left-censored) and that had not stopped flowering by the last sample date (right-censored). However, the analysis did not produce stable estimates for the onset of flowering in 2009 of *F. lenensis* (all treatments), *K. macrantha* (upper slope without water only), *P. sericea* (upper slope with water only), and for the cessation of flowering of *D. integrifolius* in 2009; therefore, these could not be interpreted confidently (see *Results*). The three-way interaction of chamber treatment  $\times$  slope–watering treatment  $\times$  year was dropped to improve stability of the parameter estimates. As a conservative way of comparing effects of treatments on the length of the flowering season, if either date of onset or cessation of flowering changed significantly in one direction without a corresponding change in the other, we acknowledged either an extension or contraction of the flowering season, as appropriate.

## RESULTS

### Community-level effects

For graminoids, both flower production and time of peak flowering were significantly affected by all three main effects: year, slope–watering, and chamber (Table 1). Specifically, OTCs reduced graminoid flower production and delayed peak flowering; flowering was earlier on the lower slope than the upper slope, and the addition of water on the upper slope increased flower production. More flowers were produced and peak flowering was earlier in 2010 than 2009 (Fig. 1A, C). In addition, there were significant interactions of slope–watering  $\times$  year and chamber  $\times$  year for graminoid

flower production, due to the more pronounced treatment effects in 2010 (Fig. 1A).

For forbs, flower production and time of peak flowering were significantly affected by slope–watering and year, but not chamber, although there was a significant interaction between chamber and slope–watering for date of peak flowering (Table 1). Specifically, similar to the graminoids, OTCs delayed peak flowering but on the upper slope only. There was significantly higher flower production on the upper slope, and, in contrast to the graminoids, peak flowering of forbs was later on the lower slope than the upper slope. Like graminoids, forbs showed earlier peak flowering in 2010 but unlike graminoids, produced more flowers at peak in 2009.

### Species-level effects: flower production

Species-level responses of flower production to topography, watering, or chamber treatment, varied among species and between years (Fig. 2, Table 2). Only three species showed a significant response to chamber, and only in 2010; the graminoids *F. lenensis* and *K. macrantha* both showed dramatically lower flower production in OTC plots relative to controls, but the annual forb *D. integrifolius* showed significantly more flowers in OTC plots. Two species, *F. lenensis* and *T. gobicus*, produced more flowers with supplemental water ( $P < 0.05$ , Tukey's test). In addition, *T. gobicus* had greater flower production on the upper slope than on the lower slope. Four species, *Carex* spp., *P. attenuata*, *A. commutata*, and *P. sericea*, showed no significant response in flower production to either chamber manipulation or supplemental water.

There was significant interannual variation in flower production, although no consistent pattern. *A. commutata* produced significantly more flowers in 2009, while *F. lenensis* and *K. macrantha* both had greater flower production in 2010. *Carex* spp. and *P. sericea* produced more flowers on the lower slope in 2010 (Fig. 2, Table 2).

### Species level: timing of onset, peak, and cessation of flowering

Chamber manipulation affected the flowering phenology of seven of the eight target species in at least one



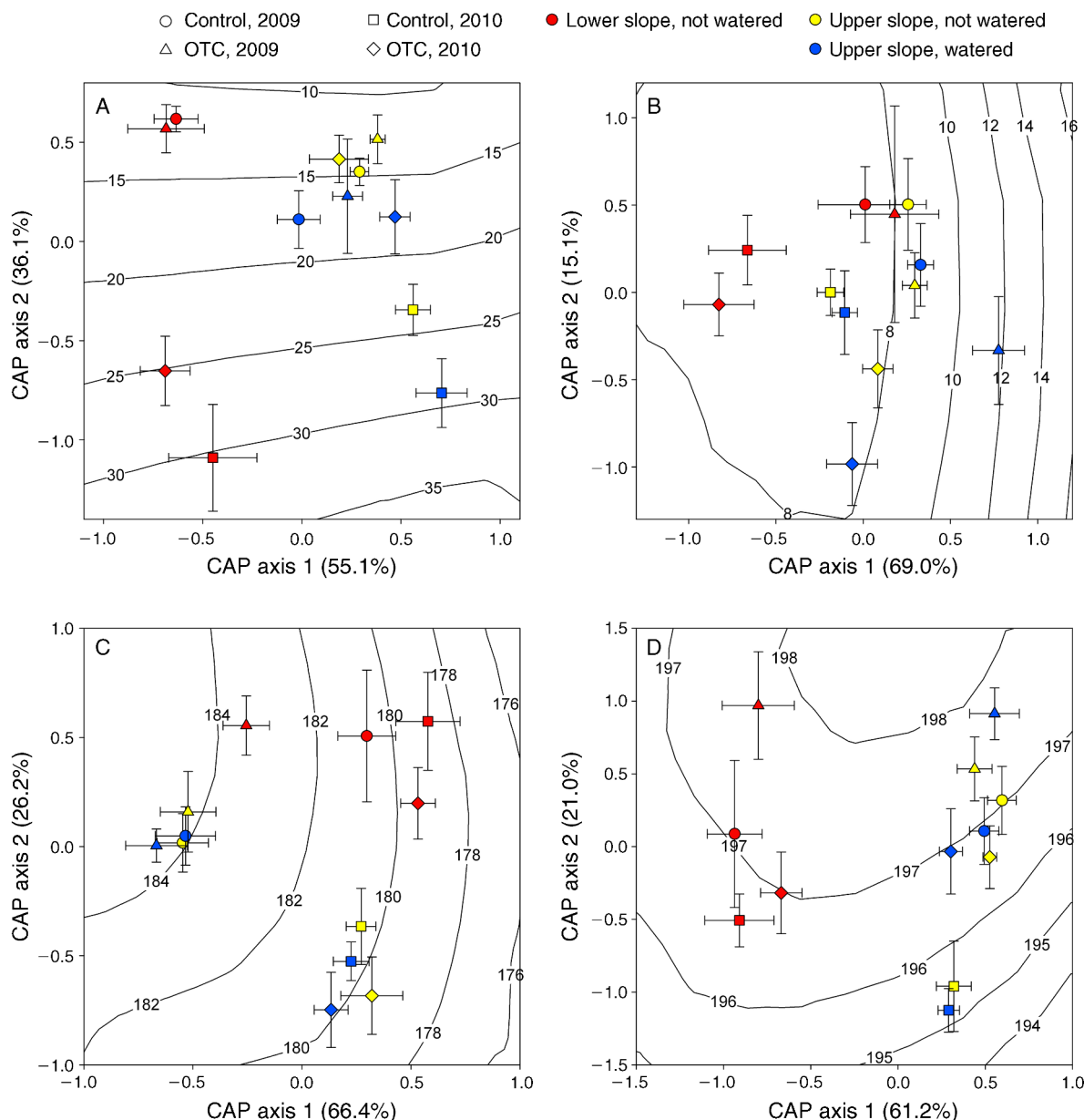


FIG. 1. (A, B) CAP (canonical analysis of principal coordinates) ordination of flower production at peak and (C, D) timing of peak for (A, C) graminoids and (B, D) forbs in northern Mongolia. Colors represent three levels of slope–watering treatment with red the lower slope, not watered; yellow the upper slope, not watered; and blue the upper slope, watered. Circles are control plots in 2009; triangles are OTC (open-top passive warming chambers) plots in 2009; squares are control plots in 2010; and diamonds are OTC plots in 2010. The overall pattern is visualized by overlaying the plots of the first two CAP axes upon the gradient (contour plots produced using *envfit* in Vegan [Oksanen et al. 2011]) of the averages of either flowering production at peak (no. flowers/percent cover) or timing of peak (as day of year; day 1 is 1 January) for the four most abundant graminoid species (A and C) and all the forb species (B and D). Error bars are SE; percentages indicate the relative contribution of each axis to the variance explained by the CAP analysis shown in Table 1.

year or in at least one of the two slope locations (Table 2). For the early-flowering species, the chamber treatment only affected cessation of flowering, with *F. lenensis* ceasing to flower earlier in OTCs compared to control plots in 2010, and *P. attenuata* ceasing to flower later in OTCs both years (Fig. 3, Table 2). OTCs had no effect on flowering time of *Carex* spp., which was the

other early-flowering species. For the mid- and late-flowering species, OTCs generally caused earlier flowering; peak flowering and cessation of flowering were earlier for *P. sericea* and *K. macrantha*. Flowering onset was earlier for *T. gobicus* on the upper slope. For *A. commutata*, flowering onset in OTCs was earlier on the lower slope but delayed on the upper slope. For the

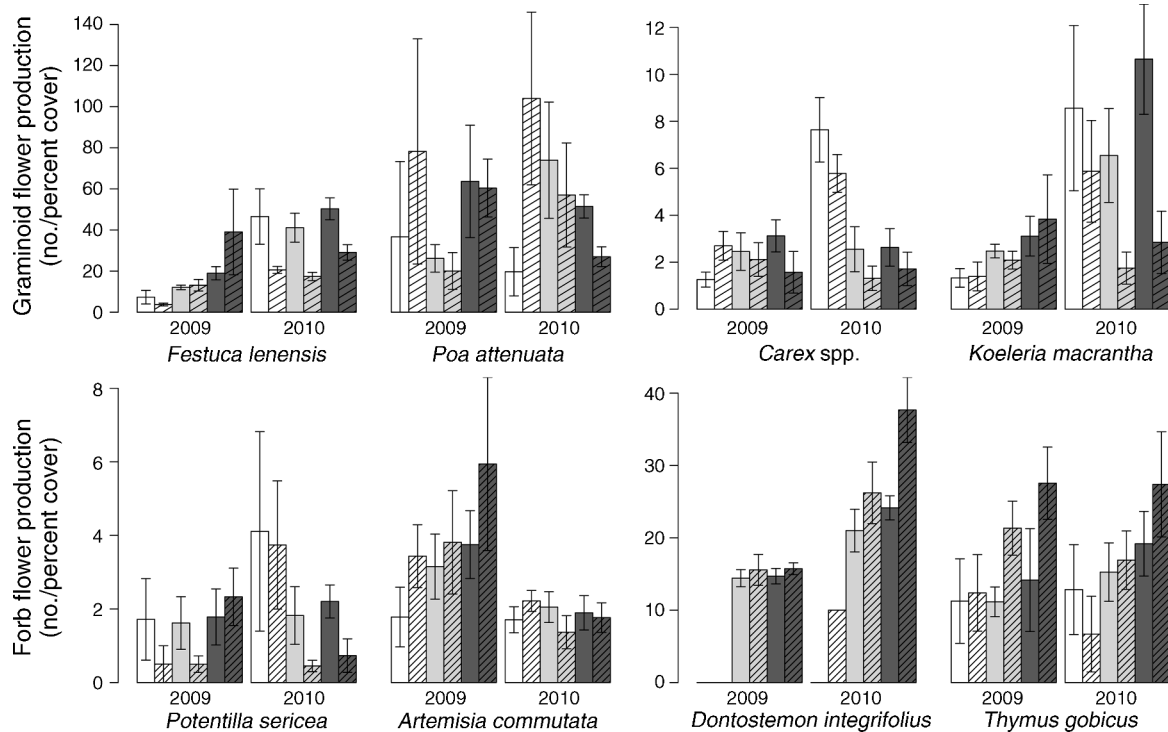


FIG. 2. Flower production in 2009 and 2010 (mean  $\pm$  SE) for the eight target species split into graminoids and forbs. The grayscale code used for the three levels of slope–watering treatment are: open, lower slope, not watered; gray, upper slope, not watered; and black, upper slope, watered. Hatched bars correspond to the chamber treatment (OTC) for each slope–watering combination.

annual *D. integrifolius*, OTCs delayed peak flowering in both years; in 2010 OTCs delayed the onset of flowering in plots without supplemental water.

For some species, the effects of chamber on the onset and/or cessation of flowering caused significant changes to the duration of the flowering season. We observed an extension of the flowering season in OTC plots for *P. attenuata* in 2009, for *T. gobicus* on the upper slope ( $P < 0.05$ , Tukey's test), and for *A. commutata* on the lower slope ( $P < 0.05$ ). In contrast, OTCs caused a contraction of the flowering season relative to controls for *F. lenensis*, *K. macrantha*, *P. attenuata*, and *D. integrifolius* in 2010, for *A. commutata* on the upper slope ( $P < 0.05$ ), and for *P. sericea* on plots without supplemental water ( $P < 0.05$ ; Fig. 3).

Watering affected flowering phenology in *K. macrantha* and *D. integrifolius*. It caused an earlier onset of flowering for both species and a delayed cessation of flowering for *D. integrifolius* in 2010, resulting in a longer flowering season for these two species (Fig. 3; based on non-overlapping confidence intervals). The accelerated failure time models produced large confidence limits in the upper-no watering for the onset of flowering of *K. macrantha* and for the cessation of flowering of *D. integrifolius* upper slope in 2009, and so we could not reliably infer the effect of watering on the

duration of the flowering season for these two species in 2009.

Topographic location had a strong effect on flowering phenology (Fig. 3). Peak flowering tended to be earlier on the upper slope, as seen in *A. commutata*, *K. macrantha*, and *P. sericea* in both years, and in *F. lenensis* in 2010. *Carex* spp. had later peak flowering on the upper slope in both years, as did *F. lenensis* in 2009, and *P. attenuata* in 2010 (Fig. 3, Table 2). Therefore, there was no consistent response between species flowering earlier or later in the season, or between graminoids and forbs. The effect of topographic location on cessation of flowering was variable; significantly earlier cessation of flowering on the upper slope was observed for *A. commutata* in both years, while *F. lenensis* and *Carex* spp. had significantly later cessation of flowering on the upper slope in 2009 and 2010, respectively.

## DISCUSSION

Community-level analysis allows the detection of emergent trends that are difficult to identify through individual species analysis due to the idiosyncratic response of species. Our results indicate that climatic warming in the Mongolian steppe could lead to a dramatic decrease in flower production at the community level, especially for the dominant grasses. This

TABLE 2. *P* values for ANOVAs of flower production and time of peak flowering, and survival analysis of onset and cessation of flowering of the eight target species.

Treatment, by flowering measurement	Graminoids				Forbs			
	<i>Carex</i> spp.	<i>Poa attenuata</i>	<i>Festuca lenensis</i>	<i>Koeleria macrantha</i>	<i>Potentilla sericea</i>	<i>Thymus gobicus</i>	<i>Artemisia commutata</i>	<i>Dontostemon integrifolius</i>
Flower production								
Chamber	0.1172	0.3679	0.0528	<b>0.0154</b>	0.1149	0.1661	0.2542	<b>0.008</b>
Year	<b>0.0038</b>	0.5647	<b>0.0001</b>	<b>0.0005</b>	0.1456	0.9828	<b>0.0041</b>	<b>&lt;0.0001</b>
Slope-watering (SW)	<b>0.0002</b>	0.6891	<b>0.0169</b>	0.3209	0.1027	<b>0.037</b>	0.3536	0.053
Chamber $\times$ year	0.2097	0.8976	<b>0.0017</b>	<b>0.0108</b>	0.6506	0.3038	0.1934	<b>0.034</b>
Chamber $\times$ SW	0.6654	0.0714	0.4121	0.6535	0.8112	0.3294	0.698	0.285
Year $\times$ SW	<b>&lt;0.0001</b>	0.1016	0.2761	0.2506	<b>0.0313</b>	0.8643	0.3028	0.068
Chamber $\times$ year $\times$ SW	0.2228	0.6521	0.6531	0.4812	0.5349	0.9709	0.9118	0.272
Date of peak flowering								
Chamber	0.085	0.2921	0.6475	<b>0.0325</b>	<b>0.015</b>	0.4511	0.2052	<b>&lt;0.0001</b>
Year	<b>&lt;0.0001</b>	0.0862	<b>&lt;0.0001</b>	0.4596	0.0792	0.203	0.2056	<b>&lt;0.0001</b>
Slope-watering (SW)	<b>0.0017</b>	0.0916	0.5581	<b>0.0014</b>	<b>0.0012</b>	0.5519	<b>&lt;0.0001</b>	0.153
Chamber $\times$ year	0.3235	0.3726	0.2138	0.572	0.7564	0.5204	0.382	<b>0.005</b>
Chamber $\times$ SW	0.5359	0.1364	0.6079	0.4911	0.4737	0.1672	0.0983	0.556
Year $\times$ SW	0.694	<b>0.0428</b>	<b>&lt;0.0001</b>	0.365	0.6121	0.2816	0.5953	0.529
Chamber $\times$ year $\times$ SW	0.8937	0.7815	0.2487	0.6368	0.8102	0.9554	0.2511	0.858
Onset of flowering								
Chamber	0.4758	0.4739	$\sim 1$	0.4244	0.3738	<b>0.0090</b>	0.5484	0.132
Year	0.1250	0.1434	<b>0.0277</b>	<b>&lt;0.0001</b>	$\sim 1$	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Slope-watering (SW)	<b>0.0145</b>	<b>0.0002</b>	$\sim 1$	<b>0.0006</b>	$\sim 1$	0.8091	<b>0.0001</b>	<b>0.004</b>
Chamber $\times$ year	0.6453	0.6796	$\sim 1$	0.4209	0.7894	0.1191	<b>0.0325</b>	<b>0.018</b>
Chamber $\times$ SW	0.2867	0.6142	0.3762	0.1922	0.5002	<b>0.0214</b>	<b>0.0010</b>	<b>0.037</b>
Year $\times$ SW	0.3036	<b>0.0068</b>	$\sim 1$	<b>0.0043</b>	0.1605	0.0601	0.1369	0.082
Cessation of flowering								
Chamber	0.2855	0.6503	<b>0.0022</b>	<b>0.0070</b>	<b>0.0006</b>	0.4002	0.2231	0.9606
Year	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0209</b>	0.9066	<b>0.0007</b>	0.3977	na
Slope-watering (SW)	<b>0.0005</b>	0.0619	0.5444	0.9895	<b>&lt;0.0001</b>	0.1967	<b>&lt;0.0001</b>	<b>0.0046</b>
Chamber $\times$ year	0.0872	<b>0.0319</b>	<b>0.0181</b>	0.1662	0.5969	0.1098	0.1114	na
Chamber $\times$ SW	0.2556	0.8505	0.1073	0.9889	<b>0.0062</b>	0.1800	0.1073	0.9606
Year $\times$ SW	<b>0.0044</b>	0.0572	<b>0.0003</b>	0.2321	<b>0.0128</b>	0.0851	0.6310	na

Notes: *D. integrifolius* was present on the upper slope only; therefore for this species SW refers to just the watering treatment. The cessation of flowering for *D. integrifolius* was analyzed for 2010 only and therefore Year was not included in the model (hence "na" in the table).

decrease in flowering in response to warming is consistent with our hypothesis that there is an interaction between warming and water stress, but differs from results of other studies performed in more mesic, cold systems, such as at high elevation or high latitude. These studies often show an increase in flower or seed production (Molau and Shaver 1997, Hollister and Webber 2000, Kudo and Suzuki 2003, Klanderud 2005, Lemmens et al. 2008). Decreased flower production by graminoids could translate into a large effect on plant community structure of the steppe (Jacquemyn et al. 2010), because graminoids represent half of the vegetative cover and are a primary source of forage for domestic and wild herbivores. At the community level, contrary to our hypothesis, climate manipulation tended to delay peak flowering of both graminoids and forbs, although the phenological responses were highly variable among species, and also depended on topographic position and year. These complex results corroborate other research that has shown not only species-specific, but also temporally and spatially variable responses in phenology (Dunne et al. 2003, 2004, Ibáñez et al. 2010).

To our knowledge, the only study of reproductive traits in which warming and water supply were both manipulated was performed in a Mediterranean system where drought induced a decrease in flower number (Llorens and Peñuelas 2005). Along the same lines, we believe the decrease in flower production was mainly driven by a decrease in soil water availability in the OTCs (Liancourt et al., *in press*; see also Aerts et al. 2004). This conclusion is supported by the increase in graminoid flower production in response to the watering treatment on the upper slope. Our ability to detect significant effects on onset, peak, and cessation of flowering of some species in the first year of our experiment indicates that phenological responses to climate manipulation can occur rapidly within this system. These changes, however, are embedded within strong annual and topographic effects, which affect flowering phenology far more than the experimental treatments. Year-to-year variation in flower production and phenology is often greater than the effect of experimental treatments simulating climate change (e.g., Hollister and Webber 2000, Aerts et al. 2004).

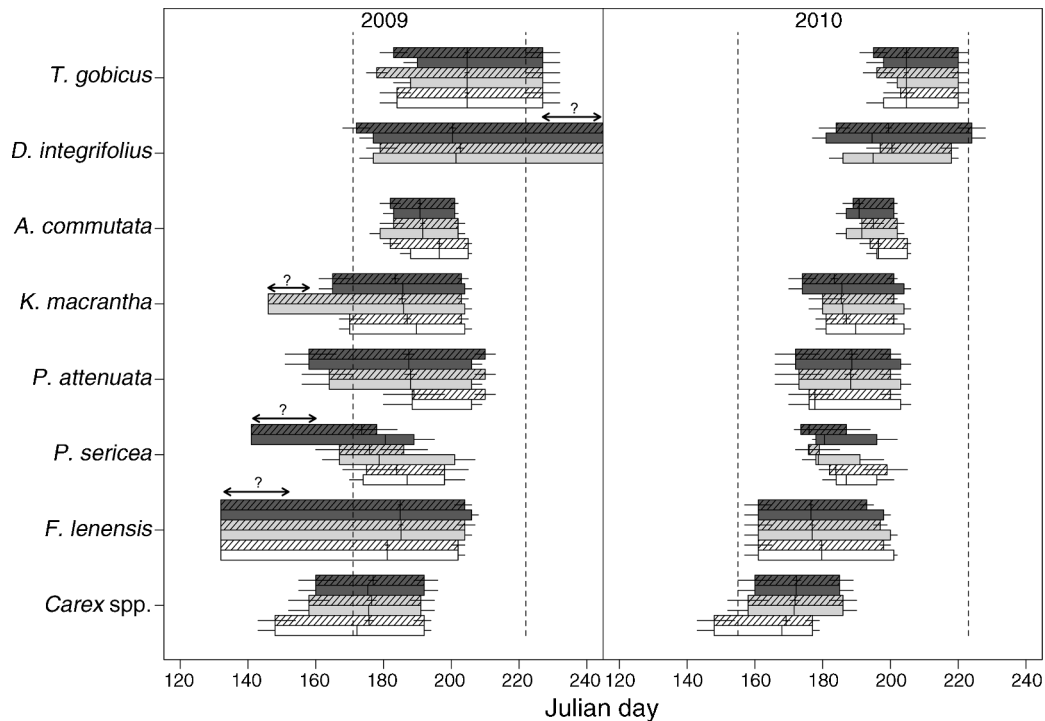


FIG. 3. Onset, peak, and cessation of flowering in 2009 and 2010 for the eight target species, ordered by rank of peak flowering date (where Julian day 1 is 1 January). The grayscale code used for the three levels of slope–watering treatment are as in Fig. 2: open, lower slope, not watered; gray, upper slope, not watered; and black, upper slope, watered. Hatched bars correspond to the chamber treatment (OTC) for each slope–watering combination. Error bars are 95% confidence limits. The question marks indicate where the accelerated failure time models did not produce good estimates (i.e., very large confidence limits) for onset or cessation of flowering.

The differential effects of our climate manipulation in successive years could be explained by differences in weather, or a cumulative effect of treatment on, for example, carbon storage patterns of the perennial plants, or an interaction between these two. For example, six species showed a contraction of the flowering season in response to warming in 2010, whereas this was seen in only one species in 2009.

The strong topographical effect is also understandable because temperature and soil moisture vary more between the upper and lower slope than between warming or watering treatments (PIRE Mongolia, *unpublished data*). The fact that species responses to climate manipulation vary between the upper and lower slope highlights the importance of considering topography within a complex landscape before drawing conclusions as to the effects of climate change at the regional scale (Dunne et al. 2004, Klein et al. 2005, Hülber et al. 2010, Scherrer and Körner 2010).

The idiosyncratic differences among the three phenological variables (onset, cessation, and time of peak flowering) for any one species underscore the need to examine the effects of climate manipulation over the whole range of the flowering period (Rathcke and Lacey 1985, Malo 2002, Miller-Rushing et al. 2008, Forrest et al. 2010), rather than just at the onset or peak of

flowering, as is frequently done. The differing responses among species in onset, cessation, and time of peak flowering are likely due to each species responding to different environmental and physiological cues (Rathcke and Lacey 1985). Changes in the synchrony of flowering among different species have the potential to affect interspecific competition for pollinators and indirect facilitation among flowering species (Rathcke 1983, Mitchell et al. 2009, Forrest et al. 2010, Tachiki et al. 2010). A change in peak flowering, meanwhile, is likely to have the greatest importance for gene flow among populations, as observed along topographic or altitudinal gradients (Hall and Willis 2006). We found no systematic response to warming among groups of species, e.g., neither early- nor late-flowering species show a differentiated response, as found in some studies (Fitter et al. 1995, Sherry et al. 2007), although this may be because we did not manipulate spring temperatures or date of snow melt, which can be critical for early-flowering species (Dunne et al. 2003, Hülber et al. 2010).

Experimental warming over the longer term is necessary in this system in order to develop and refine our understanding of climatic control of flowering phenology and to dissect the topographic, temporal, and species-specific variability. We suggest additional investigations into whether plant community composi-



tion is seed-limited and whether climate change alters the strength and nature of plant–plant and plant–pollinator interactions in order to translate the observed effects of climate change into changes in plant community structure and the provision of ecosystem services.

In summary, the timing of flowering on the steppe in northern Mongolia is vulnerable to climate change, both warming and changes in water availability. The dramatic decrease in flower production, particularly in the graminoids, and the contraction and shift in flowering phenology not only has important implications for plant community structure, but also has ramifications for the steppe's ability to support livestock herding and hence Mongolian livelihoods.

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## SUPPLEMENTAL MATERIAL

### Appendix

Figures showing relative abundance distributions for species contributing to community-level analysis, soil and air temperatures for open-top chamber (OTC) and control plots on the upper and lower slope in 2009, and peak flowering time for species included in community-level analyses (*Ecological Archives* E093-072-A1).