

Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources

J. A. SHERWOOD,¹ D. M. DEBINSKI,^{1,†} P. C. CARAGEA,² AND M. J. GERMINO³

¹Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 50011 USA

²Department of Statistics, Iowa State University, Ames, Iowa 50011 USA

³US Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho 83706 USA

Citation: Sherwood, J. A., D. M. Debinski, P. C. Caragea, and M. J. Germino. 2017. Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources. *Ecosphere* 8(3):e01745. 10.1002/ecs2.1745

Abstract. Climate change can have a broad range of effects on ecosystems and organisms, and early responses may include shifts in vegetation phenology and productivity that may not coincide with the energetics and forage timing of higher trophic levels. We evaluated phenology, annual height growth, and foliar frost responses of forbs to a factorial experiment of snow removal (SR) and warming in a high-elevation meadow over two years in the Rocky Mountains, United States. Species included arrowleaf balsamroot (*Balsamorhiza sagittata*, early-season emergence and flowering) and buckwheat (*Eriogonum umbellatum*, semi-woody and late-season flowering), key forbs for pollinator and nectar-using animal communities that are widely distributed and locally abundant in western North America. Snow removal exerted stronger effects than did warming, and advanced phenology differently for each species. Specifically, SR advanced green-up by a few days for *B. sagittata* to >2 wk in *E. umbellatum*, and led to 5- to 11-d advances in flowering of *B. sagittata* in one year and advances in bud break in 3 of 4 species/yr combinations. Snow removal increased height of *E. umbellatum* appreciably (~5 cm added to ~22.8 cm in control), but led to substantial increases in frost damage to flowers of *B. sagittata*. Whereas warming had no effects on *E. umbellatum*, it increased heights of *B. sagittata* by >6 cm (compared to 30.7 cm in control plots) and moreover led to appreciable reductions in frost damage to flowers. These data suggest that timing of snowmelt, which is highly variable from year to year but is advancing in recent decades, has a greater impact on these critical phenological, growth, and floral survival traits and floral/nectar resources than warming per se, although warming mitigated early effects of SR on frost kill of flowers. Given the short growing season of these species, the shifts could cause uncoupling in nectar availability and timing of foraging.

Key words: *Balsamorhiza sagittata*; climate change; *Eriogonum umbellatum*; montane meadows; phenology; snowpack.

Received 5 December 2016; accepted 12 December 2016. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Sherwood et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** debinski@iastate.edu

INTRODUCTION

Experimental simulations of climate change provide valuable insights for identifying and understanding the potential impacts of changing environmental conditions on ecosystems. Climate predictions indicate that temperatures, particularly daily minimum temperatures, are increasing and snowpack is decreasing (Alward 1999,

Easterling et al. 2000, Braganza et al. 2004). The western United States is already experiencing a trend toward warmer temperatures and drier conditions primarily due to decreasing snowpack (Mote 2003). Long-term trends in annual mean temperatures in the Colorado Rocky Mountains indicate that temperatures are rising an average of 0.5–1°C per decade with the largest increases occurring during the winter and summer months

(Diaz and Eischeid 2007, Ray et al. 2008, Saunders et al. 2008, Clow 2010, Rangwala and Miller 2010, 2012). As more climate changes are observed and recorded throughout the world, it is increasingly necessary to understand how these changes in daily minimum temperatures and snowpack affect ecosystems. Therefore, it is important to study not only how changing *temperatures* may impact ecosystems, but how the potential *synergistic effects* of increased temperature and decreased snowpack may affect ecosystems.

We investigated how changes in snowpack and temperature affected phenology, frost kill, and growth in a mixed sagebrush (*Artemisia* sp.) and forb montane meadow. Montane systems have a short growing season and are highly sensitive to climatic variation, particularly with respect to temperature and snow cover. Winter snowpack plays a pivotal role in meadow ecosystems, not only by providing water during the spring snowmelt, but also by acting as an insulator to plants and animals throughout the winter and in early spring when temperatures may drop below freezing during the nighttime. Snowmelt initiates springtime growth and earlier snowmelt could drive early-emerging plant species to initiate growth earlier when temperatures are still hovering near freezing, resulting in frost damage (Walker et al. 1995, Price and Waser 1998, Dunne et al. 2003, Inouye 2008, Wipf et al. 2009, CaraDonna and Bain 2016). Given the strong positive correlation between earlier flowering and earlier snowmelt, late-season snow storms and frost are likely to have a greater effect on the earlier-flowering species (Price and Waser 1998, Dunne et al. 2003, Miller-Rushing and Inouye 2009).

Snow manipulation studies provide insight into how climate change may affect these ecosystems and have shown consistently that decreased snow depth and earlier snowmelt date result in earlier plant phenology (e.g., Dunne et al. 2003, Aerts et al. 2004, Wipf et al. 2009, Wipf 2010). In addition, plant responses to changing conditions can be different than insect responses, resulting in phenological mismatches (e.g., Visser and Holleman 2001, Kudo and Ida 2013). Montane meadows support a high diversity of insect, bird, and mammal species, and each of these taxa could be adversely affected by frost-damaged plants or mismatches between plant and animal phenological patterns, resulting in problems associated

with pollination services, seed dispersal, or food resources.

The overall goal of this research was to quantify the effects of snow manipulation and passive warming on plant phenology of two forb species that are important nectar sources for the pollinator community (Auckland et al. 2004, Ogle et al. 2011). Previous warming methods have primarily relied on systems (active and passive) that increase daily maximum temperatures (e.g., Kennedy 1994, Convey and Wynn-Williams 2002, Bokhorst et al. 2008). Given that we were interested in the effect of early snowmelt on plant phenology and the potential for damaging springtime freezing or frost events, we chose to use an open-sided passive warming chamber approach design that increases *minimum* temperatures with effects most notable at night and not maximum temperatures during daytimes, which is a more concise simulation of early greenhouse gas warming effects (Germino and Smith 1999). Another benefit of the open-sided chamber (OSC) is that it requires no electricity and does not create horizontal barriers to wind, precipitation, insects, or small animals.

Our experimental manipulations allowed us to test whether plant growth and phenology (bud break, flowering, and senescence) were affected by earlier snowmelt date and/or increased temperature, particularly at night. We hypothesized that:

1. Earlier snowmelt resulting from reduced snowpack would result in earlier phenology (emergence, bud break, flowering, and senescence) and increased vegetative growth, and the combination of snow removal (SR) and warming would increase the response.
2. Warming would result in less frost damage of plant tissues and higher bud survival, whereas SR would result in greater damage.

MATERIALS AND METHODS

The study was conducted during 2010–2012 in a flat montane meadow in Grand Teton National Park, Wyoming, United States, at an elevation of 2100 m. The meadow had a relatively homogeneous plant community composition with a combination of sagebrush (*Artemisia arbuscula* ssp. *thermopola* in plots, and *Artemisia tridentata* ssp.

vaseyana in the surrounding area), flowering forbs and grasses, and a high percent cover of bare ground (on the order of 50% or more). The substrate consists of alluvium and cobbly, glacial outwash that were deposited after the Pinedale glaciers receded, resulting in a very permeable soil surface (Martin 2008). The regional climate is characterized by a mean annual precipitation of 53 cm, most of which falls as snow in the winter months. The region averages over 3.5 m of total annual snow cover, with January having the greatest accumulation of ~1 m (Western Regional Climate Center). Snow cover typically begins to accumulate in October and melts away by (or during) May. December and January are typically the coldest months with an average daily maximum temperature of -3°C , while July and August are the warmest months (average high = 25°C , respectively; Western Regional Climate Center). The typical growing season for forbs and grasses lasts until late August to early September, with maximum greenness occurring approximately mid-June (Debinski et al. 2000). Depending on snow depth and springtime temperatures, meadow vegetation typically starts to emerge and green-up in mid- to late May. The earliest plant species to emerge and green-up, as well as to senesce, are the grasses and forbs (Blaisdell 1958, Debinski et al. 2000).

We established twelve 2.4-m^2 plots at approximately 5 m distance apart and regularly assigned the following treatments to each of three plots (Appendix S1: Fig. S1): (1) heating (H), (2) snow removal (SR), (3) snow removal + heating (HSR), and (4) untreated controls (C). Note that we are using the term heating to refer to our specific treatments while warming is used to describe a broader phenomenon associated with climate change. Sites were marked for the duration of the experiment by using 12 cm wide plastic landscape edging around the perimeter of each plot buried flush with the ground. The edging did not affect movement of invertebrates or rain.

Minimum nighttime warming was achieved by adapting the OSC design devised by Germino and Smith (1999) to have a roof of clear plastic slats arrayed in a louver-like fashion as in Germino and Demshar (2008), but enlarged for use in the current study. The plastic roof of the OSC increases daily minimum temperatures of plant and soil surfaces (by $\sim 2^{\circ}\text{C}$) by passively

increasing the downwelling infrared (longwave, or thermal) radiation to plant and soil surfaces (see Germino and Smith 1999 for validation of radiation effects). The OSCs used in this study are particularly ideal in environments such as in montane meadows in Grand Teton National Park that have mostly clear skies in the growing season and minimal tree cover that would otherwise moderate radiation balances.

The OSCs were placed on the site at the time of SR (late April to early May) and remained until the end of the growing season (late September to mid-October). The OSCs consisted of a 2.4×2.4 m wood frame open to the environment on all sides. The louvered roof of the OSCs were comprised of 4 cm wide clear Optix Acrylic panels ($>95\%$ transmittance of sunlight) placed at 50° angles every 10 cm. The panels were angled in opposite directions toward the center so that the panels met at an angle in the center of the OSC. Panels were sufficiently spaced so that they did not prohibit movement of precipitation. The tops of the OSCs were approximately 30 cm from the ground to remain above maximum height of the vegetation.

We modified available snowpack to decrease available moisture and insulation in the SR treatments. For the spring SR treatment, 0.75 m of snow was removed on May 11, 2011, and 0.6 m of snow was removed a month earlier in 2012, on April 15, due to a relative warm spring and rapid snowmelt. For context, 2011 had 1052 mm of precipitation for the water year (October 1–September 30, of the following year), whereas 2012 had 846 mm of precipitation (Snowtel data from Basecamp, Wyoming, site 314; <http://www.wcc.nrcs.usda.gov/index.html>). The average annual precipitation for this site during 1981–2010 was 808 mm. Care was taken to place shoveled snow away from the plots to avoid potentially introducing more moisture from snowmelt. We were also careful at the time of SR to avoid trampling the experimental area by working along the outside edges of the plots. Approximately 2 cm of snow was left on the plots to reduce plant damage from the shovels, and allowed to melt naturally. The dense spring snowpack we removed is about 50% water by volume (<http://cdec.water.ca.gov/snow/misc/density.html>) and the amounts removed equate to approximately half of the annual precipitation. A combination of warming and snow reduction

was applied using the methods described above. In addition, three control plots were established that remained unmanipulated throughout the growing season. Three blocks of each of the four treatments were established and treatments within the blocks were randomly assigned.

Soil moisture and soil temperature were measured throughout the growing season. We installed Decagon 5TM soil moisture probes (Decagon Devices, Pullman, Washington, USA) in the center of each plot at 25 cm depth at the time of OSC placement and SR in 2011 (probes were left in place between 2011 and 2012). Soil moisture meters were placed horizontally with the flat side parallel to the soil surface in the bare soil microsites separating plants (basal gaps were ~10 to >50 cm in diameter) with as little soil disturbance and careful repacking of soil. In this xeric system, there is ample bare ground between plants, so we were able to place the meters into the soil without disturbing any plants. The total region of soil disturbance for the initial sensor placement was just over $10 \times 3.2 \times 25$ cm (the dimensions of the probe and depth of the hole). Soil moisture was measured in one-hour intervals using Em50 data loggers (Decagon Devices, Pullman, Washington, USA) from the time of SR until the end of the growing season in October. Soil surface temperatures were measured hourly using Hobo pendant temperature data loggers (Onset Computer, Bourne, Massachusetts, USA) placed in the center of each plot.

Vegetation surveys were conducted after initial snowmelt and continued throughout the growing season in 2011 and 2012. Vegetative development and reproductive phases were observed and recorded for the two dominant perennial plant species, arrowleaf balsamroot (*Balsamorhiza sagittata*) and wild buckwheat (*Eriogonum umbellatum*). *Balsamorhiza sagittata* is an early-emerging deciduous perennial forb whose shoots emerge from the soil in May (Fig. 1A), with large showy composite inflorescences on relatively long, individual stalks. The flowers and leaves senesce during the summer months, typically around the last half of June/early July. *Eriogonum umbellatum* is a woody perennial that forms broader mats with relatively more numerous and smaller evergreen leaves that green-up in the spring after turning red in the fall (Fig. 1B). Each plant forms multiple flower stalks with a single umbel

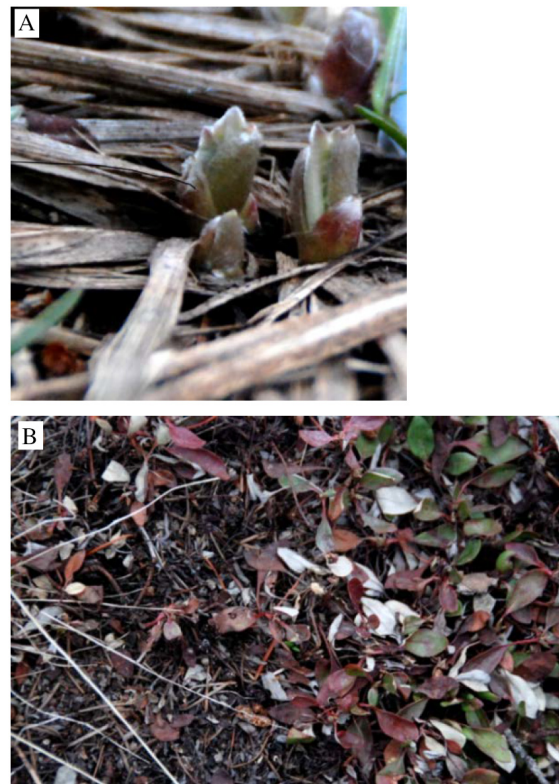


Fig. 1. The first phenological stages measured at the beginning of the growth season for (A) *Balsamorhiza sagittata* and (B) *Eriogonum umbellatum*.

containing clusters of tiny flowers beginning in June and lasting throughout most of July.

Phenology for each species was monitored and phenophase (emergence/green-up, bud break, flowering, and senescence) recorded for plants within each plot. Frost damage was also recorded; however, the resulting data differed for the species. *Balsamorhiza sagittata* blooms in early spring and its flowers are more exposed to spring frost, and *E. umbellatum* initiates growth and flowering later in the season when frosts are rarer. We also recorded the number of frost-killed buds and flowers in each plot during each sampling period, and whereas frost-killed tissues were common on *B. sagittata*, they were never evident and thus not further quantified on *E. umbellatum*.

Phenology assessments and growth measurements were recorded 1–2 times/wk from early May through late July each year. Given that the mature plant forms of *B. sagittata* and *E. umbellatum* are very different (Fig. 2A, B), we used maximum leaf

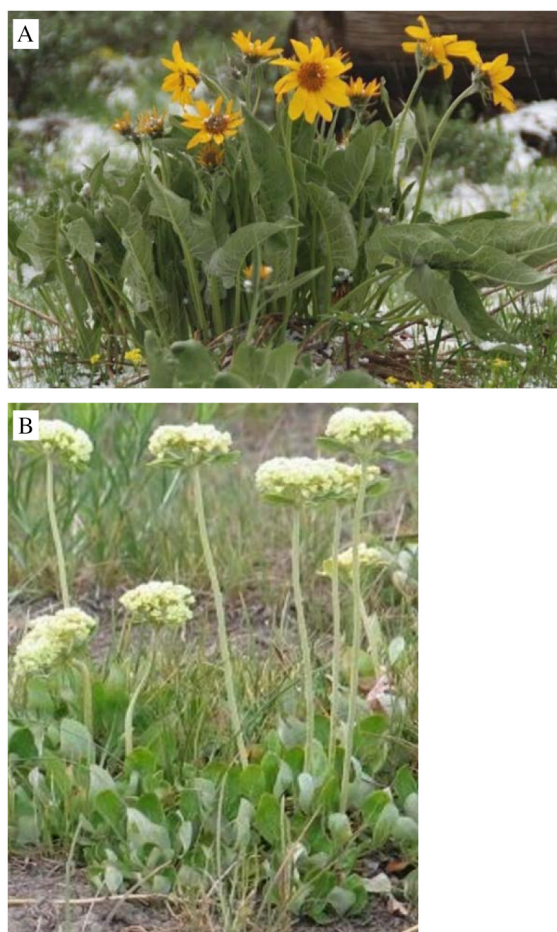


Fig. 2. Mature plant forms for (A) *Balsamorhiza sagittata* and (B) *Eriogonum umbellatum*.

height for *B. sagittata* and maximum *E. umbellatum* inflorescence height as measures of plant stature, and, indirectly, growth. For *B. sagittata*, we tracked phenology and leaf height of individual plants, whereas for *E. umbellatum*, we measured the tallest 10 inflorescences within each of the four plot quadrants and categorized them in terms of phenology.

Statistical methods for assessing effects of treatments on soil moisture and surface temperature

We used a randomization-based approach in order to evaluate the effect of warming and snow manipulation on soil moisture and surface temperature, separately for each year. We compared sets of time series data (soil moisture or temperature) to test for differences between

treatments. Randomization tests are nonparametric, so no assumptions are necessary regarding the statistical distributions of the data. We used the area under the (point-to-point) difference time series, and computed the area under this curve numerically, using Simpson's rule, in the package StreamMetabolism within the statistical software R (R Development Core Team 2015) using an approach similar to Rocchetti and De Nicolao (1990). For the temperature series data, we considered the 5 a.m. soil surface temperatures between all treatment groups (C, H, SR, and HSR). For the soil moisture data, we used hourly values measured at 25 cm depth to compare SR treatments (SR and HSR) and NoSR treatments (C and H). Appendix S1 contains additional details on the randomization test procedure. Note that in some cases, the smallest possible *P*-value was larger than 0.5, so we have included $P < 0.1$ in that case.

Statistical methods for assessing change in plant phenology and frost damage

The date for the first occurrence was calculated for each phenological event (emergence/green-up, bud break, flowering, and flower senescence) in each plot across the four treatments (C, H, SR, and HSR). The dates for the first occurrence of each phenophase were recorded as the point in time when the majority of plants (>50%) in the plots entered that phase. One of the H plots was determined to be an outlier and not included in the *B. sagittata* analysis as the plants were not fully developed or flower producing.

To assess the effects of frost damage in *B. sagittata*, we calculated the proportion of frost-killed buds and early flowers by dividing the number of frost-killed bud and early flowers by the total number of buds per plant and compared these proportions across treatments. A square root transformation was used to correct heteroskedasticity. Data for 2012 were problematic because (1) there was no variability in the control plot (all values were 1 due to 100% frost-killed buds) and (2) there was high variability in the data from the HSR treatment. For these reasons, we compared only the data from the H and SR treatments by conducting a two-sample *t* test for normal and homoskedastic data.

We calculated the maximum leaf height of *B. sagittata* as the average of the maximum

height reached for all plants in each treatment plot considered. Similarly, the maximum inflorescence height of *E. umbellatum* was calculated by averaging all the measured inflorescence heights from each quadrant within each treatment plot. We used one-way ANOVAs to compare the effect of each treatment (SR, H, and HSR) on the timing of phenological events, percentage of frost-killed buds, and overall leaf/flower height. When an effect was significant, post hoc Tukey's HSD (honest significant difference) multiple comparisons were made to assess differences between individual means for each treatment. Analyses of plant responses were performed in JMP 12 Pro (SAS Institute, Cary, North Carolina, USA) using $\alpha = 0.05$. We focus our discussion of results on the main treatment effects, but to be thorough, we have presented all comparisons.

RESULTS

Soil moisture and soil temperature

Heating treatments increased morning temperature, and SR treatments reduced soil moisture across the growing season (2011 data are shown

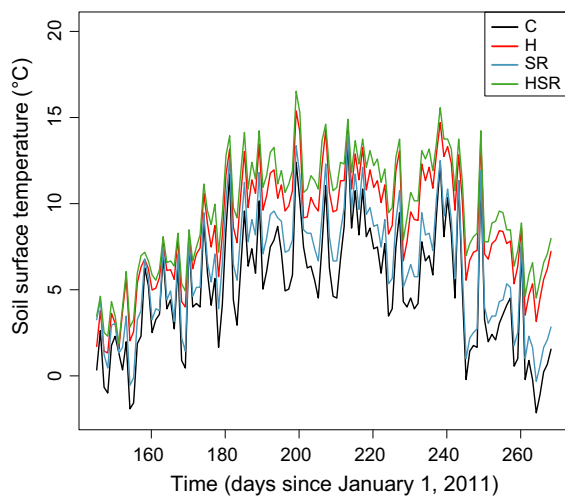


Fig. 3. Time series of the soil surface temperature in the experimental plots in 2011. Each summary series is computed as the median hourly value for the plots that received the heating treatment (heating + snow removal [HSR] and heating [H]) and the plots where there was no heating (snow removal [SR] and control [C]). $N = 4$ plots/treatment.

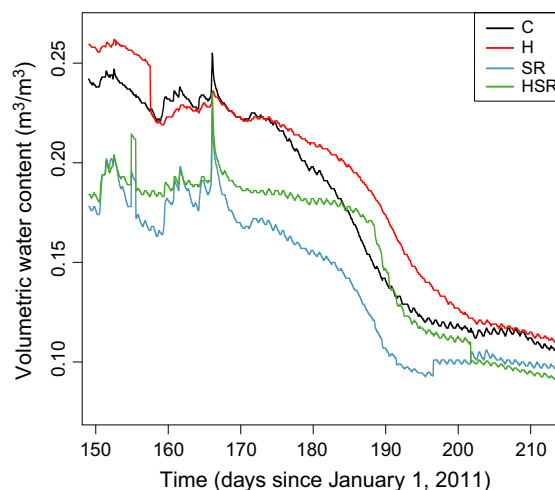


Fig. 4. Time series of the median volumetric water content of the soil (soil moisture) for the experimental plots for 2011. Each summary series is computed as the median hourly value for the plots that received the snow removal (heating + snow removal [HSR] and (snow removal [SR]) and the plots where there was no snow removal (heating [H] and control [C]). $N = 4$ plots/treatment.

as an example in Figs. 3, 4; P -values for 2011 temperature comparisons were as follows: $C < H$: 0.1, $C < SR$: 0.05, $C < HSR$: 0.05, $SR < H$: 0.1, $SR < HSR$: 0.05, $H < HSR$: 0.1. See Appendix S1 for details on how the randomization tests were performed). Snow removal significantly reduced soil moisture in both 2011 and 2012 (P -values for the test comparing SR plots to No-SR plots were 0.01 and 0.02 for 2011 and 2012, respectively). H treatments marginally increased soil moisture but only during early-season months when soil water was abundant and thus likely not limiting growth in both 2011 and 2012 (the P -values corresponding to the test comparing the H plots to the C and SR plots were 0.06 and 0.08, respectively).

Phenological responses

Snow removal with or without heating caused *Balsamorhiza sagittata* to emerge one to four days earlier than control plots, and advanced its flowering by 6 to >15 d, and advanced its bud break by 8 d in 2011 in unheated plots and 5 d in 2012 in combination with heating (HSR; Table 1; $P < 0.05$). Heating (H) had no direct effects on phenology. Snow removal advanced green-up of

Table 1. Summary of all pairwise comparisons of *Balsamorhiza sagittata* phenological events by treatment.

Comparison	Emergence		Bud break		Flowering		Senescence	
	Difference in means	<i>P</i>	Difference in means	<i>P</i>	Difference in means	<i>P</i>	Difference in means	<i>P</i>
(A) 2011								
C—SR	2.0	0.022	8.7	<0.001	15.7	<0.001	1.7	0.788
C—H	0	1	−1.3	0.584	2.0	0.824	−3.3	0.402
C—HSR	1.3	0.119	6.7	<0.001	14.3	0.001	0	1
SR—H	−2.0	0.037	−10.0	<0.001	−13.7	0.003	−5.0	0.142
SR—HSR	−0.7	0.578	−2.0	0.212	−1.3	0.915	−1.7	0.788
HSR—H	−1.3	0.172	−8.0	<0.001	−12.3	0.005	−3.3	0.402
(B) 2012								
C—SR	4.0	<0.0001	1.0	0.5784	6.0	0.0368	N/A	N/A
C—H	0	1	−2.0	0.1717	4.0	0.2363	N/A	N/A
C—HSR	4.0	<0.0001	5.0	0.0013	11.0	0.0014	N/A	N/A
SR—H	−4.0	<0.0001	−3.0	0.0368	−2.0	0.7234	N/A	N/A
SR—HSR	0	1	4.0	0.0048	5.0	0.0791	N/A	N/A
HSR—H	−4.0	<0.0001	−7.0	0.0003	−7.0	0.0303	N/A	N/A

Notes: Abbreviations for the treatments in soil moisture results are as follows: C, control; SR, snow removal only; H, heating only; HSR, snow removal + heating. Differences in means are reported as Julian days. Tukey–Kramer correction was used for multiple comparisons. Positive values indicate advances in time for the latter treatment relative to former. $P \leq 0.05$ are noted in boldface. In each comparison, $df = 7$ (one plot was not included because it had no flowering plants).

Eriogonum umbellatum by 6.5 to >13 d in unheated or heated plots and advanced bud break by about 8 d in 2012, most significantly in heated plots (Table 2; $P < 0.05$). H had no effects.

Frost damage

Frost and freezing damage resulted in significant damage to buds and early flowers of

B. sagittata in both years (Table 3). The highest proportion of frost-killed buds occurred in the SR treatment with close to 70% (66 out of 96 buds) of all buds killed during the 2011 growing season. This was significantly different from each of the heating treatments (H and HSR) where less than 2% (one out of 46 buds) of buds in H ($P = 0.001$) and 3% (two out of 63 buds) in HSR ($P = 0.004$) treatments were killed. The proportion

Table 2. Summary of all pairwise comparisons of *Eriogonum umbellatum* phenological events by treatment.

Comparison	Green-up		Bud break		Flowering	
	Difference in means	<i>P</i>	Difference in means	<i>P</i>	Difference in means	<i>P</i>
(A) 2011						
C—SR	10.7	0.028	0.5	0.813	7.3	0.109
C—H	1.3	0.967	0.7	0.655	0.0	1.000
C—HSR	13.3	0.008	0.3	0.932	3.0	0.709
SR—H	−9.3	0.052	0.2	0.990	−7.3	0.109
SR—HSR	2.7	0.803	−0.2	0.990	−4.3	0.447
HSR—H	−12.0	0.015	0.3	0.932	−3.0	0.709
(B) 2012						
C—SR	6.7	0.049	7.3	0.075	4.7	0.414
C—H	1.3	0.915	2.3	0.792	2.3	0.845
C—HSR	9.7	0.007	8.7	0.036	2.3	0.845
SR—H	−5.3	0.120	−5.0	0.269	−2.3	0.845
SR—HSR	3.0	0.506	1.3	0.949	−2.3	0.845
HSR—H	−8.3	0.016	−6.3	0.131	0.0	1.000

Notes: Abbreviations for the treatments in soil moisture results are as follows: C, control; SR, snow removal only; H, heating only; HSR, snow removal + heating. Differences in means are reported as days. Tukey–Kramer correction was used for multiple comparisons. $P \leq 0.05$ are noted in boldface. In each comparison, $df = 8$.

Table 3. Summary of all pairwise comparisons of proportion of *Balsamorhiza sagittata* frost-killed buds by treatment.

Comparison	Difference in squared means	<i>P</i>
(A) 2011		
C—SR	−0.207	0.35
C—H	0.548	0.009
C—HSR	0.503	0.02
SR—H	0.755	0.001
SR—HSR	0.710	0.004
HSR—H	0.0450	0.98
(B) 2012		
SR—H	0.92	0.002

Notes: Abbreviations for the treatments in soil moisture results are as follows: C, control; SR, snow removal only; H, heating only; HSR, snow removal + heating. Differences in means are reported as overall proportion of frost-killed buds. Values from 2011 were square-root-transformed due to unequal variances. The only comparison made in 2012 was between SR and H. Tukey–Kramer correction was used for multiple comparisons. $P \leq 0.05$ are noted in boldface. In each 2011 comparison, $df = 7$. In 2012, $df = 3$.

of frost-killed buds in the C (18 out of 48 buds) was significantly different than in both the H ($P = 0.009$) and HSR ($P = 0.02$) treatments but not than the SR treatment ($P = 0.35$). In 2012, plants emerged almost 20 d earlier compared to 2011, and thus were exposed to more freeze events during early growth. As a result, all of the buds and early flowers in the C (100%) and a majority in the SR (~95%) treatments were killed due to frost and freezing events. In addition, we noted large unexplained variability between the HSR plots. As a result, we only compared the H and SR treatments. The H treatment in 2012 again resulted in significantly less frost-killed buds and early flowers (one out of 21) than the SR treatment (100 out of 107 buds; $P = 0.002$).

Height of plants

Balsamorhiza sagittata heights were 6.26 cm taller in H and 5.4 cm taller in HSR compared to C (average height = 30.7 cm) in 2012 (Table 4; $P < 0.05$), whereas in 2011 only H significantly increased heights (difference of 6.13 cm $P = 0.03$, data not shown) over C (average height = 33.8 cm). Snow removal + heating had the largest effect on *E. umbellatum*, increasing heights by 9.5 cm compared to C (average height = 22.8 cm), while SR increased *E. umbellatum* heights by 7.83 cm in 2012 (Table 4; $P < 0.05$). No significant differences were found for *E. umbellatum* in 2011.

DISCUSSION

We have focused our assessments on two of the most widespread and conspicuous forbs in non-forested western U.S. landscapes. They occur together, but represent two contrasting life history strategies, thus allowing us to understand responses to the treatments from a more generalized perspective. Because *Balsamorhiza sagittata* is one of the first species to flower, it was an excellent species in which to assess effects of treatments on frost-killed buds. Alternatively, because *Eriogonum umbellatum* is a woody perennial with evergreen leaves, it allowed us to detect effects of treatments on the rate of leaf green-up and late-season phenological responses. In addition, *B. sagittata* is a large-leaved plant, whereas *E. umbellatum* has much smaller leaves, so it may not be surprising that they would express differential responses to changes in the amount of long-wave thermal radiation. Taken together, we were able to infer some important implications regarding expected climate change responses of alpine plants from the perspective of (1) phenology, (2) frost kill, and (3) growth.

Table 4. Comparison of 2012 *Balsamorhiza sagittata* maximum leaf height measurements and *Eriogonum umbellatum* maximum flower stalk height by treatment for all pairwise comparisons.

Comparison	Difference in means	<i>P</i>
(A) Maximum leaf height for <i>B. sagittata</i>		
C—SR	−2.87	0.36
C—H	−6.26	0.04
C—HSR	−5.41	0.05
SR—H	−3.39	0.32
SR—HSR	−2.54	0.45
HSR—H	−0.85	0.96
(B) Maximum flower stalk height for <i>E. umbellatum</i>		
C—SR	−7.833	0.027
C—H	−5.333	0.137
C—HSR	−9.500	0.009
SR—H	2.500	0.663
SR—HSR	−1.667	0.863
HSR—H	4.167	0.284

Notes: Abbreviations for the treatments in soil moisture results are as follows: C, control; SR, snow removal only; H, heating only; HSR, snow removal + heating. Differences in means are reported as height in cm. Tukey–Kramer correction was used for multiple comparisons. $P \leq 0.05$ are noted in boldface. In each comparison, $df = 8$.

Overall, we found that a reduction in snowpack had significant effects on phenology, resulting in earlier emergence, bud break (*B. sagittata*), flowering (*B. sagittata*), and green-up (*E. umbellatum*) dates. We did not detect as many synergistic effects of heating and SR as we had expected, but there is some evidence of synergy with respect to advancement of *B. sagittata* bud break and flowering, and *E. umbellatum* bud break. Heating markedly reduced frost damage on buds and increased growth in *B. sagittata*. *Eriogonum umbellatum* also showed increased growth under SR and HSR conditions, and there was some evidence of synergy between these two effects in 2012. Thus, a future climate with reduced snowpack could advance plant emergence and increase frost-killed buds, but nighttime warming could potentially mitigate frost damage and increase total plant growth.

If this type of shift in phenology of montane meadow plants occurred across the landscape, it could affect ecosystem processes because the insect and mammals that use these plants may or may not experience phenological shifts to the same degree. Given that the full growing season for *B. sagittata* is just under ~40 d (Fig. 5), a shift in bud timing by 10 d or flowering by 15 d as we observed in 2011 could have significant ecological

repercussions. Although there have been documented cases of parallel shifts in plant and insect phenology (e.g., Bartomeus et al. 2011, Rafferty and Ives 2011, Ovaskainen et al. 2013, Forrest 2015), the phenology of different organisms may be regulated differently, and result in nonparallel shifts in phenology. For example, Kudo and Ida (2013) documented a mismatch between the flowering onset of *Corydalis ambigua* and its predominant pollinator, bumble bee queens (*Bombus* spp.). In that study, *C. ambigua* appeared to have a greater response to early snowmelt and warmer spring temperatures than the *Bombus* spp. Our observations of emergence trends of *Parnassius clodius* and their primary nectar plants, *B. sagittata* (J. Sherwood, *personal observation*) and *E. umbellatum* (Auckland et al. 2004; J. Sherwood, *personal observation*), suggest that plants and pollinators in this system may respond differently to snowmelt timing and temperature.

Downscaling regional climate change projections so that we can understand the specific effect of climate change on minimum daily temperatures, and daily maximum temperatures, will be essential for predicting plant community responses. For example, some plant species exposed to higher daily minimum temperatures may experience higher respiration rates, without a corresponding increase in photosynthetic rates, which could lead to a decrease in plant productivity and growth (Hughes 2000). While these higher nocturnal respiration rates have been linked with decreases in plant productivity and yield in some plant species (Paembonan et al. 1992, Albrizio and Steduto 2003, Mohammed and Tarpley 2009), nocturnal warming increased net CO₂ exchange (uptake) for species at their upper elevation limit (Germine and Smith 1999). Species-specific and context-specific factors may also modulate the responses. Many plant species can acclimate to changes in temperature (e.g., Smith and Hadley 1974, Bunce 2008, Kositsup et al. 2009, Smith and Dukes 2013), but there may be differences in the response depending on growth rate (Atkin et al. 2006) or plant functional type (Bunce 2008, Smith and Dukes 2013).

The advancement of phenology has previously been interpreted as a positive response in terms of the fitness of the plants because it allows the plant more time for growth and resource allocation (Van der Wal et al. 2000, Saavedra 2002, Starr and

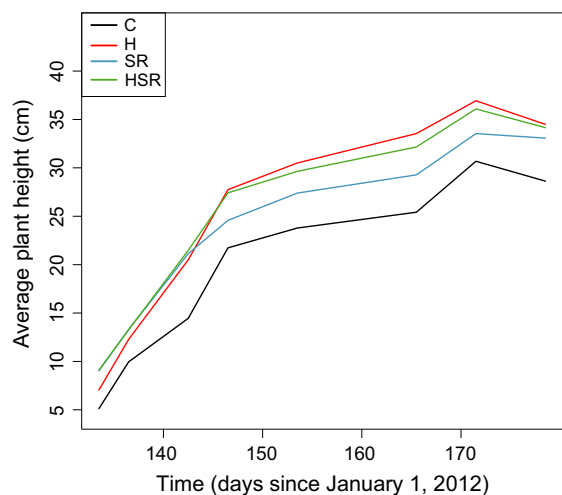


Fig. 5. Overall average leaf height (cm) of *Balsamorhiza sagittata* measured during the 2012 growing season. Average computed for each time point over the observations in four plots for control (C), snow removal (SR), and heating + snow removal (HSR), and three plots for heating (H).

Oberbauer 2003). Therefore, we could expect that earlier snowmelt could be beneficial for plants because they could potentially adapt to a longer growing season. However, there are many other factors to consider in evaluating such responses. For example, there may be a longer period of seed predation if seeds are produced earlier in the season. In addition, earlier snowmelt in an ecosystem that relies on snowpack for seasonal moisture could lead to greater period of drought exposure.

Winter snowpack plays an important role in ecosystems that rely on the insulating effects of the snow. Previous studies have examined the role that frost events may play in the survival, growth, and reproduction of alpine plants (Inouye 2001, 2008, Inouye et al. 2002, Larcher et al. 2010, Hacker et al. 2011). Exposure to low-temperature events could increase if the snow-free season is extended due to earlier snowmelt (Groffman et al. 2001, IPCC 2013). Increasing daytime temperatures are leading to earlier snowmelt and advanced plant phenology, yet springtime frost events have not been eliminated. Decreasing snow cover leaves the plants exposed to lower temperatures and potential frost events because of the lost insulating capacity of snow (Sakai and Larcher 1987, Taschler and Neuner 2004). Springtime flower budding is tightly linked to the plant's reproductive efforts, and flower buds are particularly vulnerable to frost damage. Thus, earlier plant emergence and development due to advanced snowmelt date could lead to more frequent and more serious frost damage (Molau 1997, Price and Waser 1998, Inouye et al. 2002, Inouye 2008) resulting in decreased plant reproduction. Our SR treatments further supported the importance of early-season snow cover in protecting early-emerging plant species from frost damage. If the number of buds and flowers damaged during a particularly cold, snow-free spring is widespread, it could be extremely detrimental to plant reproduction. One bad year for reproduction may not be as important in a long-lived perennial such as *B. sagittata*, but multiple such years could have an effect on population dynamics and diversity. However, if nighttime temperatures remain higher due to increased cloudiness or other factors, the early-emerging plant species may not be as greatly affected by freezing events, as shown by the combination of SR and passive warming in our experiments.

In summary, SR advanced phenological events for both plant species we examined, but heating had differential effects. Heating increased growth and reduced frost-killed buds in the early-blooming, large-leaved, and herbaceous *B. sagittata*. However, SR had a greater effect than heating on growth in the later-blooming, small-leaved, and woody *E. umbellatum*. Thus, the timing of exposure (SR) and photoperiod effects are strong drivers of phenology in this system and the susceptibility of these species to changes varied with their life history patterns.

ACKNOWLEDGMENTS

This research was supported by grants from Decagon Devices, the Xerces Society, the Center for Global and Regional Environmental Research, ISU EEOB Department, and the University of Wyoming NPS Research Station. Funding was also provided by Idaho NSF EPSCoR (EPS 0814387). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. A very special thanks go to K. McCloskey, J. Brengle, I. Waldron, K. Kindscher, and those who assisted with the field studies throughout the years: D. Nelson, J.J. Sherwood, C. Gause, A. Taylor, M. Kyer, A. Binder, K. Szcudronski, and J. Pink.

LITERATURE CITED

- Aerts, R., J. H. C. Cornelissen, E. Dorrepaal, R. S. P. van Logtestijn, and T. V. Callaghan. 2004. Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Global Change Biology* 10:1599–1609.
- Albrizio, R., and P. Steduto. 2003. Photosynthesis, respiration and conservative carbon use efficiency of four field grown crops. *Agricultural and Forest Meteorology* 116:19–36.
- Alward, R. D. 1999. Grassland vegetation changes and nocturnal global warming. *Science* 283:229–231.
- Atkin, O. K., I. Scheurwater, and T. L. Pons. 2006. High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Global Change Biology* 12:500–515.
- Auckland, J. N., D. M. Debinski, and W. R. Clark. 2004. Survival, movement, and resource use of the butterfly *Parnassius clodius*. *Ecological Entomology* 29:139–149.
- Bartomeus, I., J. S. Ascher, D. Wagner, B. N. Danforth, S. Colla, S. Kornbluth, and R. Winfree. 2011.

- Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences USA* 108: 20645–20649.
- Blaisdell, J. P. 1958. Seasonal development and yield of native plants on the upper Snake River plains and their relation to certain climatic factors. *Technical Bulletin* 1190. United States Department of Agriculture, Washington, D.C., USA.
- Bokhorst, S., J. W. Bjerke, F. W. Bowles, J. Melillo, T. V. Callaghan, and G. K. Phoenix. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology* 14:2603–2612.
- Braganza, K., D. J. Karoly, and J. M. Arblaster. 2004. Diurnal temperature range as an index of global climate change during the twentieth century. *Geophysical Research Letters* 31:L13217.
- Bunce, J. A. 2008. Acclimation of photosynthesis to temperature in *Arabidopsis thaliana* and *Brassica oleracea*. *Photosynthetica* 46:517–524.
- CaraDonna, P. J., and J. A. Bain. 2016. Frost sensitivity of leaves and flowers of subalpine plants is related to tissue type and phenology. *Journal of Ecology* 104:55–64.
- Clow, D. W. 2010. Changes in timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate* 23:2293–2306.
- Convey, P., and D. D. Wynn-Williams. 2002. Antarctic soil nematode response to artificial climate amelioration. *European Journal of Soil Biology* 38:255–259.
- Debinski, D. M., M. E. Jakubauskas, and K. Kindscher. 2000. Montane meadows as indicators of environmental change. *Environmental Monitoring and Assessment* 64:213–225.
- Diaz, H. F., and J. K. Eischeid. 2007. Disappearing “alpine tundra” Köppen climatic type in the western United States. *Geophysical Research Letters* 34: L18707.
- Dunne, J. A., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs* 73:69–86.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- Forrest, J. R. K. 2015. Plant-pollinator interactions and phenological change: What we can learn about climate impacts from experiments and observations? *Oikos* 124:4–13.
- Germino, M. J., and D. Demshar. 2008. PS 73-27: a new approach for passive warming in field experiments. Abstract in *Proceedings of the 93rd Ecological Society of America Annual Meeting*. <https://eco.confex.com/eco/2008/techprogram/P14550.htm>
- Germino, M. J., and W. K. Smith. 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell and Environment* 22:407–415.
- Groffman, P. M., C. T. Driscoll, T. J. Fahey, J. P. Hardy, R. D. Fitzhugh, and G. L. Tierney. 2001. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56:135–150.
- Hacker, J., U. Ladinig, J. Wagner, and G. Neuner. 2011. Inflorescences of alpine cushion plants freeze autonomously and may survive subzero temperatures by supercooling. *Plant Science* 180:149–156.
- Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution* 15:56–61.
- Inouye, D. W. 2001. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3:457–463.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- Inouye, D., M. Morales, and G. Dodge. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. *Oecologia* 130:543–550.
- IPCC. 2013. Climate change 2013: the physical science basis. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, New York, USA.
- Kennedy, A. D. 1994. Simulated climate-change – a field manipulation study of polar microarthropod community response to global warming. *Ecography* 17:131–140.
- Kositsup, B., P. Montpied, P. Kasemsap, P. Thaler, T. Améglio, and E. Dreyer. 2009. Photosynthetic capacity and temperature responses of photosynthesis of rubber trees (*Hevea brasiliensis* Müll. Arg.) acclimate to changes in ambient temperatures. *Trees* 23:357–365.
- Kudo, G., and T. Y. Ida. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94:2311–2320.
- Larcher, W., C. Kainmüller, and J. Wagner. 2010. Survival types of high mountain plants under extreme temperatures. *Flora* 205:3–18.

- Martin, L., 2008. Hydrogeology and water-supply wells, Grand Teton National Park. Natural Resource Technical Report NPS/NRPC/WRD/NRTR—2008/091, National Park Service, Fort Collins, Colorado, USA.
- Miller-Rushing, A. J., and D. W. Inouye. 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species. *American Journal of Botany* 96:1821–1829.
- Mohammed, A.-R., and L. Tarpley. 2009. Impact of high nighttime temperature on respiration, membrane stability, antioxidant capacity, and yield of rice plants. *Crop Science* 49:313.
- Molau, U. 1997. Phenology and reproductive success in arctic plants: susceptibility to climate change. Pages 153–170 in W. C. Oechel, et al., editors. *Global change and arctic terrestrial ecosystems*. Springer, New York, New York, USA.
- Mote, P. W. 2003. Trends in snow water equivalent in the Pacific Northwest and their climatic causes. *Geophysical Research Letters* 30:1601.
- Ogle, D., D. Tilley, J. Cane, L. St. John, K. Fullen, M. Stannard, and P. Pavék. 2011. Plants for pollinators in the Intermountain West. Plant Materials Technical Note 2A (revised). U.S. Department of Agriculture – Natural Resources Conservation Service, Boise, Idaho, USA.
- Ovaskainen, O., S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova, N. Kutenkova, A. Shcherbakov, E. Meyke, and M. del Mar Delgado. 2013. Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences USA* 110:13434–13439.
- Paembonan, S. A., A. Hagihara, and K. Hozumi. 1992. Long-term respiration in relation to growth and maintenance processes of the aboveground parts of a hinoki forest tree. *Tree Physiology* 10:101–110.
- Price, M. V., and N. M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79:1261–1271.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rafferty, N. E., and A. R. Ives. 2011. Effects of experimental shifts in flowering phenology on plant – pollinator interactions. *Ecology Letters* 14:69–74.
- Rangwala, I., and J. R. Miller. 2010. Twentieth century temperature trends in Colorado's San Juan Mountains. *Arctic, Antarctic, and Alpine Research* 42: 89–97.
- Rangwala, I., and J. R. Miller. 2012. Climate change in mountains: a review of elevation-dependent warming and its possible causes. *Climatic Change* 114:527–547.
- Ray, A. J., J. J. Barsugli, K. B. Averyt, K. Wolter, M. Hoerling, N. Doesken, B. Udall, and R. S. Webb. 2008. Climate change in Colorado: a synthesis to support water resources management and adaptation. CU-NOAA Western Water Assessment, Boulder, Colorado, USA.
- Rocchetti, M., and G. De Nicolao. 1990. CURT: a randomization test for statistical comparison between experimental curves. *Computer Methods and Programs in Biomedicine* 31:207–213.
- Saavedra, F. 2002. Testing climate change predictions with the subalpine species *Delphinium nuttallianum*. Pages 201–249 in S. Schneider and T. Root, editors. *Wildlife responses to climate change: North American studies*. Island Press, Washington, D.C., USA.
- Sakai, A., and W. Larcher. 1987. Frost survival of plants: responses and adaptation to freezing stress. Springer-Verlag, Berlin, Germany.
- Saunders, S., C. H. Montgomery, T. Easley, and T. Spencer. 2008. Hotter and drier: the West's changed climate. The Rocky Mountain Climate Organization and the Natural Resources Defense Council, New York, New York, USA.
- Smith, N. G., and J. S. Dukes. 2013. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO₂. *Global Change Biology* 19:45–63.
- Smith, E. M., and E. B. Hadley. 1974. Photosynthetic and respiratory acclimation to temperature in *Ledum groenlandicum* populations. *Arctic and Alpine Research* 6:13–27.
- Starr, G., and S. F. Oberbauer. 2003. Photosynthesis of Arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* 84: 1415–1420.
- Taschler, D., and G. Neuner. 2004. Summer frost resistance and freezing patterns measured in situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. *Plant, Cell and Environment* 27:737–746.
- Van der Wal, R., N. Madan, S. Van Lieshout, C. Dormann, R. Langvatn, and S. D. Albon. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* 123:108–115.
- Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B: Biological Sciences* 268:289–294.

- Walker, M. D., R. C. Ingersoll, and P. J. Webber. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 76:1067–1083.
- Wipf, S. 2010. Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology* 207:53–66.
- Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change* 94:105–121.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1745/full>