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Experimentally simulating environmental change in a montane meadow system via reduced snowpack and passive warming: soil and plant responses

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Experimentally simulating environmental change in a montane meadow system via reduced snowpack and passive warming: soil and plant responses

by

Jill Ann Sherwood

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This thesis is dedicated to everyone who believed in me.

Especially Amber Nicole Stumbaugh.
Your wisdom, strength, humor, perservence, and love will always live within me.
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CHAPTER 1. GENERAL INTRODUCTION

Introduction

Increasing evidence predicts that global climatic patterns are changing rapidly as a result of anthropogenic production of greenhouse gases, including CO$_2$ (IPCC 2007). Atmosphere-Ocean General Circulation Model (AOGCM) simulations for the Intergovernmental Panel on Climate Change (IPCC) estimate a 1.4° - 5.8°C temperature increase during the period from 1990–2100 (Cubasch et al., 2001; Notaro et al., 2006). The degree of warming is not, however, occurring at the same rate or direction in all locations. Models show that high altitude and latitude regions will experience a greater degree of warming, and that warming is more pronounced in the winter than the summer (Mote et al., 2005; Trenberth et al., 2007). In addition, models predict an increase in cloudiness will result in less radiant heat loss at night thus leading to a faster increase in nighttime temperatures than daytime temperatures (Alward et al., 1999). The impacts of increasing temperatures are already apparent in advancement of spring events (such as flowering), and have been recorded in many species (Beebee, 1995; Bradley et al., 1999; Walther et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003). In addition, increased temperatures are also likely to affect other abiotic factors, such as the amount of winter snow cover and the timing of springtime snowmelt.

Snow cover in the Northern hemisphere has been rapidly decreasing, mainly due to an earlier snowmelt (Brown, 2000; Frei & Robinson 1999; Rikiishi et al., 2004). The duration of the snow-free period between 1972 and 2000 in the Northern Hemisphere has increased by five to six days per decade, while disappearance of spring snow cover has been three to five days earlier per decade (Dye 2002; Bjork & Molau 2007). Regional models of global climate change within the Rocky Mountains region predict not only warmer temperatures, but also diminished amounts of precipitation falling as snow, decreased snowpack, and an increase in extreme weather events (Reiners et al., 2003; Zimmerman et al., 2006; Adam
et al., 2009). Since the 1970s, snow pack has declined in the mountains of the western United States due to rising temperatures, leading to advancement in snowmelt date (Clow, 2010).

Many ecological processes are closely linked to the timing of snowmelt. Snowpack volume is directly correlated with snowmelt date (Ostler et al., 1982; Price & Waser, 1998). Shallow snow packs melt earlier than heavy snow packs and typically result in an earlier growing season (Price & Waser, 1998; Arft et al., 1999; Inouye et al., 2002; Dunne et al., 2003). Snow is a crucial factor in systems where snow melt determines the start and length of the growing season, and that also rely on winter snow pack for the majority of available water during the summer. Phenology, the study of the timing of recurring natural events, can be a tool for assessing climate change impacts on plant growth and development. Responses to climatic changes are likely to have a wide variability across species, even when subjected to similar climatic trends (Parmesan & Yohe, 2003; Visser & Both, 2005; Parmesan, 2006). Climate warming has already affected the phenology of a number of species over the past 20 to 140 years (Walther et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003). The most important factors for plant development are temperature, date of snowmelt, and photoperiod (e.g. Price & Waser, 1998; Blionis et al., 2001; Keller & Korner, 2003). In montane systems, plant phenologies are closely related to snowmelt timing and early season temperature regimes (Billings & Bliss, 1959; Fareed & Caldwell, 1975; Galen & Stanton, 1991; Kudo, 1992; Walker et al., 1995; Inouye et al., 2002; Totland & Alatalo 2002; Dunne et al., 2003) and snowmelt date is a good predictor of flowering time (Inouye et al., 2002). Dunne et al., (2003) studied the effects of climate change on flowering phenology in subalpine meadows. The results from that study showed that the timing of flowering in most species was consistently and strongly related to date of snowmelt for all spatial scales studied, especially in earlier flowering species. Snow is also important for thermal insulation, which is regulated by depth and density of the snow pack. Extreme temperatures are dampened at the soil surface directly under the snow,
and many organisms rely on the insulating capacity of snow cover for heat retention when temperatures are near freezing (Billings & Bliss, 1959; Marchand, 1987; Halfpenny & Ozanne, 1989; Auerbach & Halfpenny, 1991; Pomeroy & Brun, 1999; Jones & Pomeroy, 1999). Monson et al., (2006) reported that shallower snow packs have less insulation potential, resulting in colder soil temperatures. In montane regions, such as those found in the Greater Yellowstone Ecosystem where springtime temperatures fluctuate above and below freezing, potential melting of snow cover during the first warm spring days, followed by periods of cold weather and below freezing temperatures, leads to more plant exposure to frost and freezing temperatures. Thus, under a climate with less snow and earlier snowmelt, montane plants could face a trade-off between exploiting the prolonged growing season and experiencing greater frost events and lower overall temperatures.

Increasing temperatures, decreasing snowpack, and advancing snowmelt dates will likely have impacts on ecological communities at a variety of levels, from the individual to the population, community, and ecosystem. The challenge for scientists studying climate change is to quantify these responses. Scientists must carefully select study organisms that are good indicators of such changes. In order to predict how montane plants will respond to climate change, it is necessary to understand key phenological and growth responses to climatic conditions. Given that montane meadow plants are highly sensitive to variations in precipitation and temperature, they can provide us with a study system useful in understanding potential future climatic changes.

There have been several experimental studies assessing the effects of a changing abiotic environment (e.g., shifts in the date of snowmelt or warming) on plant phenology. However, as far as we know, there have been only a few experimental studies examining increasing nighttime temperatures in combination with snow manipulation. In this study, we utilized open-sided passive warming chambers that are believed to increase minimum nighttime
temperatures. We also performed springtime snow removal to mimic a decrease in snow cover. We examined the effects of these treatments on soil moisture and soil temperature. We also studied responses from the perspective of plant phenology to determine whether increasing minimum temperatures or decreasing soil moisture would affect their development.

**Thesis Organization**

This thesis is organized into three chapters. Chapter 1 is a general introduction to the research presented in chapter 2. Chapter 2 is an article to be submitted for publication to *Global Change Biology*. It focuses on original research that I conducted to first, test whether passive warming chambers and snow removal would alter temperature and available soil moisture, and secondly, to study the effects of altering soil moisture and temperature on selected montane meadow plants. Chapter 3 provides an overall conclusion to this research.

**References**


CHAPTER 2. EXPERIMENTALLY SIMULATING CLIMATE CHANGE IN A MONTANE MEADOW SYSTEM VIA REDUCED SNOWPACK AND PASSIVE WARMING: SOIL AND PLANT RESPONSES

A paper to be submitted to Global Change Biology

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Abstract
Global and regional climate patterns suggest that the environment in the western United States is trending towards warmer and drier conditions. The ecological effects of climate change could include shifts in distribution and phenological changes for many plants and animals. This study provides an initial examination of climatic and phenological (timing of key biological events) trends in an effort to understand how montane plants may be affected by climatic changes. To explore the consequences of increased temperatures and decreased snow cover, we conducted an experiment in a montane meadow where snow removal and passive heating were used to mimic the effects of predicted environmental changes. We manipulated soil temperature using open-sided passive warming chambers, and soil moisture by manually removing snow in the spring of 2010 and 2011. Our treatments included control, snow removal, passive warming, and snow removal + passive warming. We measured soil temperature at the surface and soil moisture at a 25cm depth to confirm that open-sided passive warming chambers and manual snow removal had the intended effects on temperature and moisture. In 2011, we recorded plant phenological response dates for emergence (green-up), budding, flowering, and senescence in three common perennial plants (Arrowleaf Balsamroot (*Balsamorhiza sagitatta*), Wild Buckwheat (*Eriogonum umbellatum*), and Western Groundsel (*Senecio integerrimus*)) in each of the treatments. Frost damage was recorded in Arrowleaf Balsamroot (*Balsamorhiza sagitatta*) in 2011.

We concluded that open-sided passive warming chambers significantly increased soil minimum nighttime temperatures at a 25 cm depth but had no impact on maximum daily temperatures. The range between the 25 cm soil maximum daily temperature and the minimum daily was significantly increased due to the increase in minimum temperatures. Soil moisture at 25 cm depth was decreased throughout the season in the snow removal treatment when compared to the control in 2011 but not 2010, when there was less snow to remove. Soil moisture was not significantly different in 2010 or 2011 when any of the other treatments were compared.
Plant responses to the treatments differed between the three species measured. Time to emergence was significantly increased in *B. sagitatta* in the snow removal and passive warming treatments but not when snow removal and passive warming were combined. Budding time was also advanced in *B. sagitatta* in the snow removal and snow removal + passive warming treatments but not the passive warming only treatments. Green-up time was advanced in *E. umbellatum* in the snow removal and snow removal + passive warming treatments. The treatments had no impact on the *S. integerrimus*.

**Introduction**

Future climate change predictions point to temperature increases, changes in precipitation, and the occurrence of increased extreme weather events (King 2005; Tebaldi *et al.*, 2006; IPCC 2007). Global climatic patterns have shown increased temperatures since the 1970s (IPCC 2007). Warming over land surfaces has increased, primarily due to an increase in the nighttime minimum temperatures, which has been associated with an increase in cloudiness (Kukla *et al.*, 1994; Alward *et al.*, 1999). The increase in nighttime minimum temperatures has almost doubled that of the increase in daily maximum temperatures (Kukla *et al.*, 1994; Alward *et al.*, 1999). The consequences of increased daily minimum temperatures and warming are likely to impact ecosystems at multiple levels. A better understanding of how ecological systems are affected by changing conditions will be necessary for further mitigation of the effects of climate change on ecosystems.

Changes in ecosystems at higher altitudes and latitudes may be subject to larger, more rapid changes (Harte & Shaw 1995; Kim *et al.*, 2002; Thuiller *et al.*, 2005). During the period from 2003 – 2007, the western United States had an average increase of 3°Celsius when compared to the 20th century average (Saunders *et al.*, 2008). Temperature increases will likely lead to a decrease in the duration of snow cover (IPCC 2007). Climatic model predictions indicate a temperature increase as high as 4 – 5°C by the end of century and a 37% reduction in
snowpack (Zimmerman et al., 2006). Mote (2003) reported that springtime mountain snowpack showed widespread declines since 1950 at most locations, with largest declines at lower elevations, indicating temperature effects. It is also predicted that the snowline will recede to higher elevations with changes in global and regional climates (Regonda & Rajagopalan 2004; Stewart et al., 2004; Lapp et al., 2005).

Many montane systems, such as some areas found in Grand Teton National Park in the Rocky Mountains of the USA, are particularly dependent on water from snowmelt (Harte et al., 1992), and such systems are also defined by strong hydrological gradients (Debinski et al., 1999). In the montane systems of the Greater Yellowstone Ecosystem, the majority of the annual precipitation falls as snow (Shaw 1958; Harte et al., 1992; Mote 2003). These montane systems contain a diverse plant community that supports a wide variety of species including insects, birds, and mammals (Swanson et al., 2007). Since minimum nighttime temperatures are increasing at such a high rate, the impact and the associated consequences of these increases could include decreased duration and quantity of snowpack, longer growing seasons for plants, shifts in competitive interactions, or changes in the ratio of photosynthetic rate to respiratory rate in some plant species (Alward et al., 1999).

Plant physiology and plant productivity are sensitive to increases in minimum nighttime temperatures (Germino & Smith 1999; Wan et al., 2002; Zhou et al., 2007; Sherry et al., 2008). In addition, springtime snowmelt in high altitude settings influences the phenology of flowering forbs where snowpack is significant (Walker et al., 1995; Inouye 2008). Environmental changes (i.e. increasing temperatures), which may impact snow distribution and snow cover, have been shown to be tightly linked to shifts in plant phenologies (Walker et al., 1995; Inouye 2008; Wipf et al., 2009). The relationship between temperature and snowmelt and the associated plant responses highlight the importance of examining how these interactions may impact plant phenology and plant
community composition. Changing the timing of plant phenophases and growth exposes the plants to varying weather conditions, including late spring frosts, which increases the probability of frost damage (Inouye et al., 2002; Inouye 2008). Since snowpack acts as an insulator for plants and other organisms when springtime temperatures are below or near the freezing point, decreased snowpack or earlier snowmelt is likely to result in more frost damage to the plant tissues and buds of the earlier blooming plants. Thus, changes in minimum daily temperature and snow depth are likely to impact ecosystems in various ways at many different levels.

Experimental simulations of climate change have been useful in identifying the potential impacts of changing environmental conditions on ecosystems. Active (i.e. infrared lamps or heating cables) and passive warming methods (i.e. open-top chambers, shelters, or covers) have been used to increase temperatures (i.e. Kennedy 1994; Convey and Wynn-Williams 2002; Bokhurst, et al., 2008). Each warming method has advantages and disadvantages when used in ecosystem manipulations that include change in light or moisture regimes or alterations of wind patterns or atmospheric exposure (Beier et al., 2004). In addition, many of the warming experiments assume that daily maximum temperatures will be the driving force in ecosystem changes. Given that the daily minimum temperatures are increasing faster than daily maximum temperatures, it is important to evaluate alternative ways of experimentally simulating increased minimum temperatures that will have minimal impacts on light, moisture, wind and exposure.

Previous snow manipulation studies have shown that decreased snow depth and earlier snowmelt date results in earlier plant phenologies (i.e. Dunne et al., 2003; Aerts et al., 2004; Wipf et al., 2009; Wipf 2010). As more climate changes are observed and recorded throughout the world, it will become increasingly necessary to understand how these changes in daily minimum temperatures and snowpack may impact ecosystems. Therefore, it is important to study not only
how changing temperatures will impact systems but also how snowpack factors into these responses and the potential effect of the combination of increased temperature and decreased snow pack on ecosystems.

Here we present an experimental method for simulating expected changes in daily minimum temperatures and available snowpack associated with climate change using louvered open-sided chambers to passively increase minimum nighttime temperatures and manipulation of spring snowpack to decrease available moisture and insulation. We expected that the louvered open-sided chambers (OSCs) would increase minimum daily soil temperature, manipulating snow would lead to decreased soil moisture throughout the growing season, and the combination of these methods would have interactive effects. We used the open-sided passive warming chambers because of they were designed to reduce heat loss at night by decreasing long-wave infrared radiation loss at night. This results in an increase in the daily minimum temperature, which is consistent with temperature changes already being recorded. Treatment effects were compared to determine if they would result in changes to temperature and soil moisture. We also assessed the effects of the treatments on plant phenology and bud survival in dominant forbs in a montane meadow ecosystem.

The overall goal of this research was to quantify the effects of snow manipulation and passive warming on abiotic soil characteristics and plant phenologies of three plant species that are important nectar sources for the pollinator community (Auckland et al., 2004; Sherwood unpublished data). These analyses provide short-term indications of how climatic changes due to decreased available soil moisture and increased temperature are manifested in montane meadow plants.

Our experimental manipulations allowed us to test the following hypotheses:

1. Soil temperature under the passively warmed plots will be higher than the soil temperature in the unwarmed plots, and this difference will occur primarily at night, resulting in a decrease in the daily temperature range ($T_{\text{max}} - T_{\text{min}}$).
2. Soil moisture in the snow removal plots will be lower than the soil moisture in the plots where snow was not removed.
3. Earlier snowmelt from snowpack reduction will result in earlier emergence, flowering, and senescence of forbs.
4. Passive warming will result in earlier emergence, budding, flowering, and senescence of forbs.
5. Passive warming will result in less plant tissue damage and higher bud survival (resulting from exposure to freezing temperatures and frost), while snow removal will result in greater damage.
6. Combined effects of snow removal and passive warming on both soil moisture and plant responses will be stronger than either treatment alone.

**Materials and Methods**

The study was conducted in a flat sagebrush (*Artemisia sp.*) meadow at an elevation of 2100 meters within a relatively homogeneous plant community composition located in Grand Teton National Park, WY during 2010-2011. The vegetation within this meadow is a combination of sagebrush, flowering forbs and grasses with a high percentage cover of bare ground. The substrate consists of alluvium and cobbly, glacial outwash that were deposited after the Pinedale glaciers receded, resulting in a very permeable soil surface (NPS 2008). The regional climate is characterized by a mean annual precipitation of 63.9 cm, most of which falls as snow in the winter months. The region averages over 3 m of annual snow cover, with January having the greatest accumulation of approximately 1 m. Snow cover in the valley typically disappears in April or May. December and January are typically the coldest months with an average high of –3°C, while July and August are the warmest months (average high = 25°C, respectively) (Western Regional Climate Center). 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 senesce, are the grasses and forbs (Blaisdell 1958; Debinski *et al.*, 2000). 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).

We established twelve 2.5 m² plots at approximately 5 m distance apart and regularly assigned the following treatments to each of three plots: (1) passive warming (H), (2) snow removal (SR), (3) snow removal + passive warming (HSR) and (4) untreated controls (C). Sites were marked for the duration of the experiment by using 12 cm high 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 temperature manipulation used for the passive warming treatments was achieved using louvered open-sided chambers (OSC’s) (developed by Matthew Germino, USGS). The OSC’s were placed on the site at the time of snow removal (late April to early May, depending upon the year) and remained until the end of the growing season (late September to mid-October). The OSC’s consisted of two 1.25m x 2.5m wooden structures placed side by side on the treatment plot covering the 2.5m x 2.5m total plot area. The sides of the frames were open to the environment on all sides. The louvered tops of the OSC’s were comprised of 4cm wide x 1.25m long Optix® Acrylic panels placed at a 50 degree angle every 10cm. The panels were angled in opposite directions toward the center so that the panels met at an angle in the center of the OSC. The tops of the OSC’s were approximately 30 cm from the ground to account for the maximum height of the vegetation. The OSC’s were designed to slightly increase daily minimum temperatures (approximately 2°C) by reducing the amount of long-wave IR lost to the environment at night, thereby increasing the net balance of long-wave IR that would otherwise be radiated back to the environment. During the daytime, solar energy is accumulated under the OSC’s. The OSC’s used in this study are particularly ideal in environments, such as in montane meadows in Grand Teton National Park, dominated by mostly clear skies and minimal tree cover. We compared treatment effects by examining the
differences in soil daily maximum, daily minimum, and daily temperature range (difference between maximum and minimum) between the H and no H (unwarmed) treatments.

In the reduced snow depth treatments, snow cover was manually reduced using shovels to remove 1-3 m of snow in the spring of each year before snowmelt (late April to early May, depending upon the year). Our previous studies have shown that removing snow in early May in this region resulted in an almost 50% reduction in soil moisture throughout the growing season. A small amount of snow (approximately 2 cm) was left on the plots to reduce plant damage from the shovels. We were careful at the time of snow removal to avoid trampling the experimental area. If significant amounts of snow fell after the plots were set up, the snow was removed immediately.

A combination of passive 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.

Abiotic measures of soil characteristics, including soil moisture and soil temperature, were measured throughout the growing season. We installed Decagon 5TM soil moisture/temperature probes (Decagon Devices, Inc.) in the center of all of the plots at a 25 cm depth at the time of OSC placement and snow removal. Soil moisture was measured in 1-hour intervals using Em50 dataloggers (Decagon Devices, Inc.) from the time of snow removal until the end of the growing season in October.

In addition to the data collected on temperature and moisture, vegetation was surveyed during the growing season in 2011. The start of each phenophase (emergence/green-up, budding, flowering, and flower senescence) was recorded for the three dominant perennial plant species Arrowleaf Balsamroot (Balsamorhiza sagitatta), Wild Buckwheat (Eriogonum umbellatum), and Western
Groundsel (*Senecio integerrimus*) at least once weekly from the date of snowmelt and continuing through the summer months. Both *Balsamorhiza sagitatta* and *Senecio integerrimus* are deciduous perennial forbs whose shoots emerge from the soil in the spring and leaves die back in the fall. Therefore, the first phenological stage for these plant species is emergence. However, *Eriogonum umbellatum* is an herbaceous perennial evergreen with mat-like leaves which turn red in the fall. Therefore, the first phenological stage for *E. umbellatum* is the greening of leaves (not emergence), and our results for *E. umbellatum* include date of leaf green-up, whereas these data are not appropriate for the other two species. For *E. umbellatum*, we recorded the date at which approximately half of the leaves had turned green. Data for flower senescence in *E. umbellatum* were not included in the analyses because senescence was not captured in all plots during the field season due to constraints in field season length. The dates for each phenophase were recorded as the point in time when the majority of plants in the plots entered that phase. Frost-killed buds were measured and recorded during each sampling period.

**Statistical methods for soil moisture/temperature**

Non-parametric permutation statistical analyses were used to analyze soil moisture and temperatures differences of time series data between treatment groups where correlations exist among time points. Time series analyses were based on hourly data and each year was considered separately.

To test our hypotheses, we first identified the treatment groups being compared for each hypothesis. Treatments (C, H, SR, and HSR) were considered individually in the soil moisture analyses after initial testing revealed that soil moisture differed in treatments at points along the growing season. For example, when testing our hypothesis that soil moisture content in the snow removal plots would be higher than in the control plots, the two groups were defined by the two treatments (C and SR), where each contained three series (or replicates). Hypothesis testing for temperature differences was conducted differently than for
soil moisture. We combined all passively warmed plots (H and HSR) and all plots that were not passively warmed (C and SR) based on initial analyses showing that soil temperature at 25 cm did not differ significantly over the season in non-snow removal and snow removal plots. Therefore, when testing our hypothesis that the daily minimum temperatures are higher in the warmed plots compared to the unwarmed plots, we had two groups (unwarmed versus warmed) with six individual series (replicates) per treatment.

We next generated hourly time series plots using the median value (soil moisture or temperature) of the treatments within each group at every time point throughout the growing season. With times series denoted by $M_1$ and $M_2$, and subscripts denoting treatment group, we calculated the difference between the median values for every time point, where the difference $D = M_1 - M_2$, resulting in a difference time series $D$. The comparison between the time series was then reformulated in terms of the difference series $D$. To test whether the series $D$ was statistically significant, we defined a difference index. While there may be several ways to approach this problem, we based our analysis on the calculation of the area under the curve, which we denote by $A$. The main advantage of using the area under the curve as a comparison index is that we do not ignore the fact that data were collected in a sequential fashion (i.e., over time), as would the sample average or the median of the time series $D$. We compute the area under the curve numerically, using Simpson's rule, implemented in the package StreamMetabolism within the statistical software R (R development Core Team).

To assess the statistical significance of the observed difference, denoted here by $A_{obs}$, we constructed a permutation test. Permutation tests (also known as randomization tests) were originally introduced by R. A. Fisher (1935). The governing principle for this test is that the distribution of the desired test statistic under the null hypothesis is generated by computing the test statistic for all possible rearrangements of the data. If the observed test statistic is very unlikely under this distribution, there is strong support for the alternative hypothesis.
For our purposes, the rearrangements consisted of changing group membership. Under the null hypothesis of no difference between the groups, we redefined group membership for all the treatments by randomly permuting the treatments between the two groups, and keeping the group size (number of series) the same as the original one. For each rearrangement \( i \), we computed the difference curve, \( D_i \), and obtained the area under that curve \( A_i \), \( i = 1, \ldots, N \), where \( N \) is the number of all possible permutations of the series between the two groups. The probability (\( p \)-value) that there is a statistically significant difference between the groups is calculated as the number of \( A_i \) that are more extreme than \( A_{\text{obs}} \), divided by the total number of permutations. When comparing groups which contain only three replicate series, there were only 20 total possible combinations, and so the maximum attainable significance level is 1/20, or 0.05.

Significant differences were determined in three ways. First, we looked at the \( p \)-value for each hypothesis. However, due to the limitations of the available data in some cases, it was impossible to obtain \( p \)-values lower than the often used significance level of 0.05. Given that we are not able to achieve a value less than 0.05 by design, we generated histograms of all possible values of \( A_i \), and compared the location of the observed difference, \( A_{\text{obs}} \), within the distribution of all the values of \( A_i \) from the permutation test. If \( A_{\text{obs}} \) lies within the distribution, then we concluded that there were no differences between groups. And finally, we plotted all the difference series obtained in the permutation test to account for the time component. From this we identified the observed series. If the observed series was fully contained within the set of possible series, we concluded that there were no differences.
Statistical methods for assessing change in plant phenology

Our analysis of the plant data was based on mean dates for each phenological stage and the average number of frost-killed buds. Because of the nature of these data, we used simple statistical methods to determine if there were differences between treatments (C, H, SR, and HSR). Differences in the mean date for each phenological phase (emergence, budding, flowering, and senescence) and average number of frost-killed buds were evaluated with pairwise t-tests comparing each treatment (snow removal, passive warming and snow removal + passive warming) with the control. In addition, we evaluated differences between all treatments because we hypothesized that the combination of snow removal + passive warming would show a greater phenological plant response than any other treatment (C, H, SR), and also that the passive warming treatments would serve to protect the plants from frost damage. Statistical analyses for plant phenology and frost damage were performed in SAS 9.2 (SAS Institute).

Results

Soil temperature at 25cm depth:

Time series data for both maximum and minimum temperatures were plotted throughout the growing season for 2010 and 2011 (Fig. 1). Our results supported the hypothesis that the daily minimum soil temperature at 25cm under the open-sided chambers (passive warming) remained higher than the soil temperature in the unwarmed plots (minimum daily soil temperatures under the open-sided chambers were ~1-5 °C higher than the soil temperatures without passive warming). These results were consistent between 2010, shown in Figure 2, (p=0.005) and 2011 (p= 0.017), data not shown. The degree of difference between the minimum daily temperatures in passively warmed and unwarmed plots varied throughout the growing season with the largest differences occurring after mid-summer (Fig. 1). A comparison of the soil temperature in the warming treatment versus the unwarmed treatment revealed that daily maximum soil
temperature was not significantly different over the growing season between the treatments in either 2010 or 2011 (Fig. 1). In addition, an examination of the temperature range (difference between the daily maximum temperature and the daily minimum temperature) revealed that the temperature range in the warming treatments was lower than the range in the unwarmed treatments. In 2010, the range was moderately significant with p=0.057 (Fig. 2) while the range difference in 2011 was statistically significant with p=0.01 (data not shown). These results reinforce the hypothesis that the warming treatments suffer less heat loss and therefore maintain a higher nighttime temperature.

Soil moisture at 25cm depth:

The median soil moisture values at 25cm depth for each time series were plotted for 2010 and 2011 over the growing season (Fig. 3). Examination of the graphs for 2010 reveals that there may be a difference in soil moisture between control and snow removal treatments during the first part of the growing season, but very little difference exists during the second part of the growing season. The difference in soil moisture for 2011, however, is large throughout the entire growing season. In order to test if the differences are statistically significant, we compare the results of the permutation tests between individual treatments.

Permutation tests comparing the individual treatments of control versus snow removal indicate that there are no significant differences between the treatments in 2010. The observed test statistic lies well within the range of all possible values (dotted line in the top left panel in Fig.4), and in the series of differences (dark line in the bottom left panel in Fig. 4). However, in 2011, the differences were statistically significant (Fig. 4: p =0.05). In addition, both the observed test statistic and the difference series have the highest values throughout the time period measured (Fig. 4; right top and bottom panels, respectively), indicating a consistent difference over the growing season.
When examining the graphs of the median soil moisture values in the comparison of the control versus passive warming treatments, there appears to be no difference between the treatments in 2010 or 2011 (Fig. 5). Tests of the differences support the conclusion that there are no differences in soil moisture between the control and warming treatments in either year for the entire growing season (Fig. 5; p=0.7, both years).

The overall soil moisture trend in median time series graphs for 2010 and 2011 indicates that soil moisture was lower in the snow removal + passive warming treatments when compared with the control. However, permutation tests revealed no significant differences between these treatments for either year.

Finally, we tested the differences between the snow removal + passive warming treatments and all of the other treatments to determine whether there were larger differences in soil moisture when snow removal was combined with passive warming. Graphs of the median soil moisture values over the time period in 2011 indicate that the soil moisture in snow removal + passive warming treatment is lower than the median of all of the other treatments. This trend remains when each of the treatments (control, snow removal, and passive warming) are compared individually (data not shown). This is consistent with the data from 2010. However, the results from the permutation tests indicate that there were no statistically significant differences when the snow removal + passive warming treatment was compared individually to each of the other treatments, or to the group of all other treatments combined (Table 1).

**Plant Phenology**

The snow removal treatment affected the phenology of two of the three most abundant plant species *Balsamorhiza sagitatta* and *Eriogonum umbellatum*, but the effects were manifested in different ways. Shoots of *B. sagitatta* had already emerged in the snow removal treatments when we first started measuring plant phenology. Based on the height of the shoots in non-snow removal plots, we
were able to determine an approximate date for shoot emergence in the snow removal plots by comparing shoot heights. The approximate emergence dates for the snow removal and snow removal + passive warming treatments were very similar. There were also no significant differences between control and passive warming only. However, the removal of snow tended to advance shoot emergence date in *B. sagitatta* by approximately 3-4 days when compared with control and passive warming (*p*-value=0.002). In addition, snow removal + passive warming advanced emergence when compared with control and passive warming only (*p*-value=0.022). For *E. umbellatum*, the date at which approximately half of the leaves were green, was advanced by an average of 11 days in the snow removal treatment (*p*-value = 0.007) and 14 days in the snow removal + passive warming treatment (*p*-value = 0.0015) when compared with control. When comparing plots that had the snow removal treatment (+/- passive warming), we also found a significantly advanced green-up in *E. umbellatum* when compared with the passive warming treatment only (Fig. 6). The snow removal treatment advanced green-up date by approximately 8 days (*p*-value = 0.02) and the snow removal + passive warming treatment advanced green-up date by approximately 12 days (*p*-value=0.004) compared to the passive warming only treatment. In addition, the plots that had passive warming + snow removal had slightly advanced green-up dates when compared to controls, although the results were not significant. There were no differences between the snow removal and snow removal + passive warming treatments (Fig. 6).

Budding, flowering, and senescence patterns also differed among species in response to treatments. The snow removal treatment significantly increased budding date in *B. sagitatta* by approximately 10 days when compared with the control (*p*-value= 0.02) and 18 days when compared with passive warming only (*p*-value=0.0007). There was also a significant advance in budding date (~16 days) between the passive warming only and snow removal + passive warming treatments (*p*-value=0.0015). There were no statistically significant differences in budding date between the snow removal treatments and the snow removal +
passive warming in *B. sagitatta*. The snow removal, passive warming treatments or the combination had no effect on the time to bud or flower in *E. umbellatum*.

Senescence date of the *B. sagitatta* flowers tended to be earlier in snow removal plots, although this difference was not statistically significant. The snow removal, passive warming treatments, and the combination of treatments had no effect on the time to bud or flower in *E. umbellatum*. We were unable to record flower senescence in *E. umbellatum* in all of the plots; therefore, our analysis did not include this phenological state in this species.

There were no statistically significant differences in plant phenology for *S. integrerrimus* with any of the treatments.

**Frost Damage**

The proportion of frost-killed flower buds was a response variable observed only in *B. sagitatta*, because it is the earliest species to emerge and flower. The proportion of frost-killed flower buds in *B. sagitatta* was significantly higher in the plots where the snow was removed. The average number of frost-killed buds in the snow removal treatment was 0.71, while the average in the control plots was 0.39. The average number of frost-killed buds in the snow removal treatment was significantly greater than all other treatments (Table 2). In addition, the average number of frost-killed buds was also significantly higher in the control when compared with the passive warming and snow removal + passive warming treatments. There were no frost-killed buds in either *E. umbellatum* or *S. integrerrimus* because both of these plant species emerge and flower later in the season.

**Discussion**

Climate predictions for the western United States, and specifically regions above 2,000 m in elevation, indicate that minimum daily temperatures are increasing and snow pack is decreasing. Our first objective in this study was to test whether
we could alter environmental conditions (soil temperature and soil moisture at 25cm depth) using open-sided passive warming chambers and snow removal methods. Our results confirm that the open-sided chamber design can successfully simulate the predicted increase in minimum daily temperatures without affecting maximum daily temperatures. The temperature under the warming chambers was consistently higher in the plots that were covered with open-sided warming chambers. Climate change predictions indicate that the minimum daily temperatures are increasing at a faster rate than the daily maximum temperatures (IPCC 2007). The increase in daily minimum temperatures can affect ecosystems at many levels. Specifically, plants exposed to higher daily minimum temperatures may experience higher respiration rates without an increase in photosynthetic rates, which can lead to a decrease in plant productivity and growth (Hughes 2000). Higher nighttime respiration rates have been linked with decreases in plant productivity and yield in some plant species (Paembonan et al., 1992; Albrizio & Steduto, 2003; Mohammed & Tarpley 2009). However, an increase in daily minimum temperatures has the potential to lead to changes in plant communities, as some plant species have the potential to respond favorably to changing conditions which could be detrimental to others.

Based on previous studies, we hypothesized that springtime snow removal could, in fact, lead to a decrease in soil moisture that would be evident throughout the growing season. We were able to show that in years with sufficient snow (e.g., 2011), snow removal can reduce soil moisture at a 25cm depth throughout the season. Soil moisture was not significantly different between the snow removal and non-snow removal plots in 2010. Our hypothesis that the addition of passive warming would exacerbate the effects of the snow removal treatment and further reduce soil moisture was not consistent between the years. The warming + snow removal treatment in 2010 exhibited lower soil moisture when compared with the other treatments, but this difference was not seen in 2011. In some cases in 2011, the soil moisture was slightly higher in plots that were passively warmed, although not significantly. One explanation for why these differences might have
occurred relates the average snow depth per year. In 2010, average snow depth in the plots at the time of snow removal was approximately 0.25 m, whereas, average snow depth in the plots at the time of snow removal in 2011 was approximately 1 m. The small amount of snow in 2010 may not have provided enough soil moisture, especially at the 25cm depth, to create significant differences when comparing the snow removal treatments with the non-snow removal treatments. Therefore, we suspect that the differences noted in the warming + snow removal treatments between the years may also be attributed to snow depth.

Utilizing these simulation methods, we observed effects on plant phenology that provide important insights into what we might expect from the predicted changes in climate. Differences in the timing of phenophases were noted among the different treatments in two of the three plant species. These manifestations of differences were not uniform among the plant species, but each of these species has a slightly different life form, and as such the interspecific differences may not be so surprising. The timing of the first phenophase (emergence or green-up) was significantly earlier in two species, *Balsamorhiza sagitatta* and *Eriogonum umbellatum* when snow was removed. The *E. umbellatum* plants that were exposed to the snow removal and passive warming + snow removal treatments greened-up an average of 8 - 14 days earlier than those in the control and passive warming treatments. Snow removal and passive warming advanced the phenology (emergence and bud date) of *Balsamorhiza sagitatta*. 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 (Starr & Oberbauer 2003, van der Wal et al., 2000; Saavedra 2002). 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. Decreasing snow cover also leaves the plants exposed to lower temperatures and potential frost events because snow acts as an insulator.
Previous studies have examined the role that frost events may play in the survival, growth, and reproduction of alpine plants (Germino & Smith 1999; Inouye 2000; Inouye et al., 2002; Inouye 2008). It is predicted that the number of low temperature events could increase if the snow free season is extended due to earlier snowmelt (Groffman et al., 2001; IPCC 2007). Thus, earlier plant emergence and development due to advanced snowmelt date could lead to more frequent and more serious frost damage (Molau, 1997; Price & Waser, 1998; Inouye et al., 2002). We were able to show in our snow removal plots that frost damage in an early emerging species does, in fact, occur. However, those damage events may be less likely to occur with increases in minimum nighttime temperatures, as was shown by the snow removal + open-sided passive warming chambers. Therefore, decreasing snow cover and increasing nighttime temperatures may cancel out the negative impacts from frost damage.

The results from this study provide insight into how climate change could change the phenology of montane meadow plants, and ultimately impact ecosystem processes. Our field experiment revealed that reduced snow cover and increased minimum daily temperatures has the potential to change the phenology of montane meadow plants, but these changes may depend on the plant’s lifecycle and growth patterns. Therefore, climate change simulation studies, such as this, have potential issues that confound interpretation of the results. Given the difference in snowfall between 2010 and 2011, it is difficult to accurately predict the effects of snow cover reduction on soil moisture between years because environmental conditions were not similar. In addition, the interpretation of the soil moisture results was directly affected by the amount of soil moisture available. Further, temperature, precipitation, photoperiod, nutrient availability, and other outside factors can affect plant growth. Therefore, it can be challenging to separate the interacting factors and confidently state that one factor is, indeed, the causal factor. Despite these challenges, climate change simulation experiments are informative in testing specific abiotic and biotic responses. As with many other fields of ecology, longer-term studies and interdisciplinary
approaches that incorporate physiology, growth, reproductive, and landscape interactions will help to more fully discover the drivers of the change in plant phenology and potential impacts on ecosystems.

Acknowledgements
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References


Table 1. Results of the permutation tests for physical soil measurements based on the hypotheses presented. Number of extremes (defined as values greater than the observed value) was calculated from the permutation test and used to calculate p-values. Significant p-values (defined as 0.05 or less) are indicated in bold font. Moderately significant p-values (defined as values approaching 0.05) are in italics. Abbreviations for the treatments in soil moisture results are as follows: C = Control; SR = snow removal only; H = passive warming only; HSR = snow removal + passive warming.

<table>
<thead>
<tr>
<th>Year</th>
<th>Variable tested</th>
<th>Hypothesis</th>
<th>p-value</th>
<th>Number of extremes per total permutations</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>Soil Moisture (25cm)</td>
<td>HSR &lt; All treatments</td>
<td>0.170</td>
<td>38 of 220</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HSR &lt; C</td>
<td>0.350</td>
<td>7 of 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HSR &lt; SR</td>
<td>0.100</td>
<td>2 of 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HSR &lt; H</td>
<td>0.200</td>
<td>4 of 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SR &lt; C</td>
<td>0.700</td>
<td>14 of 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H &lt; C</td>
<td>0.700</td>
<td>14 of 20</td>
</tr>
<tr>
<td></td>
<td>Max Soil Temperature Tmax</td>
<td>unwarmed = warmed (C, SR) = (H, HSR)</td>
<td>0.600</td>
<td>554 of 924</td>
</tr>
<tr>
<td></td>
<td>Min Soil Temperature Tmin</td>
<td>unwarmed &lt; warmed (C, SR) &lt; (H, HSR)</td>
<td><strong>0.005</strong></td>
<td>5 of 924</td>
</tr>
<tr>
<td></td>
<td>Soil Temperature Range (Tmax - Tmin)</td>
<td>unwarmed &lt; warmed (C, SR) &gt; (H, HSR)</td>
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<td>53 of 924</td>
</tr>
<tr>
<td>2011</td>
<td>Soil Moisture (25cm)</td>
<td>HSR &lt; All treatments</td>
<td>0.190</td>
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<td></td>
<td>HSR &lt; SR</td>
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<td></td>
<td></td>
<td>HSR &lt; H</td>
<td>0.100</td>
<td>2 of 20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SR &lt; C</td>
<td><strong>0.050</strong></td>
<td>1 of 20</td>
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<tr>
<td></td>
<td></td>
<td>H &lt; C</td>
<td>0.700</td>
<td>14 of 20</td>
</tr>
<tr>
<td></td>
<td>Max Soil Temperature Tmax</td>
<td>unwarmed = warmed (C, SR) = (H, HSR)</td>
<td>0.786</td>
<td>726 of 924</td>
</tr>
<tr>
<td></td>
<td>Min Soil Temperature Tmin</td>
<td>unwarmed &lt; warmed (C, SR) &lt; (H, HSR)</td>
<td><strong>0.017</strong></td>
<td>65 of 924</td>
</tr>
<tr>
<td></td>
<td>Soil Temperature Range (Tmax - Tmin)</td>
<td>unwarmed &lt; warmed (C, SR) &lt; (H, HSR)</td>
<td><strong>0.011</strong></td>
<td>10 of 924</td>
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Table 2. Summary of the pairwise $t$-test results from the comparison of the means of average number of frost-killed buds by treatment. Significant $p$-values (defined as 0.05 or less) are indicated in bold font.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Comparison Treatment</th>
<th>Difference in means</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Snow Removal</td>
<td>0.3173004</td>
<td>0.0388</td>
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<tr>
<td>Control</td>
<td>Passive Warming</td>
<td>0.3756729</td>
<td>0.0192</td>
</tr>
<tr>
<td>Control</td>
<td>Snow Removal + Passive Warming</td>
<td>0.3732919</td>
<td>0.0197</td>
</tr>
<tr>
<td>Snow Removal</td>
<td>Passive Warming</td>
<td>0.6929733</td>
<td>0.0007</td>
</tr>
<tr>
<td>Snow Removal</td>
<td>Snow Removal + Passive Warming</td>
<td>0.6905923</td>
<td>0.0007</td>
</tr>
<tr>
<td>Snow Removal + Passive Warming</td>
<td>Passive Warming</td>
<td>0.002381</td>
<td>0.9857</td>
</tr>
</tbody>
</table>
Figure 1

a) 2010

b) 2011
Figure 2

- Daily RANGE
  - $p$-value = 0.57

- Daily MAX
  - $p$-value = 0.601

- Daily MIN
  - $p$-value = 0.005
Figure 3

Volumetric Water Content (m$^3$/m$^3$)

Time
(days since January 1)

- Snow Removal 2011
- Control 2011
- Snow Removal 2010
- Control 2010
Figure 4

2010

\[ p\text{-value}=0.7 \]

2011

\[ p\text{-value}=0.05 \]

Frequency

Integrated Difference

Volumetric Water Content Difference (m^3/m^3)

Time (days since January 1)
Figure 5

Volumetric Water Content (m$^3$/m$^3$)

Time (days since January 1)

Heating, 2011
Control, 2011
Heating, 2010
Control, 2010

2010
$p$-value=0.7

2011
$p$-value=0.7

Frequency

Integrated Difference

Integrated Difference
Figure 6

(a) 

(b)
FIGURE LEGENDS

Figure 1: Time series of the Minimum (Min) and Maximum (Max) Daily Temperatures for 2010 (top) and 2011 (bottom) showing temperature differences between the unwarmed and the passively warmed plots (warmed) over the course of the growing season. Solid lines are maximum daily temperatures. The dashed lines represent minimum daily temperatures. Black lines depict unwarmed values. Red lines represent warmed values.

Figure 2: Results of the Randomization Tests for Temperature, 2010. The first row of graphs shows the histograms of the sampling distribution for the corresponding test statistic, with the observed test statistic marked by the vertical dotted line, for each of the three characteristics analyzed (daily minimum temperatures, daily maximum temperatures, daily temperature ranges). The second row shows (in grey) all the possible time series of the differences in daily minimum temperatures, daily maximum temperatures, or daily temperature ranges between the two groups (Heating and No Heating). The corresponding observed time series of differences is marked by the solid black line.

Figure 3: Summary time series of the median volumetric water content of the soil (soil moisture) for the data collected in the Control and Snow Removal plots for both 2010 and 2011. Each summary series is computed as the median hourly value for the plots that received the snow removal treatment (red line) and the plots where the snow was not removed (black line).

Figure 4: Results of the Randomization Tests for comparing Soil Moisture in the Passive Warming and Control treatments. The first row of graphs shows the histograms of the sampling distribution for the corresponding test statistic, with the observed test statistic marked by the vertical dotted line. The second row shows (in grey) all the possible time series of the differences in soil moisture between the two treatments. The corresponding observed time series of differences is marked by the solid black line.
**Figure 5:** Summary time series and randomization test results for the comparison of volumetric water content (soil moisture) between control and passively warmed (heated). The top plot shows the summary series of the soil moisture for the data collected in the control and passively warmed plots. Each summary series is computed as the median hourly value for the data in each of the three plots corresponding to a treatment, separately, for 2010 and 2011. The graphs on the bottom show the histograms of the sampling distribution for the corresponding test statistic, with the observed test statistic marked by the vertical dotted line.

**Figure 6:** The phenology of montane meadow species after manipulations of snow depth and passive warming: a) *Balsamorhiza sagitatta*, and b) *Eriogonum umbellatum*. Bars represent the mean date when a phenological stage was reached; error bars=1SE.
CHAPTER 3. GENERAL CONCLUSIONS

Anthropogenic climate change is expected to dramatically alter the natural fluctuations in precipitation and temperature (Easterling et al., 2000; Houghton et al., 2001; Alley et al., 2003; Alley et al., 2007). Increased inter and intra annual variability in rainfall is expected, with mean annual air temperatures rising 4°C by the year 2100 (Christensen et al., 2007). Future projections of precipitation in the western United States point to a decrease in snow cover and increase in temperatures. Understanding the influences of decreased snowpack and earlier snowmelt date will have major implications throughout many ecological systems. Plants are able to respond to the current levels of climate variability, but we need to be able to better predict how plants will respond to predicted climate change scenarios.

This study was conducted in an effort to better understand whether our chosen methods of utilizing springtime snow removal to decrease soil moisture and using open-sided passive warming structures to increase minimum daily soil temperatures would provide us with the expected changes in soil moisture, soil temperature, and plant phenological responses. In our analyses, we were able to confirm that the open-sided passive warming chambers did, in fact, increase minimum daily soil temperatures, without affecting maximum daily temperatures, resulting in a decrease in the range between the maximum and minimum daily temperatures. This was fairly consistent between 2010 and 2011. However, our attempt to experimentally reduce soil moisture at a 25cm depth did not provide consistent results between the two years. Soil moisture differences among treatments were only significant in 2011 when the snow removal treatment was compared with the control. In the Greater Yellowstone Ecosystem, there is a considerable natural variability of the snow cover, and traits related to snow cover such as timing of snowmelt, mainly as a result of fluctuations in precipitation and temperature. Therefore, it is possible that interannual variation results in variability between years. In addition, because we used a time-series
approach to analyses, soil moisture was averaged over the entire growing season despite the fact that there was variability within the season. Future analyses might include examining soil moisture and temperature differences at certain specific times during the growing season. This might provide us with a better understanding of how the soil moisture might change during the growing season.

Our results from the plant phenology studies varied among species, with *Balsamorhiza sagitatta* showing a response to the snow removal and passive warming treatments via advanced emergence. Budding dates of *B. sagitatta* were advanced in snow removal + passive warming when compared with control plots. *Eriogonum umbellatum* showed an earlier green-up in response to snow removal, and the combination of snow removal + passive warming advanced budding time. The treatments had no effect on the phenology of *Senecio integrerrimus*. Given the different natural histories and growth characteristics of the three plant species, it isn’t surprising that they responded in different ways.

The impacts of climate change are a central issue of the 21st century that will require the efforts of many people working from different angles. Information gained from climate change research has the potential to play an important role in the formation of climate change policies and conservation strategies. Scientific evidence can provide managers and policy makers a basis for decision-making. This research provided important contributions to the understanding of the impacts of climate change by improving our understanding how plant species may respond to environmental changes. And finally, this study helped to fill current gaps in knowledge, but additional research is needed to better understand the complex mechanisms and interactions that drive plant phenology across species.
APPENDIX A. EXPERIMENTAL DESIGN PHOTOS FOR CHAPTER 2

Control: No Treatment

Passive Warming

Snow Removal

Passive Warming and Snow Removal
APPENDIX B. SUPPLEMENTAL FIGURES FOR CHAPTER 2

![Histograms for daily minimum, maximum, and temperature range](image)

Figure 1: Results of the Randomization Tests for Temperature, 2011. The first row of graphs shows the histograms of the sampling distribution for the corresponding test statistic, with the observed test statistic marked by the vertical dotted line, for each of the three characteristics analyzed (daily minimum temperatures, daily maximum temperatures, daily temperature ranges). The second row shows (in grey) all the possible time series of the differences in daily minimum temperatures, daily maximum temperatures, or daily temperature ranges between the two groups (Heating and No Heating). The corresponding observed time series of differences is marked by the solid black line.
Figure 2: Results of the Randomization Tests for comparing the differences in volumetric water content of the soil (soil moisture) between the snow removal and control treatments for 2010 and 2011. The first row of graphs shows the histograms of the sampling distribution for the corresponding test statistic, with the observed test statistic marked by the vertical dotted line. The second row shows (in grey) all the possible time series of the differences in soil moisture between the two treatments. The corresponding observed time series of differences is marked by the solid black line.