

LESSONS FROM THE OLD SCHOOL: PHENOLOGICAL RESPONSES OF THE  
HORSETAIL *EQUISETUM ARVENSE* TO EXPERIMENTAL AIR AND SOIL WARMING IN  
INTERIOR ALASKAN BOREAL FOREST

by  
Will Q. Hendricks  
B.S. University of Michigan, 2013

A Thesis submitted in Partial Fulfillment of the Requirements  
for the Degree of

Master of Science  
in  
Biological Sciences

University of Alaska Fairbanks  
August 2024

APPROVED:

Christa Mulder, Committee Chair  
Teresa Hollingsworth, Committee Member  
Stefanie Ickert-Bond, Committee Member  
Diane Wagner, Chair  
Department of Biology and Wildlife  
Karsten Hueffer, Dean  
College of Natural Science &  
Mathematics  
Richard Collins, Director  
Graduate School



© Copyright by Will Hendricks  
All Rights Reserved

## **Dedication**

I dedicate this text to my dad who dreamed of publishing research as a scientist, and always believed that I would. I dedicate my degree to my mom who channeled her academic passion for Buddhist philosophy into a career in social work in support of her family.

## Abstract

Although there are many studies on plant phenological shifts due to climate change, few of them focus on the phenological responses of seedless vascular plant species to warming climate. The boreal forest biome contains ~ 30% of the carbon stored by forests globally and horsetails with their circumboreal distribution are abundant in the boreal forest. Understanding the phenological response of horsetails to warming air and the timing of ground thaw is an important component for understanding how much carbon will be fixed by plants in the boreal biome in the future warmer climate. To examine the effects of air and soil warming on the phenology of *Equisetum arvense* L. in interior Alaskan boreal forest near Fairbanks, Alaska, we carried out a two-by-two full factorial warming experiment using open topped warming chambers (air warming) and snow removals to advance ground thaw (soil warming). Warming soil by 1 °C caused *E. arvense* to emerge sooner, and warming air by 0.7 °C caused *E. arvense* to grow faster and advance to photosynthetic activity sooner. Warmed *E. arvense* stems also entered senescence earlier than stems in un-warmed control plots, but the advance was greater in the spring, leading to an overall maximum extension of their growing season by 6%, or 6.7 days, for plants that were exposed to both air and soil warming. This is double the average growing season extension of 3% (1.5 days) documented in similar warming experiments of arctic seed plants, and more than the mean growing season extension per decade for seed plants in Europe (4.8 days) and China (6.2 days). Such season expansion at relatively low temperature increases suggests that *E. arvense* has potential to fix more carbon in future boreal forests.

## Acknowledgements

I would like to thank my advisor Dr. Christa Mulder for her support and encouragement through the unexpected twists and turns of my graduate experience throughout which she was a wise and energetic presence. Our shared interest in and enthusiasm for horsetails has been a motivator for me through the designing, implementation, and writing of my thesis research. This thesis has been prepared as a manuscript for publication in the journal *Botany*, for which Christa and I will be the authors. Thank you, Christa, for your patience and input in the editing of this thesis.

I would also like to acknowledge my committee members Dr. Teresa Hollingsworth, and Dr. Steffi Ickert-Bond for their comments, guidance, and feedback. Teresa helped remind me that there are more plants out there than horsetails. Steffi guided me through plant evolution, the fossil record, and kept me grounded as I learned about deep time. I am grateful for your time and insight.

Many friends and family members helped carry me through this program. Max Plichta enthusiastically donated precious summer weekend days to help me with field work and was consistently encouraging. Max asked how I was doing, and told me I was valuable, regardless of my productivity. Lainey Gallenberg, the friendly wizard of figures and data management, helped me at the beginning, middle and end of this process, and I am grateful for her contributions that preserved fistfuls of hair on my head.

My colleagues at the National Ecological Observatory Network were universally supportive. Chris Baird asked me what more he could do to help daily. Lori Petruski carried our team, and I might not have enrolled without her encouragement. Josh Monroe was a time-management inspiration. Abbey VandenBerg's optimism and courage is contagious.

Sarah Ebeler-Monroe is the best field technician I have ever met. Admittedly not a plant person, she diligently conducted the field measurements for this project better than I could have done myself. Sarah worked six days a week rain or shine, all the while braving the many mosquitos and moose that wouldn't leave our plots. She was the only applicant for the position, and I think she took the job because she knew I needed the help.

My faithful field partner Lila knew exactly where not to sit and sat there anyway. Thanks for being my adventure buddy.

Laura Weingartner in many ways lived my graduate experience as much as I did: I can't imagine success without her support. She is an incredible artist, writer, lab mate, roommate, and teammate. She built me up, helped me write emails, make figures, organize my thoughts, and understood my 'process' without judgment. Let's go sit in the sun, or go swimming, or dancing.

## Table of Contents

Copyright .....	iii
Dedication .....	iv
Abstract .....	v
Acknowledgements .....	vi
Table of Contents .....	viii
List of Figures .....	x
List of Tables .....	xi
Chapter 1: Lessons from the old school: phenological responses of the horsetail <i>Equisetum arvense</i> to experimental air and soil warming in interior Alaskan boreal forests. ....	1
1.1 Introduction .....	1
1.2 Methods .....	5
1.2.1 Study Area Description and Site Selection .....	5
1.2.2 Treatments .....	5
1.2.3 Phenological Phases .....	6
1.2.4 Field Measurements .....	6
1.2.5 Statistical Analyses .....	8
1.3 Results .....	10
1.3.1 Effect of Treatments on Soil and Air Temperature .....	10
1.3.2 Effect of Treatments on Emergence .....	10
1.3.3 Effect of Treatments on Growth .....	10
1.3.4 Effect of Treatments on Photosynthetically Active Period (PAP) .....	11
1.3.5 Effect of Treatments on Phenology .....	11
1.3.6 Effect of Treatments on Rhizome Biomass .....	12



1.4 Discussion.....	12
1.5 References.....	16
1.6 Figures.....	23
1.7 Tables.....	29

## List of Figures

Figure 1.1 Schematic of a site containing four plots of the full factorial experimental design with two factors and two levels for each factor (treatment and control).....	23
Figure 1.2 Study timeline (upper panel) showing dates treatments were applied to plots, and general patterns of snow depth, <i>E. arvensis</i> emergence.....	24
Figure 1.3 Proportion of the total <i>E. arvensis</i> stems that emerged by treatment from May 1 through June 19 .....	25
Figure 1.4 Mean heights of <i>E. arvensis</i> stems over time.....	26
Figure 1.5 Length of photosynthetically active period (PAP) by treatment. ....	27
Figure 1.6 Mean phenology scores for <i>E. arvensis</i> treatments by observation bout with spring phenology left and fall phenology right .....	28

## List of Tables

Table 1.1 Site locations and elevations.....	29
Table 1.2 Results of repeat measures ANOVA for our four response variables. The models are structured the same way: response variable ~ Plot + Time * Treatment.....	30

## **Chapter 1: Lessons from the old school: phenological responses of the horsetail *Equisetum arvense* to experimental air and soil warming in interior Alaskan boreal forests.**

### **1.1 Introduction**

Hendricks, W. Q., Mulder, C. P. H. (2024). Lessons from the old school: phenological responses of horsetails (*Equisetum arvense*) to experimental air and soil warming in interior Alaskan boreal forests. This manuscript was prepared to be submitted to *Botany*.

Boreal forests are the largest terrestrial biome on the planet, covering about 35% of the North American continent (Brandt, 2009) and accounting for ~ 30% of the carbon storage of the world's forests (Pan et al., 2011). With an increase in mean temperatures in interior Alaska at a rate estimated at double to four times the global average (Wendler & Shulski, 2009; Rantanen et al., 2022), understanding the phenological response of plants to experimental warming is a critical component of understanding how species in boreal forest plant communities might respond to the warmer climate they will inhabit in the future. In addition to a warmer climate, observations and models indicate increasing winter precipitation in the form of snow in interior Alaskan boreal forests (Wendler et al., 2017; *SNAP Community Climate Charts*, 2024). The combination of warmer temperatures and increased snow depth decouples ground thaw timing from spring warming so that warmer springs are not necessarily accompanied by earlier ground thaw. This decoupling effect of climate warming on temperatures and snowmelt dates has been observed in the Arctic, where researchers noted a lack of influence of warmer springs on the timing of the first phases of plant phenological responses due to extra time needed to melt deeper snowpack (Bjorkman et al., 2015). Thus, studies examining plant phenological response to warming need to distinguish between the effects of air warming and the timing of ground thaw to better understand the mechanisms that drive plant phenological responses to warming and predict changes under various possible climate conditions. An experimental approach manipulating air temperature and ground thaw simulates the complex effects of climate change in boreal systems better than experimental designs only manipulating air warming.

Humans have observed and recorded the seasonal life history of organisms – phenology – for thousands of years, understanding the importance of recording the timing of animal species movements or plant activity through seasons for planning harvesting activities (Piao et al., 2019).

Currently phenology is used as a tool in measuring the impacts of a changing climate on organisms. Although not all plant species show a phenological response to temperature, and responses are difficult to predict at the species level or at small spatial scales (Roslin et al., 2021), meta-analyses of observations of thousands of taxa over hundreds of years indicate that increases in temperature lead, on average, to a temporal advance of life history events (e.g., Parmesan & Yohe, 2003; Thackeray et al., 2016; Roslin et al., 2021). However, in experimental studies over shorter time scales, plant species display a range of phenological responses to increased air temperature (e.g., Wipf et al., 2009; Bjorkman et al., 2015; Jabis et al., 2020). In temperate regions with a distinct growing season plant species show, on average, advancement of early season phenological events and, to a lesser degree, a delay in the fall (Collins et al., 2021; Davis et al. 2022). Yet one constant in phenological literature is a lack of attention to seedless vascular plants common in the boreal forest such as ferns and horsetails of the Polypodiopsida, and the clubmosses, fir mosses and spike mosses of the Lycopodiopsida. These clades are nearly completely excluded from studies of plant phenological responses to warming despite the fact they are living representatives of ancient groups of plants that have survived large changes in global climate.

Originating an estimated 431 million years ago (MYA) (Testo & Sundue, 2016), the *Equisetaceae* represents one of the oldest families of land plants with extant members (Gifford et al., 1989; Elgorriaga et al., 2018; Christenhusz et al., 2021). Within the *Equisetaceae*, *Equisetum* L. is the only extant genus, and represents one of the oldest genera of vascular plants (Husby, 2013; Vanneste et al., 2015; Christenhusz et al., 2021). Fossils from the Jurassic and even the Triassic period display all the major characters shared by modern *Equisetum*, resulting in an estimated minimum age of the genus of 175 MYA (Elgorriaga et al., 2018; Christenhusz et al., 2021). With such ancient roots, members of the genus *Equisetum* have survived drastic changes in global climate and atmospheric composition (Ekart et al., 1999; Elgorriaga et al., 2018; Voosen, 2019; Scotese et al., 2021). Considering their history of survival through historical climate change, the lack of studies devoted to the ecology and phenology of modern *Equisetum* is striking.

The lack of representation of *Equisetum* in studies on the boreal forest's response to climate change is also noteworthy considering the genus is a prominent member of the plant boreal plant

community. For example, in one survey of plant diversity and abundance in interior Alaskan boreal forests, *Equisetum* was the 6<sup>th</sup> most encountered of 29 vascular plant genera present in the study area (National Ecological Observatory Network (NEON), 2021). In another survey of vascular plant diversity and abundance in interior Alaskan boreal forest riparian habitat, *Equisetum* was the most encountered genus of the 52 found (Hollingsworth, 2020). One of the common *Equisetum* species in interior Alaska, the field horsetail, *Equisetum arvense* L. has a circumboreal distribution verging on global, as it is considered a weed species of international concern, especially in Australia and New Zealand (Randall, 2017).

In interior Alaska, the growing season is short, and *E. arvense* appears aboveground as small herbaceous shoots soon after snow melts in the spring (Hendricks, personal observation) and quickly develop into either photosynthetically active vegetative stems, or short-lived spore-bearing reproductive stems that are largely achlorophyllous (Apple, 1985). Aboveground stems are produced annually and emerge from subterranean buds born on perennial rhizomes. Belowground tissues of *E. arvense* constitute the majority of the plant's biomass even when above ground tissues are at their seasonal maximum (Williams, 1979). Because *E. arvense* buds are below ground, the timing of emergence is likely closely tied to the timing of ground thaw, which is increasingly recognized in alpine and high latitudes as a key trigger of early season phenology, and an important factor in the duration of a plant's growing season (e.g., Wipf, 2010; Jacques et al., 2015; Jabis et al., 2020; Montgomery et al., 2020).

Phenological responses in the fall also play a role in determining the duration of the growing season of boreal plants. For example, if *E. arvense* stems emerge earlier in the spring due to advanced ground thaw or warmer air temperatures, an equal advance of fall senescence could mean no change in its photosynthetically active period. Conversely, no change or a delay in the timing of fall senescence would provide a longer period of photosynthetic activity and a corresponding potential for *E. arvense* to fix more carbon. Mechanisms responsible for senescing vascular plants such as photoperiod, air temperature, patterns of precipitation, or a combination of these factors (e.g., Gill et al., 2015; Lang et al., 2019; Sun et al., 2023) are complex and likely optimized at the species level (e.g., Gill et al., 2015; Serrano-Bueno et al., 2021). Alternatively, some plants of high latitudes have a growing season with a fixed duration where senescence is controlled not by external conditions like temperature or photoperiod, but by genetic or

potentially other unidentified mechanisms (Khorsand et al., 2015; Semenchuk et al., 2016). In the case of a fixed duration of photosynthetic activity, the timing of senescence would be entirely dependent on the timing of the emergence of stems in the spring and remain unaffected by differences in factors like air temperature. On average plants in boreal and arctic systems show delay of fall senescence with experimental warming (e.g., Montgomery et al., 2020; Collins et al., 2021), although a study of the phenology of two perennial forbs in the boreal zone showed one species had no change and the other only a slight advancement of senescence timing (Jacques et al., 2015). The mechanisms driving senescence of *E. arvense* are completely unknown: they could be primarily abiotic, primarily driven by stem age, or a combination of both. Therefore, earlier stem emergence could but does not necessarily correspond with an expansion of the photosynthetically active period for *E. arvense*.

Seedless vascular plants are an important component of the rapidly warming boreal forest plant community, but they have been excluded from phenological studies in the region. This has led to a bias in phenological studies toward younger lineages of plants that have not been historically confronted with climate warming. Broadly, we set out to document the phenology of a common and abundant seedless vascular plant in the boreal forest region, using methods like those employed by National Phenological Network for seed plants. Specifically, we examined the phenological response of *E. arvense* to manipulations of air temperature and the timing of ground thaw. We developed three hypotheses. First, as with other plants with subterranean buds and/or early spring phenological niches, advancing ground thaw will lead to advanced emergence. Second, given that temperature is a primary factor affecting the rate of plant development, and optimal growth for many economically important crop plants and tree species (including boreal tree species) occur at temperatures that are relatively high compared to springtime temperatures in interior Alaskan boreal forests (Went, 1953; Way & Oren, 2010; Hatfield & Prueger, 2015), we hypothesize that experimentally increasing spring air temperature would increase the rates of *E. arvense* growth and development. Third, we hypothesize that the combination of earlier emergence associated with advanced ground thaw and quicker development due to warmer spring air temperature will result in an increased duration of the photosynthetically active period for *E. arvense*. Understanding responses of *E. arvense* to advanced ground thaw and warmer air will help answer the question of how this taxon will increase or decrease carbon fixation in future boreal forests.

## 1.2 Methods

### 1.2.1 Study Area Description and Site Selection

We conducted our experiment within a 15 km<sup>2</sup> area on the traditional lands of the Dena people of the lower Tanana River near Fairbanks Alaska (64.86 °N, 147.84 °W, elevation 150 m), primarily on the University of Alaska Fairbanks campus. Most of interior Alaska is dominated by black spruce forest; however, our study sites were within forests of *Betula neoalaskana* Sarg. (Alaska paper birch), *Pcpulus tremuloides* Michx. (quaking aspen), and *Picea glauca* (Moench) Voss (white spruce) which are common on south facing slopes or in well drained upland areas (Viereck et al., 1983; Hollingsworth, 2004). The silt loam upland soils in these broadleaf forests developed from loess originating from glacial outwash streams (Viereck et al., 1983; Ping et al., 2005). The climate is continental with long cold winters and short warm summers (Ping et al., 2005).

Our study was conducted in 2023, a year with cold spring temperatures. In April 2023 the average temperature was -5.8 °C, 6.7 °C below the 30-year average of 0.9 °C (SD = 2.8 °C) (Arguez et al., 2010; Menne et al., 2012). These cool temperatures delayed deciduous tree leaf-out by eight days compared to the 50-year average of May 8th (Anderson et al., 2023). We selected ten sites with deciduous tree overstory in boreal forest composed predominantly of *B. neoalaskana* and *P. tremuloides*. Sites had similar elevation, slope, and aspect; most sites were flat except sites 1, and 2 which had slopes of 10% and aspects of southwest and west respectively (Table 1.1).

### 1.2.2 Treatments

To assess the phenological response of *E. arvensis* to warmed air and soil, we employed a full-factorial experiment with two factors (advanced ground thaw and air warming) and two levels of each factor (control and treatment). Each site contained four 1 m<sup>2</sup> experimental plots, and sites were replicated 10 times. We used a shovel around the perimeter of each plot to mechanically sever rhizomatous connections in the top 30 – 50 cm of soil to ensure independence from water, nutrient, or carbohydrate inputs transported via rhizome from *E. arvensis* outside the plot. Because *E. arvensis* forms clonal patches and the average size of these



individuals is unknown, we located sites at least 50 m apart and assumed each site contained an individual *E. arvensis* clone (Figure 1.1).

To advance ground thaw date and to increase soil temperature, we manually removed snow using shovels in the late spring. We removed snow until leaf litter was exposed but were careful not to disturb the litter layer. We applied snow removal treatments on April 23, when snow depth was 60 cm and daily high and low temperatures were mild — in the eight days after snow removals daily lows averaged  $-5.4^{\circ}\text{C}$  and daily high temperatures averaged  $5.9^{\circ}\text{C}$  (Menne et al., 2012; *Alaska Climate Research Center*, 2024).

To warm air temperature at experimental plots, we installed polyvinyl open-top chambers (OTCs). OTCs were 130 cm wide at the base, and 121 cm tall aluminum frames covered with polyvinyl chloride plastic film (Nantucket Distributing, Middleboro, MA) which were modified by removing a trapezoid of plastic between each of the ribs between 7 and 14 cm from the top of the chamber (except for the side with the zipper). Removing the top of the greenhouse in this way creates a roughly  $300\text{ cm}^2$  opening which moderates heating effects, allows air flow, and permits precipitation to reach plants. OTCs were applied on April 30, 16 days before leaf-out of the broadleaf tree overstory.

### 1.2.3 Phenological Phases

Phenological phases for the study species were based broadly on National Phenological Network methods (Denny et al., 2014) (Figure 1.2). Vegetative stems are labeled with an “A,” reproductive stems are labeled with a “B,” and increasing numerical value corresponds to increasing phenological advancement. A1 Vegetative emergence: emerging vegetative stems (< 10 cm tall) are scaly, unbranching, largely lacking green color. B1 Reproductive emergence: emerging reproductive stems (< 10 cm tall) are differentiated from emerging vegetative stems by the presence of an immature strobilus at the apex of the emerging shoot. A2 Greening: greening stems (10 – 25 cm tall) begin to become green and develop branches, and the internodes between branch whorls begin to be distinguishable between scales. A3 Vegetative maturity: stems were vegetatively mature (25 – 50 cm tall) when completely green, and stem branches are clearly to fully developed. B3 Reproductive maturity: stems were reproductively mature when their strobili

were open and spore release was visible to the naked eye. Reproductive stems were no longer considered to be mature when they had finished releasing spores and began to wither and droop. A4 Color change: this phase is the initiation of senescence and is marked by progressive yellowing inward from stem branch tips until all aboveground tissues are yellow. A5 Death: This phase marks advanced senescence, and stems were considered dead when they become grey or white, and stems begin to wilt and collapse.

#### **1.2.4 Field Measurements**

We recorded ambient air temperature to the nearest 0.1°C at each plot with two HOBO pendant temperature loggers (UA-002-64; Onset Computer Corporation, Pocasset, MA, USA) on a stake 50 cm above ground level. Air temperature sensors were installed concurrently with OTCs, while soil temperature sensors were installed on May 18 when the ground thawed sufficiently for us to install two HOBO pendant temperature loggers 10 cm below the soil surface in each plot. OTC warming efficacy diminishes with increasing canopy cover, so OTCs were removed on June 9 – 10. All temperature sensors were removed on September 29, the day of our final observation, at which point most stems were dead.

We visited all sites over the course of two days, a period we refer to hereafter as a bout. Starting May 1, we conducted two bouts each week to capture the onset of vegetative and reproductive stem emergence. By May 15 stems were emerging at most plots, so we increased bout frequency to three times each week. On June 12, phenological development of *E. arvense* stems had slowed and bout frequency was reduced to twice per week. We paused phenological observations on June 23 when most vegetative stems were mature and reproductively mature stems had withered. By September 4 vegetative stems began to yellow, and we resumed phenological observation bouts once weekly until September 29 when most stems were dead.

To measure phenological advancement, we counted stems in each phenological stage for each experimental plot on each observation day. To measure *E. arvense* stem heights, we recorded the vertical height from ground level for 10 stems in each phenological phase present in each plot on each observation day. Stems were selected haphazardly within plots and were measured to the nearest 1 cm increment. Because *E. arvense* stems reach their maximum height

at maturity, we discontinued stem height measurements when most vegetative stems had reached maturity.

Rhizome biomass was collected in two soil cores per plot (30 cm long, 4.5 cm diameter). Soil cores were pooled by plot and rinsed in a 2 mm mesh soil sieve to separate soil from plant root material. Rhizomes were oven dried at 65° C for 48 hours and weighed to nearest 0.01 g.

### **1.2.5 Statistical Analyses**

All statistical analyses were performed using R Statistical Software version 4.3.0 (R Core Team 2023). For one-way analysis of variance (ANOVA) tests, and Tukey honest significant difference (TukeyHSD) tests we used the *stats* package (version 4.2.3). For our repeated measures ANOVA analyses we used the *rstatix* package (version 0.7.2).

To understand how maximum air temperatures were affected by OTC treatments, daily plot mean temperatures were averaged over the period OTCs were in place (April 30 – June 10) and analyzed with a one-way analysis of variance ANOVA test with site as a random variable. Similarly, we tested the snow removal effect on soil temperature using plot average soil temperature. Plot soil temperatures across a month-long period starting when soil temperature sensors were installed (May 18 – June 17) were analyzed with a one-way ANOVA test where site was included as a random variable.

To assess treatment effect on *E. arvense* emergence we first calculated the proportion of the maximum number of emerged stems for each plot on each bout. We ran a repeated measures ANOVA with proportion of emerged stems as the response variable; explanatory variables included warming treatment (4 levels), time as a within-subjects variable, and site identity as a blocking variable. We chose to treat the warming treatments as a single variable with four levels of treatment rather than as two variables with two levels because we were primarily interested in the interaction between warming treatments and time, and a three way interaction between soil warming, air warming, and time, would have been difficult to interpret.

To estimate mean *E. arvense* stem height in each plot on each day we used the mean height of stems in each phase and weighted by the number of stems present in that phase. To evaluate treatment effects of increased air and soil temperature on stem heights over time, we ran repeated

measures ANOVA with stem height as the response variable, explanatory variables included warming treatment (4 levels), time as a within-subjects variable, and site identity as a blocking variable.

To calculate the length of the photosynthetically active period for *E. arvense*, we started by calculating the proportion of stems in each phase on each day to the maximum number of stems observed in that phase at each plot. We used these proportional phase data to calculate a photosynthetically active period (PAP) for each plot. We defined PAP as the period starting the first day 50% or more of *E. arvense* stems reached the A2 greening vegetative phase through the first day 50% of stems in each plot reached the A4 color change phase. To identify a treatment effect on the duration of the photosynthetically active period for *E. arvense*, we ran a two-way ANOVA with photosynthetically active period as the response variable, soil temperature, air temperature, and their interaction as explanatory variables, and site identity as a blocking variable.

We used phenology scores to assess treatment effects on *E. arvense* stem senescence. To calculate average phenology scores for each plot on each day, we assigned numerical values to each successive phenological phase (1 = A1 emerging vegetative & B1 emerging reproductive, 2 = A2 greening vegetative, 3 = A3 mature vegetative & B3 mature reproductive, 4 = A4 color change, 5 = A5 death) (Eq. 1.1).

$$Phenology\ Score = \frac{\Sigma(Phase\ Value * Phase\ Stem\ Count)}{\Sigma(Stem\ Count)} \quad (1.1)$$

To evaluate treatment effects on *E. arvense* senescence (the period of the beginning of senescence to the end of observations, September 4 – September 29) we used the phenology scores as a response variable in repeated measures ANOVA; warming treatment (4 levels) as explanatory variables, time as a within-subjects variable, and site identity as a blocking variable.

To test whether differences in air temperature alone could account for variation in developmental rates between treatments, we examined whether there were differences in cumulative growing degree days required to advance from emergence to vegetative maturity. Cumulative growing degree days were calculated for each plot as the sum of mean daily air temperatures above 0° C for the period starting when the phenology score was 1 (emerging) and

ending at 3 (vegetative maturity). We ran an ANOVA with cumulative growing degree days required to advance emerging *E. arvense* stems to maturity as the response variable, warming treatment (4 levels) as explanatory variables, and site identity as a random blocking variable.

Treatment effects on rhizome mass were analyzed in a one-way ANOVA with site as a random variable and rhizome dry mass as the response variable.

## **1.3 Results**

### **1.3.1 Effect of Treatments on Soil and Air Temperature**

To understand treatment effects on soil temperature we tested air and soil temperatures over the period OTCs were deployed at plots (May 18 – June 17). Snow removal treatments increased soil temperatures 1 °C on average ( $F_{1,27} = 17.466$ ,  $p < 0.001$ ), while OTCs had no effect on soil temperature compared to controls. Looking at air temperatures over the same period, snow removal treatments had no effect on air temperature and OTCs increased air temperature 0.7°C on average ( $F_{1,27} = 93.017$ ,  $p < 0.001$ ) compared to controls.

### **1.3.2 Effect of Treatments on Emergence**

The snow removal treatment and associated soil warming showed a significant correlation with earlier emergence at the beginning of May compared to plots that did not have snow removed (Table 1.2, Figure 1.3). Plants in snow removal treatments experienced warmer soil and emerged earlier. In fact, on our first observation bout on May 1-2 every snow removal treatment plot contained emerging *E. arvense* stems. In contrast, we first observed stems emerging in plots without snow removals on May 8, and it wasn't until May 22 that every plot where snow had not been experimentally removed contained emerging stems. The OTC treatment and associated increase in air temperature had no effect on patterns of emergence (Figure 1.3).

### **1.3.3 Effect of Treatments on Growth**

The OTC treatment and associated increase in air temperature had a significant positive effect on *E. arvense* growth, as measured by height in May and early June, as compared to plots without the OTC treatment. However, by the end of June, these differences in growth between

treatments were no longer observed (Figure 1.4; Table 1.2). We continued to measure stem heights into July but were not able to sample all plots due to the presence of a recalcitrant resident moose, so these unbalanced later observations were not included in the analyses. However, these height data omitted from statistical analyses showed a pattern of stems converging in overall height suggesting treatments did not have a substantial effect on the maximum overall height reached by *E. arvense* stems at maturity.

### **1.3.4 Effect of Treatments on Photosynthetically Active Period (PAP)**

We compared the length the photosynthetically active period (PAP) across our treatment groups. Both soil warming ( $F_{1, 36} = 18.181$ ,  $p < 0.001$ ) and air warming ( $F_{1, 36} = 5.306$ ,  $p = 0.027$ ) treatments significantly influenced the *E. arvense* PAP. Plants that received only the air warming treatment showed an increase in PAP by 2.1 days while plants exposed only to soil warming showed an increased PAP of 4.1 days as compared to controls. Plots receiving both types of warming exhibited the largest PAP increase of 6.7 days as compared to controls, but this did not constitute an interaction ( $F_{1, 36} = 0.62$ ,  $p < 0.808$ ) (Figure 1.5).

### **1.3.5 Effect of Treatments on Phenology**

We report here on the phenology of the vegetative stems only; there were too few plots with reproductive stems (40 % of plots) to allow for analysis. We examined phenological advancement separately for spring development and fall senescence (Figure 1.6). Repeated measures ANOVA detected significant positive warming treatment effects for air and soil warming treatments on spring phenological advancement from A1 emerging vegetative to A2 greening to A3 mature vegetative (phenology scores of 1, 2, and 3 respectively) with a significant interaction between time and treatment (Table 1.2). This was reflected in the lack of a significant difference between treatments in growing degree days (GDD) required for *E. arvense* stems to progress from emergence to maturity (air-warmed plants required 140.2 GDD, soil-warmed plants required 144.2 GDD, air & soil-warmed plants required 147.3 GDD, and untreated plants required 135.5 GDD,  $F_{3, 27} = 1.14$ ,  $p = 0.351$ ).

We tested air and soil warming effects on *E. arvense* stem senescence using phenology scores in the fall starting in early September, when plants began to progress from the A3 mature

vegetative phase to the A4 color change phase and ending at the end of September, when most plants had reached the A5 death phase (phenology scores 3, 4, and 5 respectively) (Figure 1.6, Table 1.2). Plants in control plots were the latest to senesce. Plants that received only OTC treatments were the earliest to change color, while later in September plants that experienced snow removal treatments were the first to have the majority of stems die.

### 1.3.6 Effect of Treatments on Rhizome Biomass

The mean rhizome biomass in plots was 0.74 g (SD = 0.32 g), which indicated a high degree of variation between samples. ANOVA of dry *E. arvense* rhizome biomass did not detect any statistically significant difference between treatments and control plots ( $F_{3, 36} = 0.362$ ,  $p = 0.781$ ).

## 1.4 Discussion

We investigated the phenological and physiological response of *E. arvense* to air and soil warming (ground thaw). Ground thaw via snow removal caused *E. arvense* stems to emerge sooner. Air warming, although it had no effect on the timing of emergence, caused *E. arvense* stems to develop faster. Our results agree with a consensus in the literature for high latitude and alpine plants demonstrating that early phenological activity is driven primarily by snowmelt date rather than air temperature (Wipf et al., 2009; Wipf, 2010; Bjorkman et al., 2015; Mulder & Spellman, 2019; Jabis et al., 2020). Both air and soil warming extended the photosynthetically active period (PAP) for *E. arvense* and the effects were additive to a maximum increase of 6%. Plants exposed to air and soil warming experienced earlier senescence, but the size of the shift was more pronounced in the spring than it was in the fall, leading to overall increases in PAP driven primarily by earlier emergence due to advanced ground thaw resulting from snow removal.

Spring photosynthesis is important for understory plants in broadleaf forests, particularly those like *E. arvense* that emerge before canopy closure (Lapointe, 2001; Neufeld & Young, 2014). We observed *E. arvense* stems emerging as soon as snow melted from plots, regardless of our snow manipulations, often before snow had completely melted from the surrounding area. This suggests snowmelt date is the critical initial phenological trigger for this species, and that *E. arvense* is an example of a plant species that occupies an especially early phenological niche.

While plants in snow removal treatments senesced earlier than air warmed and control plants, the differences in end-of-season phenology were small and likely not biologically significant when compared to larger differences in early phenology. Similar growing season extensions driven primarily by spring phenological advancement were seen in other heat manipulation experiments in Northern Minnesota on perennial herbaceous rhizomatous plants and shrubs (including one species of fern) over multiple years (Jacques et al., 2015; Rice et al., 2018).

Though the season extension for warmed *E. arvense* was driven by early emergence resulting from soil warming via snow removal, we noted the growth rate of *E. arvense* stems in soil warming treatments alone was slower than all other treatments including the growth rate of control plants. In April 2023, the average temperature was -5.8 °C, 6.7 °C below the 30-year average of 0.9 °C (SD = 2.8 °C) which suggests the pattern we see could be a result of colder than average spring temperatures and not a direct effect of snow removal treatments (Arguez et al., 2010; Menne et al., 2012). Plants that emerged earlier due to snow removal experienced colder air temperatures compared to the other treatments. Early emergence into relatively colder weather increased the time required for plants to transition from emerging to greening for plants in snow removal treatments. Plants that emerged later (i.e., no snow removal treatment) emerged into warmer air temperatures and took fewer days from emergence to greening. We find support for this finding in our analysis of growing degree days (GDD) that indicated no difference in GDD required for plants across treatments to advance from emergence to maturity. It remains unknown what relative ability *E. arvense* possess to respond to earlier, warmer springs as compared to other plants in interior Alaska with a similar life history to their own (e.g., *Rubus chamaemorus* L and *Mertensia paniculata* (Aiton) G. Don) for which growth of aboveground tissues initiates from buds on perennial subterranean tissues (Apple, 1985). Furthermore, we were not able to assess the effect of our treatments on reproductive *E. arvense* stems, so we don't know how warmer or colder temperatures may impact spore production. This lack of fertile shoots could be partially related to shade inhibition of fertile shoot growth as of our plots all of which were under broadleaf tree canopy (Andersson & Lundegårdh, 1999). Regardless, the potential advantage of earlier emergence and increased access to sunlight through open spring canopy may be offset by the risk associated with an earlier loss of frost hardiness and potential resulting damage from early season cold temperatures (e.g., Wipf et al., 2009; Richardson et al., 2018), although vulnerability of *E. arvense* to frost damage after emergence is unknown.



Air temperature and snowmelt date are predicted to continue to change in interior Alaska. In the next 80 years in Fairbanks, medium emissions models (RCP 6.0) predict air temperature to increase 4.2° C to 7° C, and winter precipitation to increase by 3.5 mm to 8.8 mm (Scenarios Network for Alaska and Arctic Planning 2024), leading to earlier snowmelt dates in spring (Lader et al., 2020). Our experimental design simulated air warming of + 1° C and soil warming of + 0.7 ° C. Even at these relatively low warming levels and smaller shifts in ground thaw date than predicted for the near future, plants treated with both air and soil warming had a 6% (6.7 days) longer PAP compared to controls. This response is double the average growing season extension of 3% (1.5 days) and double the mean season extension in similar OTC experiments of arctic seed plants (Collins et al., 2021). The growing season extension for *E. arvensis* of 6.7 days is also more than the mean observed seed plant growing season extension rates per decade in Europe (4.8 days) and China (6.2 days), though it is on par with the 6–11 day average season extension seen in an air and soil warming study in a boreal-temperate ecotone system (Piao et al., 2019; Montgomery et al., 2020; Collins et al., 2021). Considering 2023 was a year characterized by colder than average April temperatures, we anticipate the 6% increase we documented in PAP is an underestimate of the potential phenological response of *E. arvensis* to warmer air temperatures and advancing ground thaw.

Although we noted an expansion of the growing season for warmed *E. arvensis* plants, we did not detect a corresponding increase in belowground biomass. Our data showed high variability in rhizome mass, even within treatments, likely related to uneven spatial distribution of rhizomes in the soil. We were therefore unlikely to detect a difference in rhizome biomass between treatments on the order expected (< 10%), even if one existed. However, the demonstrated extension of the growing season described in this study, paired with predictions of earlier snowmelt dates and warmer air temperatures, suggests that *E. arvensis* could fix and store more carbon in future interior Alaska climate. It is unknown how much *E. arvensis* biomass exists in the boreal forest but considering the abundance of the species in aboveground surveys of interior Alaska flora, and that much of the biomass of this species exists belowground, the total biomass across its circumboreal range is likely large in comparison with other understory nonwoody vascular plants. We do know *E. arvensis* can grow and colonize some disturbed areas quickly. In one study, horsetails colonized agricultural fields that had been tilled 16 times just as quickly as fields tilled once, ultimately colonizing a hectare completely in six years (Clouter & Watson

1985). Increases of carbon fixation by this group would influence the carbon budget of the boreal region and knowing whether *E. arvensis* can expand its growing season is the first step in determining to what extent its capacity to fix and store carbon in the boreal region may increase in the future.

Future greenhouse studies of *E. arvensis* in pots subjected to warmer air and soil temperatures, and collection of the belowground biomass of the entire organism at the end of the study, are needed to understand exactly how much an increase in PAP might translate to an increase in biomass. Further effort should also be invested in understanding temperature optima for *E. arvensis* growth and photosynthesis rates to determine the range where fixation rates are positive. For example, the dominant tree species of the interior Alaska region display lower photosynthesis rates at warmer predicted summer temperatures though acclimation to warmer temperature may lead to an increase in CO<sub>2</sub> assimilation rates (Stinziano & Way, 2014). To understand the full range of impacts of climate change on carbon cycling in boreal forests, future phenology studies need to include seedless vascular plants, especially in boreal forests they are common. We demonstrate that simple methods like those used to record phenologies of seed plants are adequate to detect such responses. *E. arvensis* is an example of a seedless vascular plant species that could be added to the target taxon lists of large phenological networks with little to no need to modify existing observational methods or techniques. Additionally, we recommend the inclusion of *E. arvensis* and other seedless vascular plants into large phenological networks such as the National Phenology Network and NatureWatch.

## 1.5 References

- Alaska Climate Research Center* (USW00026411). (2024). <https://akclimate.org/data/data-portal/>
- Anderson, J., Elsner, C., Fathauer, T., & Euskirchen, E. (2023). *Greenup values for interior Alaska 1976—Present* (knb-lter-bnz.300.31). Bonanza Creek LTER. <https://doi.org/10.6073/pasta/3a8af33974f5da4819e4b0e3e1bf2dd3>
- Andersson, T. N., & Lundegårdh, B. (1999). Field horsetail (*Equisetum arvense*)—effects of potassium under different light and nitrogen conditions. *Weed Science*, 47(1), 47–54. <https://doi.org/10.1017/S0043174500090640>
- Apple, M. (1985). Phenology of *Equisetum*. *Graduate Student Theses, Dissertations, & Professional Papers*. University of Montana. <https://scholarworks.umt.edu/etd/7384>
- Arguez, A., Durre, I., Applequist, S., Squires, M., Vose, R., Yin, X., & Bilotta, R. (2010). *U.S. Climate Normals Product Suite (1990-2020)*. NOAA National Climatic Data Center. <https://doi.org/10.7289/V5PN93JP>
- Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M., & Henry, G. H. R. (2015). Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, 21(12), 4651–4661. <https://doi.org/10.1111/gcb.13051>
- Brandt, J. P. (2009). The extent of the North American boreal zone. *Environmental Reviews*, 17(NA), 101–161. <https://doi.org/10.1139/A09-004>
- Christenhusz, M. J. M., Chase, M. W., Fay, M. F., Hidalgo, O., Leitch, I. J., Pellicer, J., & Viruel, J. (2021). Biogeography and genome size evolution of the oldest extant vascular plant genus, *Equisetum* (*Equisetaceae*). *Annals of Botany*, 127(5), 681–695. <https://doi.org/10.1093/aob/mcab005>
- Collins, C. G., Elmendorf, S. C., Hollister, R. D., Henry, G. H. R., Clark, K., Bjorkman, A. D., Myers-Smith, I. H., Prevéy, J. S., Ashton, I. W., Assmann, J. J., Alatalo, J. M., Carbognani, M., Chisholm, C., Cooper, E. J., Forrester, C., Jónsdóttir, I. S., Klanderud, K., Kopp, C. W., Livensperger, C., ... Suding, K. N. (2021). Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications*, 12(1), Article 1. <https://doi.org/10.1038/s41467-021-23841-2>

- Davis, C. C., Lyra, G. M., Park, D. S., Asprino, R., Maruyama, R., Torquato, D., Cook, B. I., & Ellison, A. M. (2022). New directions in tropical phenology. *Trends in Ecology & Evolution*, 37(8), 683–693. <https://doi.org/10.1016/j.tree.2022.05.001>
- Denny, E. G., Gerst, K. L., Miller-Rushing, A. J., Tierney, G. L., Crimmins, T. M., Enquist, C. A. F., Guertin, P., Rosemartin, A. H., Schwartz, M. D., Thomas, K. A., & Weltzin, J. F. (2014). Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology*, 58(4), 591–601. <https://doi.org/10.1007/s00484-014-0789-5>
- Ekart, D. D., Cerling, T. E., Montanez, I. P., & Tabor, N. J. (1999). A 400 million year carbon isotope record of pedogenic carbonate: Implications for paleoatmospheric carbon dioxide. *American Journal of Science*, 299(10), 805–827.
- Elgorriaga, A., Escapa, I. H., Rothwell, G. W., Tomescu, A. M. F., & Cúneo, N. R. (2018). Origin of *Equisetum*: Evolution of horsetails (Equisetales) within the major euphyllophyte clade Sphenopsida. *American Journal of Botany*, 105(8), 1286–1303. <https://doi.org/10.1002/ajb2.1125>
- Gifford, E. M., Foster, A. S., & Foster, A. S. (1989). *Morphology and evolution of vascular plants* (3rd ed). W.H. Freeman and Co.
- Gill, A. L., Gallinat, A. S., Sanders-DeMott, R., Rigden, A. J., Short Gianotti, D. J., Mantooth, J. A., & Templer, P. H. (2015). Changes in autumn senescence in northern hemisphere deciduous trees: A meta-analysis of autumn phenology studies. *Annals of Botany*, 116(6), 875–888. <https://doi.org/10.1093/aob/mcv055>
- Hatfield, J. L., & Prueger, J. H. (2015). Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes*, 10, 4–10. <https://doi.org/10.1016/j.wace.2015.08.001>
- Hollingsworth, T. N. & Bonanza Creek LTER. (2020). *Point Bar Vegetation Survey of Bonanza Creek LTER Research Plots (2007-Present)*. <https://doi.org/10.6073/PASTA/C3D2B72E7BA403FA565160853C048222>
- Hollingsworth, T. N. (2004). Quantifying variability in the Alaskan black spruce ecosystem: Linking vegetation, carbon, and fire history. *University of Alaska Fairbanks ProQuest Dissertations & Theses*.

- Husby, C. (2013). Biology and functional ecology of *Equisetum* with emphasis on the giant horsetails. *Botanical Review*, 79(2), 147–177.
- Jabis, M. D., Winkler, D. E., & Kueppers, L. M. (2020). Warming acts through earlier snowmelt to advance but not extend alpine community flowering. *Ecology*, 101(9), e03108. <https://doi.org/10.1002/ecy.3108>
- Jacques, M., Lapointe, L., Rice, K., Montgomery, R. A., Stefanski, A., & Reich, P. B. (2015). Responses of two understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: Early emergence is the key to enhanced reproductive output. *American Journal of Botany*, 102(10), 1610–1624. <https://doi.org/10.3732/ajb.1500046>
- Khorsand Rosa, R., Oberbauer, S. F., Starr, G., Parker La Puma, I., Pop, E., Ahlquist, L., & Baldwin, T. (2015). Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. *Global Change Biology*, 21(12), 4520–4532. <https://doi.org/10.1111/gcb.13040>
- Lader, R., Walsh, J. E., Bhatt, U. S., & Bieniek, P. A. (2020). Anticipated changes to the snow season in Alaska: Elevation dependency, timing and extremes. *International Journal of Climatology*, 40(1), 169–187. <https://doi.org/10.1002/joc.6201>
- Lang, W., Chen, X., Qian, S., Liu, G., & Piao, S. (2019). A new process-based model for predicting autumn phenology: How is leaf senescence controlled by photoperiod and temperature coupling? *Agricultural and Forest Meteorology*, 268, 124–135. <https://doi.org/10.1016/j.agrformet.2019.01.006>
- Lapointe, L. (2001). How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum*, 113(2), 151–157. <https://doi.org/10.1034/j.1399-3054.2001.1130201.x>
- Menne, M. J., Durre, I., Korzeniewski, B., McNeill, S., Thomas, K., Yin, X., Anthony, S., Ray, R., Vose, R. S., Gleason, B. E., & Houston, T. G. (2012). *Global Historical Climatology Network—Daily (GHCN-Daily), Version 3.31*. NOAA National Centers for Environmental Information. <https://doi.org/10.7289/V5D21VHZ>
- Montgomery, R. A., Rice, K. E., Stefanski, A., Rich, R. L., & Reich, P. B. (2020). Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. *Proceedings of the National Academy of Sciences USA*, 117(19), 10397–10405. <https://doi.org/10.1073/pnas.1917508117>

- Mulder, C. P. H., & Spellman, K. V. (2019). Do longer growing seasons give introduced plants an advantage over native plants in Interior Alaska? *Botany*, 97(6), 347–362.  
<https://doi.org/10.1139/cjb-2018-0209>
- National Ecological Observatory Network (NEON). (2021). *Plant presence and percent cover (DPI.10058.001): RELEASE-2021* (p. 819.0 MB). <https://doi.org/10.48443/ABGE-R811>
- Neufeld, H. S., & Young, D. R. (2014). Ecophysiology of the Herbaceous Layer in Temperate Deciduous Forests. In F. Gilliam (Ed.), *The Herbaceous Layer in Forests of Eastern North America* (pp. 35–95). Oxford University Press.  
<https://doi.org/10.1093/acprof:osobl/9780199837656.003.0003>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993.  
<https://doi.org/10.1126/science.1201609>
- Parnesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Ping, C. L., Michaelson, G. J., Packee, E. C., Stiles, C. A., Swanson, D. K., & Yoshikawa, K. (2005). Soil catena sequences and fire ecology in the boreal forest of Alaska. *Soil Science Society of America Journal*, 69(6), 1761–1772. <https://doi.org/10.2136/sssaj2004.0139>
- R Core Team. (2023). *R: A language and environment for statistical computing*. (4.2.3) [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Randall, R. P. (2017). *A global compendium of weeds* (3rd edition). Weeds Society of Western Australia.
- Rantanen, M., Karpechko, A. Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, 3(1), 168.  
<https://doi.org/10.1038/s43247-022-00498-3>



- Rice, K. E., Montgomery, R. A., Stefanski, A., Rich, R. L., & Reich, P. B. (2018). Experimental warming advances phenology of groundlayer plants at the boreal-temperate forest ecotone. *American Journal of Botany*, *105*(5), 851–861. <https://doi.org/10.1002/ajb2.1091>
- Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Furze, M. E., Seyednasrollah, B., Krassovski, M. B., Latimer, J. M., Nettles, W. R., Heiderman, R. R., Warren, J. M., & Hanson, P. J. (2018). Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature*, *560*(7718), Article 7718. <https://doi.org/10.1038/s41586-018-0399-1>
- Roslin, T., Antão, L., Hällfors, M., Meyke, E., Lo, C., Tikhonov, G., Delgado, M. del M., Gurarie, E., Abadonova, M., Abduraimov, O., Adrianova, O., Akimova, T., Akkiev, M., Ananin, A., Andreeva, E., Andriychuk, N., Antipin, M., Arzamascev, K., Babina, S., ... Ovaskainen, O. (2021). Phenological shifts of abiotic events, producers and consumers across a continent. *Nature Climate Change*, *11*(3), 241–248. <https://doi.org/10.1038/s41558-020-00967-7>
- Scotese, C. R., Song, H., Mills, B. J. W., & Van Der Meer, D. G. (2021). Phanerozoic paleotemperatures: The earth's changing climate during the last 540 million years. *Earth-Science Reviews*, *215*, 103503. <https://doi.org/10.1016/j.earscirev.2021.103503>
- Semenchuk, P. R., Gillespie, M. A. K., Rumpf, S. B., Baggesen, N., Elberling, B., & Cooper, E. J. (2016). High Arctic plant phenology is determined by snowmelt patterns but duration of phenological periods is fixed: An example of periodicity. *Environmental Research Letters*, *11*(12), 125006. <https://doi.org/10.1088/1748-9326/11/12/125006>
- Serrano-Bueno, G., Sánchez De Medina Hernández, V., & Valverde, F. (2021). Photoperiodic signaling and senescence, an ancient solution to a modern problem? *Frontiers in Plant Science*, *12*, 634393. <https://doi.org/10.3389/fpls.2021.634393>
- SNAP Community Climate Charts*. (2022). SNAP Community Climate Charts. Retrieved February 6, 2022, from <https://snap.uaf.edu/tools/community-charts>
- Stinziano, J. R., & Way, D. A. (2014). Combined effects of rising CO<sub>2</sub> and temperature on boreal forests: Growth, physiology and limitations. *Botany*, *92*(6), 425–436. <https://doi.org/10.1139/cjb-2013-0314>
- Sun, Q., Chen, G., Li, B., Zhu, J., Chen, X., & Yuan, W. (2023). Multiple factors induce temporal shifts in herbaceous plant leaf senescence dates on the Qinghai–Tibetan Plateau.

- Agricultural and Forest Meteorology*, 334, 109441.  
<https://doi.org/10.1016/j.agrformet.2023.109441>
- Testo, W., & Sundue, M. (2016). A 4000-species dataset provides new insight into the evolution of ferns. *Molecular Phylogenetics and Evolution*, 105, 200–211.  
<https://doi.org/10.1016/j.ympev.2016.09.003>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. <https://doi.org/10.1038/nature18608>
- Vanneste, K., Sterck, L., Myburg, A. A., Van de Peer, Y., & Mizrachi, E. (2015). Horsetails are ancient polyploids: evidence from *Equisetum giganteum*. *The Plant Cell*, 27(6), 1567–1578.  
<https://doi.org/10.1105/tpc.15.00157>
- Viereck, L. A., Dyrness, C. T., Cleve, K. V., & Foote, M. J. (1983). Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Canadian Journal of Forest Research*, 13(5), 703–720. <https://doi.org/10.1139/x83-101>
- Voosen, P. (2019). Project traces 500 million years of roller-coaster climate. *Science*, 364(6442), 716–717. <https://doi.org/10.1126/science.364.6442.716>
- Way, D. A., & Oren, R. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: A review and synthesis of data. *Tree Physiology*, 30(6), 669–688. <https://doi.org/10.1093/treephys/tpq015>
- Wendler, G., Gordon, T., & Stuefer, M. (2017). On the precipitation and precipitation change in Alaska. *Atmosphere*, 8(12), 253. <https://doi.org/10.3390/atmos8120253>
- Wendler, G., & Shulski, M. (2009). A century of climate change for Fairbanks, Alaska. *Arctic*, 62(3), 295–300.
- Went, F. W. (1953). The effect of temperature on plant growth. *Annual Review of Plant Physiology*, 4(1), 347–362. <https://doi.org/10.1146/annurev.pp.04.060153.002023>
- Williams, E. D. (1979). Studies on the depth distribution and on the germination and growth of *Equisetum arvense* L (field horsetail) from tubers. *Weed Research*, 19(1), 25–32.  
<https://doi.org/10.1111/j.1365-3180.1979.tb01513.x>



Wipf, S. (2010). Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, 207(1), 53–66. <https://doi.org/10.1007/s11258-009-9653-9>

Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94(1–2), 105–121. <https://doi.org/10.1007/s10584-009-9546-x>

## 1.6 Figures

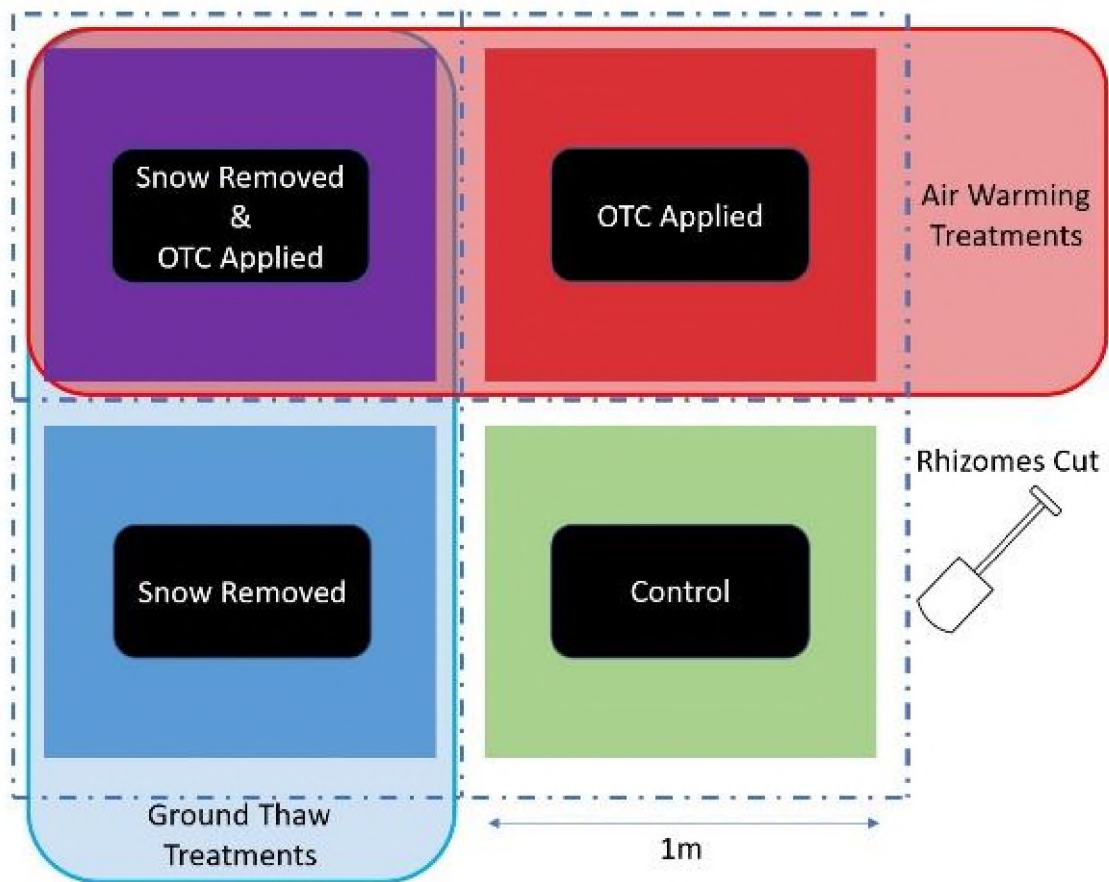


Figure 1.1 Schematic of a site containing four plots of the full factorial experimental design with two factors and two levels for each factor (treatment and control). The dotted line at the perimeter of each plot indicates severed rhizomes to a soil depth of 30 – 50 cm.

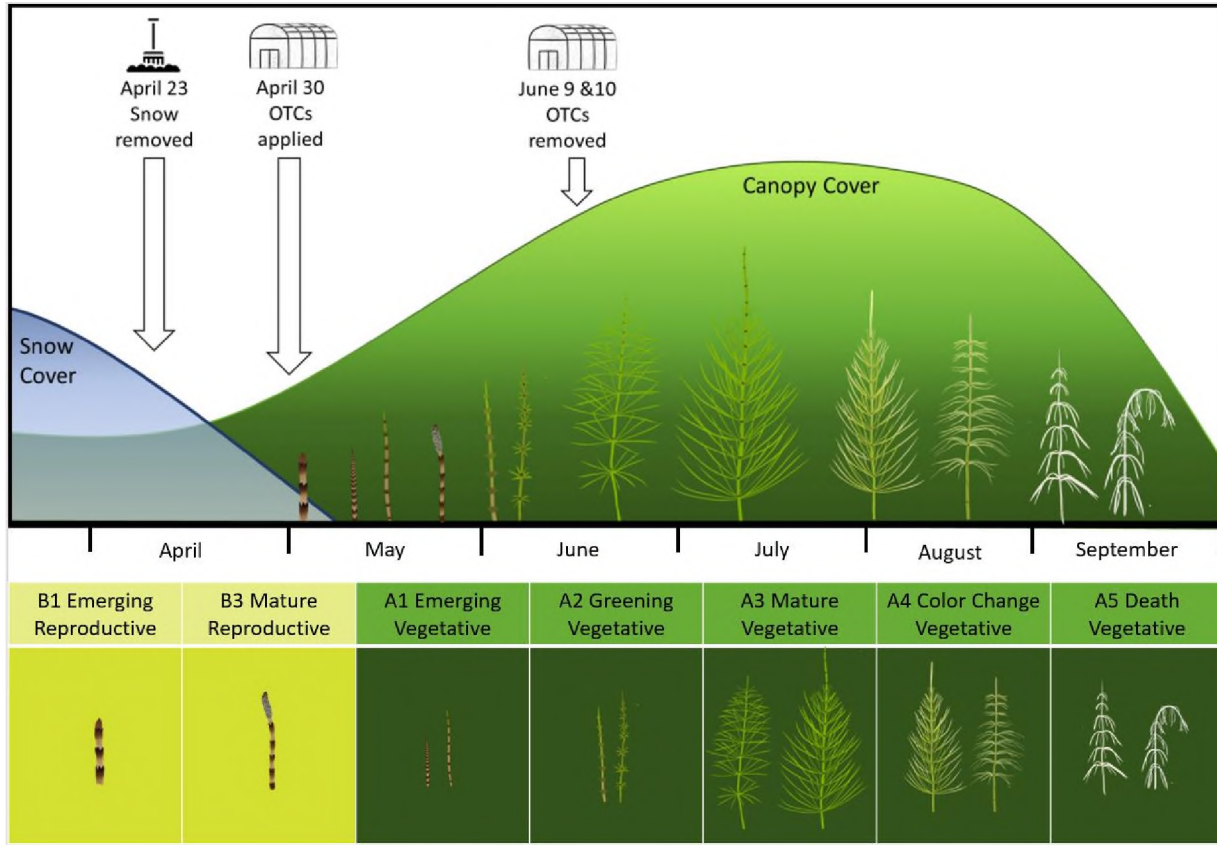


Figure 1.2 Study timeline (upper panel) showing dates treatments were applied to plots, and general patterns of snow depth, *E. arvense* emergence and development, and canopy cover change over time. *E. arvense* phenological phases (lower panel) are illustrated with examples of each phase.

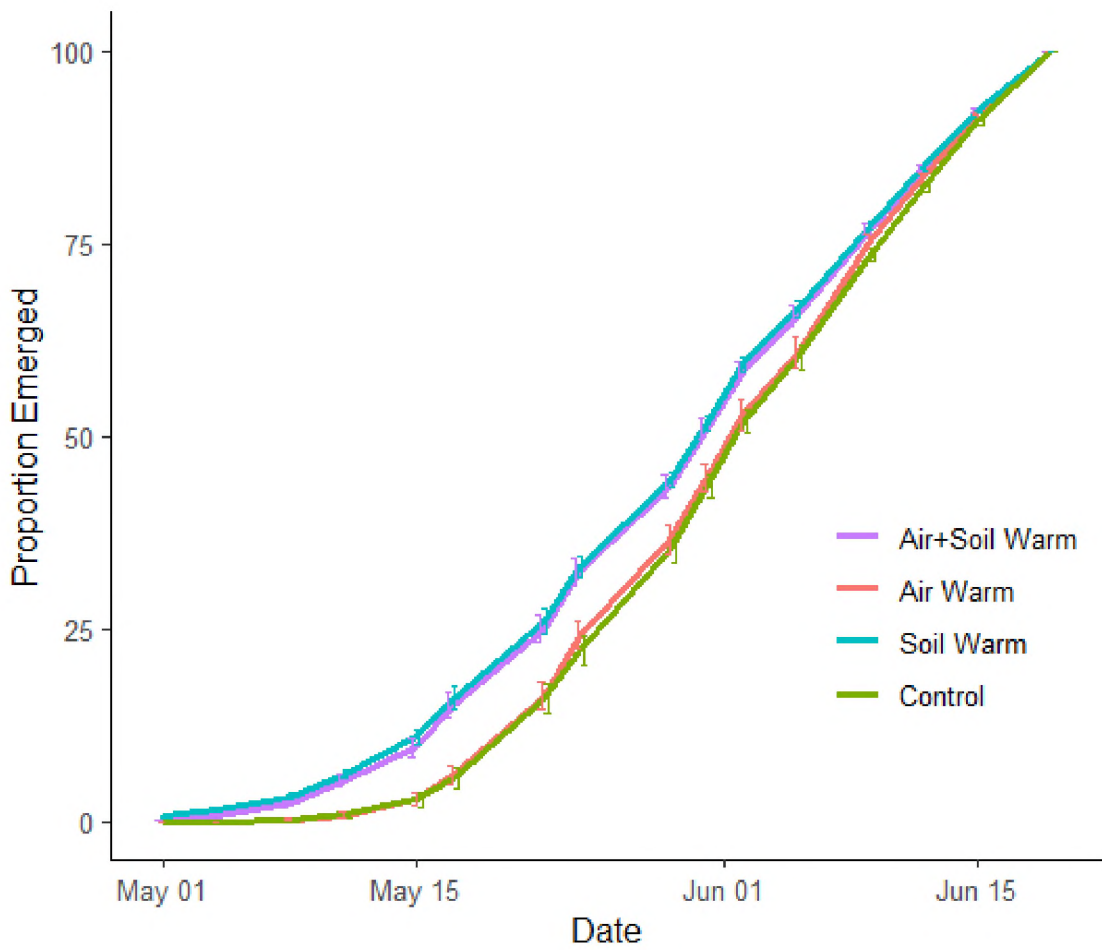


Figure 1.3 Proportion of the total *E. arvense* stems that emerged by treatment from May 1 through June 19. Error bars represent one standard error of the mean.

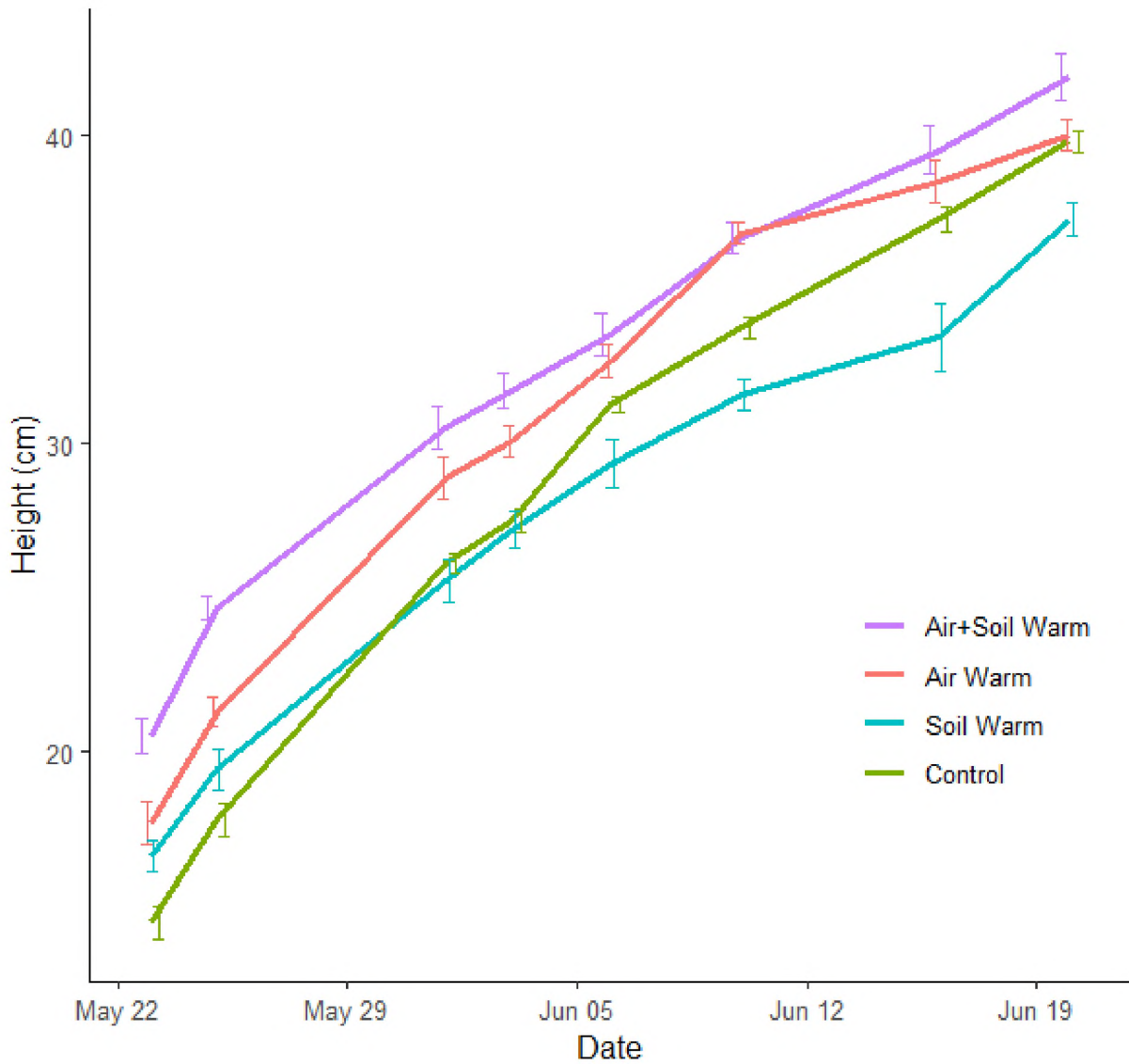


Figure 1.4 Mean heights of *E. arvense* stems over time. Error bars represent one standard error of the mean.

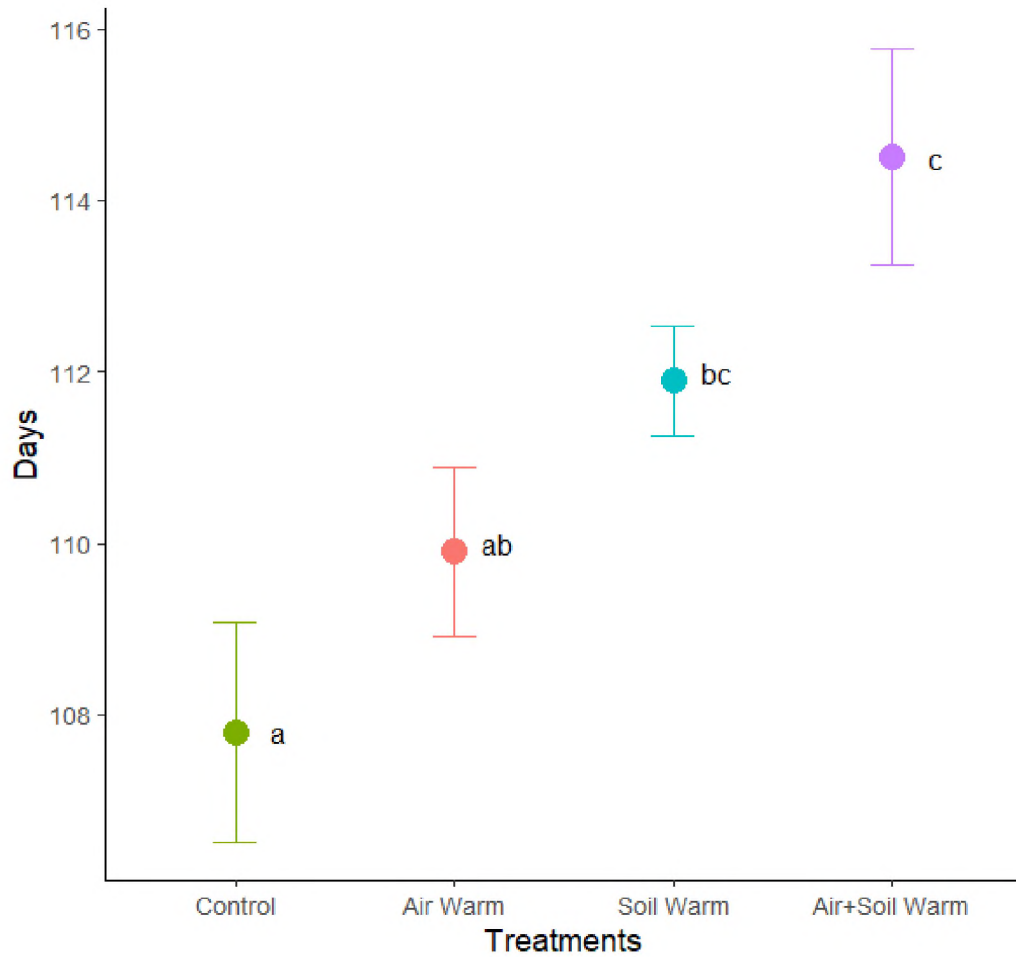


Figure 1.5 Length of photosynthetically active period (PAP) by treatment. Different letters indicate significant differences following a Tukey HSD test. Error bars represent one standard error of the mean.

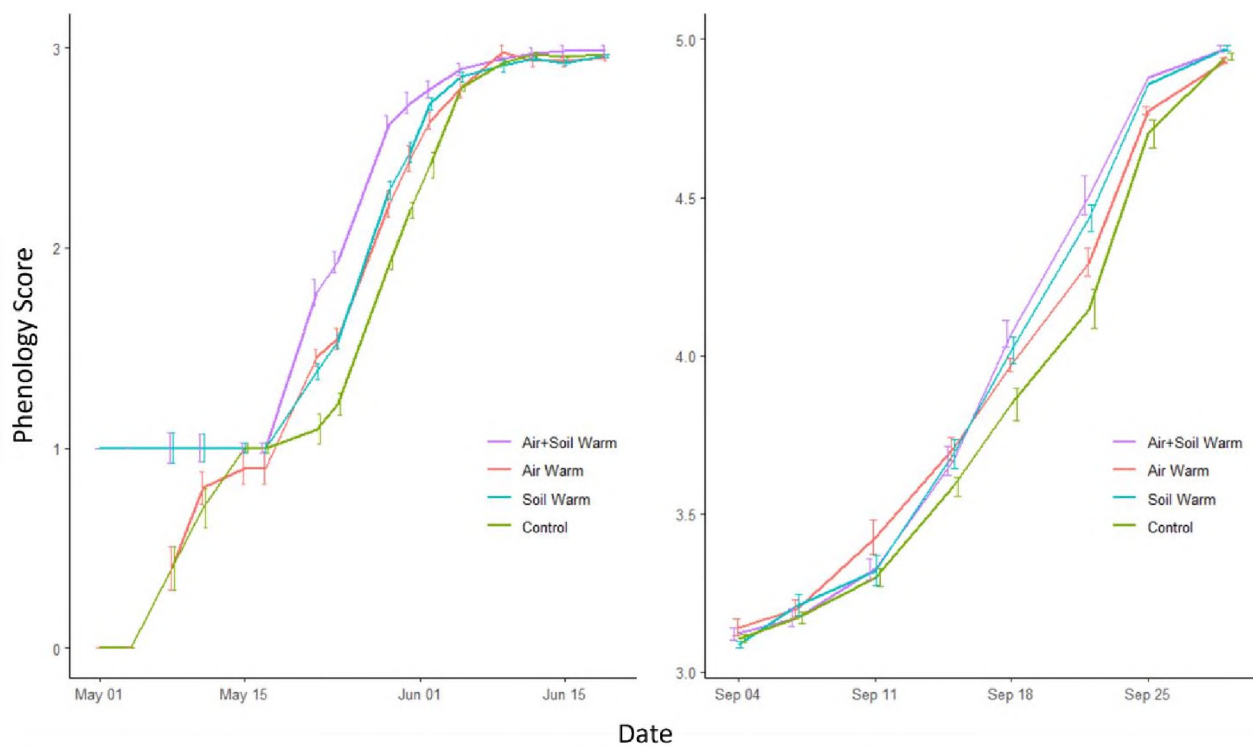


Figure 1.6 Mean phenology scores for *E. arvense* treatments by observation bout with spring phenology left and fall phenology right. Error bars represent one standard error of the mean.

## 1.7 Tables

Table 1.1 Site locations and elevations.

	Latitude	Longitude	Elevation (m)	Slope	Aspect
Site 1	64.8981° N	-147.8141° W	227	10%	SW
Site 2	64.8981° N	-147.8150° W	212	10%	W
Site 3	64.8611° N	-147.8467° W	182	~0	NA
Site 4	64.8608° N	-147.8479° W	183	~0	NA
Site 5	64.8609° N	-147.8573° W	181	~0	NA
Site 6	64.8615° N	-147.8559° W	181	~0	NA
Site 7	64.8627° N	-147.8585° W	171	~0	NA
Site 8	64.8639° N	-147.8595° W	166	~0	NA
Site 9	64.8766° N	-147.8669° W	212	~0	NA
Site 10	64.8756° N	-147.8680° W	213	~0	NA



Table 1.2 Results of repeat measures ANOVA for our four response variables. The models are structured the same way: response variable ~ Plot + Time \* Treatment.

ANOVA Model	Effect	Df	F value	p-value
Proportion of Stems Emerged	Time	1	10627.9	<0.001
	Treatment	3	19.3	<0.001
	Treatment:Time	3	0.2	0.872
Horsetail Height	Time	1	2417.3	<0.001
	Treatment	3	56.2	<0.001
	Treatment:Time	3	7.9	<0.001
Spring Phenology	Time	1	4588.8	<0.001
	Treatment	3	40.1	<0.001
	Treatment:Time	3	25.9	<0.001
Fall Phenology	Time	1	2585.9	<0.001
	Treatment	3	3.7	0.012
	Treatment:Time	3	1.4	0.253