THESIS

EFFECTS OF ALTERED SEASONALITY ON PLANT PHENOLOGY AND FUNCTION

IN ARCTIC TUNDRA

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2015

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ABSTRACT

EFFECTS OF ALTERED SEASONALITY ON PLANT PHENOLOGY AND FUNCTION IN

ARCTIC TUNDRA

Altered seasonality is one of the many consequences of climate change that is affecting plant

communities worldwide. Warmer temperatures, altered precipitation patterns, and changes in

duration of snow cover are a few of the seasonal changes taking place. These abiotic cues are key

drivers of the annual life cycles of plants, and effects of their changes vary across ecosystems,

plant communities, and individual species. Regardless, changes in vegetative phenology, through

earlier and/or later leaf greening and senescence, determine the timing and extent of the growing

season. The consequent impacts on ecosystem function include feedbacks to local climate,

changes in trophic interactions, altered nutrient cycling and plant community dynamics, and

changes in plant production and carbon balance.

Because Arctic ecosystems are undergoing more rapid climate change relative to lower

latitudes, plant community responses there may be indicative of changes to come in other

systems. In the Arctic, seasonal changes are characterized by warmer temperatures and altered

duration of snow cover. While landscape-scale observations of Arctic regions suggest a general

trend towards earlier onset of greening, later plant senescence, and increased aboveground

production, experiments are needed to determine the species and mechanisms that are driving

these trends. Over three years, we experimentally altered the timing of snowmelt and increased

temperature in moist acidic tundra. We investigated plant phenological and functional response

to these changes.

First, we asked how early snowmelt and warming affect the timing of leaf appearance and expansion, and whether spring phenological shifts would affect aboveground production of individual species. Earlier leaf expansion and growth are expected with warmer temperatures; however, in seasonally snow-covered ecosystems, timing of snowmelt may be an additional cue of plant species green-up. We found that altered seasonality led to earlier plant growth, but aboveground plant production varied among species. Further, variation in the timing of leaf expansion across functional groups due to evolved plant strategies rather than within functional groups due to experimental climate change corresponds with patterns of increased aboveground plant production. As a result, we predict that climate change will alter plant communities by increasing the abundance of early-growing plant species, even those that do not shift the timing of leaf expansion.

Second, we asked how altered seasonality would affect the timing and rate of plant community senescence, and how air and soil microclimate influences these processes. The timing of plant senescence is thought to be primarily controlled by photoperiod; however, recent studies have shown that environmental cues such as temperature and soil water content can modify timing of senescence. In the Arctic, where photoperiod decreases rapidly in August, senescence may not shift as climate warms due to strong photoperiod control. We tested alternative models of senescence to determine if microclimate (air temperature, soil temperature, and soil moisture), or start of season phenology events affect the onset and rate of community senescence. All three microclimate predictors partially explained variation in timing of onset of senescence, suggesting that photoperiod is not the sole control on this process in Arctic plant communities. Rather, increased air and soil temperatures along with drier soil conditions, led to acceleration in the onset of senescence at a community level. Our data suggest that climate

change could result in a shorter peak season due to earlier onset of senescence, which could

decrease potential carbon uptake in moist acidic tundra.

ACKNOWLEDGEMENTS

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CHAPTER ONE: INTRODUCTION

Over the last 30+ years, the ecology of plant communities has been altered by climate change (Walther et al. 2002, Parmesan 2006, Walther 2010). Plant community dynamics are driven in large part by abiotic factors, including temperature, precipitation and snow cover; changes to these drivers have resulted in altered seasonality of ecosystems. Response to altered seasonality varies by region, plant community type, and individual species. However, observed responses across ecosystems include shifts in species relative abundance (Willis et al. 2008, Elmendorf et al. 2012), range shifts (Parmesan and Yohe 2003, Walther et al. 2005, Gottfried et al. 2012), and changes in aboveground plant production (Myneni et al. 1997, Knapp and Smith 2001, Wang et al. 2012). Changes in species' phenology at individual and community levels are also widespread (Miller-Rushing and Primack 2008, Thompson and Clark 2008). Phenology is the study of periodic events that occur in the life cycle of plants or animals (Cleland et al. 2007). Plant phenology is sensitive to variation in climate and therefore is a strong source of evidence of species' responses to the direct and indirect effects of climate change. Additionally, modeling and experimental approaches have shown that phenological shifts can serve as an indicator of functional responses (e.g., ecosystem productivity) (Schwartz 1998, Cleland et al. 2007, Richardson et al. 2013).

Changes in vegetative phenology (i.e., leaf expansion, development and senescence) determine the timing and length of the growing season. Landscape-scale observations from remote sensing data indicate that spring green-up is occurring earlier in temperate and northern latitudes (Myneni et al. 1997, Zhou et al. 2001, Jia et al. 2003, Buitenwerf et al. 2015). There is also evidence that leaf senescence in fall is being delayed due to warmer temperatures (Jeong et

al. 2011, Dragoni and Rahman 2012, Zhu et al. 2012). Together, these observations suggest that the growing season is being extended at both ends. However, remotely sensed data cannot detect individual species' responses, and these may vary in direction in response to altered seasonal cues (Fitter and Fitter 2002, Menzel et al. 2006). Earlier and/or later leaf expansion and senescence of individual species determine the change in growing season length for the plant community, and differences in life history strategies (e.g., early-greening vs late-greening) may explain variation in response to altered seasonality (Steltzer and Post 2009).

Extension in growing season length at either end of the season affects multiple aspects of ecosystem function. Plant species' phenology is often coupled to interactions with species at other trophic levels, such as the relationship between plants and their insect pollinators. If species respond differently to a change in the same cue, the resulting mismatch may be detrimental to fitness for both species (Parmesan 2006). For example, when flowering of a spring ephemeral species advanced due to warming without a concurrent advance in its primary pollinator, seed production decreased (Kudo and Ida 2013). Likewise, dissimilarities in phenological shifts across a plant community may result in decreased complementarity (Cleland et al. 2006, Sherry et al. 2007), contributing to shifts in species relative abundance. Changes to land surface phenology can alter physical properties of the landscape, resulting in feedback to local climate. For example, the expansion of woody shrubs in the Arctic (Sturm et al. 2001, Tape et al. 2006) has an overall positive feedback to climate, resulting in enhanced local warming due to reduced albedo by the taller and darker shrub canopies (Penuelas et al. 2009, Richardson et al. 2013, Pearson et al. 2013). Finally, a longer growing season is expected to result in increased carbon storage in plant biomass (Peñuelas and Filella 2001).

Because Arctic ecosystems are undergoing more rapid climate change relative to lower latitudes, plant community responses there may be indicators of changes to come in other ecosystems. In the Arctic, seasonal changes are characterized by warmer temperatures (~ 1°C/decade (Christensen et al. 2013)), earlier snowmelt (3-5 days/decade) and later snowfall (Serreze et al. 2000, Dye 2002, Hinzman et al. 2005, Zeng et al. 2011). While landscape-scale observations of Arctic regions suggest that phenology is advancing in spring and being delayed in fall (Zeng et al. 2011, Zhu et al. 2012, Buitenwerf et al. 2015), experiments are needed to determine the species and mechanisms that are driving these trends. The effect of growing season changes on carbon balance in Arctic regions is of particular interest because of the large stocks of carbon stored in slowly decomposing permafrost soils (Post et al. 1982). Even small changes in length of the growing season can greatly affect carbon storage; for example, Euskirchen et al. (2006) estimates that net carbon uptake increases by 5.3 g $C/m_2/yr$ for each day of growing season extension.

Warmer spring temperatures and early snowmelt are expected to advance spring plant phenology in the Arctic. Earlier leaf appearance and expansion, in turn, is expected to lead to increases in aboveground productivity and net ecosystem productivity. However, ecosystem processes (i.e., productivity) may respond in multiple ways to earlier onset of spring, depending on other ecological constraints or indirect effects of warming in the ecosystem (Richardson et al. 2010). In Chapter 2, we ask the following questions: 1) How will early snowmelt with and/or without warming affect the timing of spring phenological events and aboveground net primary production (ANPP)?, and (2) Will earlier growth as characterized by earlier leaf expansion lead to greater growth as characterized by ANPP during peak season?

Warmer temperatures are also expected to delay leaf senescence in the Arctic, contributing to an overall increase in growing season length. Although a trend towards delayed senescence at a landscape scale has been demonstrated, senescence processes have shown mixed direction of response to warming experiments. Further, the mechanism controlling senescence processes in the Arctic are relatively poorly studied (Richardson et al. 2012, Gallinat et al. 2015) and represent a significant knowledge gap in terrestrial ecosystem models. In Chapter 3, we address the question: Does microclimate (air temperature, soil temperature, and soil moisture) explain variation in the onset and rate of senescence at a community level in moist acidic tundra?

To answer the questions posed in Chapter 2 and 3, we altered the seasonality of moist acidic tundra in Arctic Alaska, by advancing the timing of snowmelt and warming air temperatures during the snowfree period. Plant phenological and functional responses were monitored over three years.

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CHAPTER TWO: ALTERED SEASONALITY DUE TO EXPERIMENTAL CLIMATE

CHANGE LEADS TO EARLIER GROWTH BUT NOT MORE GROWTH IN ARCTIC

TUNDRA

Introduction

Seasonality in temperate to polar ecosystems is shifting through earlier seasonal warming

and changes in precipitation regimes that lead to earlier snowmelt (Schwartz et al. 2006, Hayhoe

et al. 2007, Ernakovich et al. 2014). Plant community responses are apparent, through changes in

timing of life cycle events such as leaf expansion and flowering (i.e., phenology) (Miller-

Rushing and Primack 2008, Thompson and Clark 2008), shifts in species relative abundance

(Willis et al. 2008, Elmendorf et al. 2012a), species' range shifts (Parmesan and Yohe 2003,

Walther et al. 2005, Gottfried et al. 2012), and greater aboveground plant production (Myneni et

al. 1997, Knapp and Smith 2001, Wang et al. 2012). These observations of altered seasonality

and plant community changes correspond to the period of increasing global temperatures, but

experiments are still needed to determine mechanisms and develop predictive models as climate

change continues (Pau et al. 2011, Richardson et al. 2012).

Temperature and photoperiod are known plant phenological cues that determine the

timing of spring events, such as bud burst, leaf emergence and canopy development, and

flowering (Cleland et al. 2007, Körner and Basler 2010, Polgar and Primack 2011). Experimental

warming studies using different techniques, such as active warming through overhead infrared

heaters or passive warming with open-top chambers, demonstrate that many species begin

growth and flowering earlier in warmed vs control plots (Cleland et al. 2006, Sherry et al. 2007,

Post et al. 2008, Bloor et al. 2010, Reyes-Fox et al. 2014). However, responses can vary with

some species not shifting or delaying the timing of spring events under warmed conditions

(Hollister et al. 2005a, Oberbauer et al. 2013, Reyes-Fox et al. 2014, Marchin et al. 2015). Similarly, long-term observations of phenological response to climate warming over time show an overall advance in timing of spring of an estimated 5-6 days/°C (Wolkovich et al. 2012), but with interspecific variation (Fitter and Fitter 2002, Menzel et al. 2006). The variation in response suggests that phenology is cued by other environmental variables for species within and across diverse plant communities from tundra, grassland, and forest biomes. For example, photoperiod limits plant development from occurring prior to when day length extends beyond some threshold duration and is a common constraint for many temperate tree species (Körner and Basler 2010, Basler and Körner 2014). Photoperiod also likely affects seasonal plant development in alpine tundra plant communities, but may be less important in the Arctic where day length is long during the period of time when seasonal warming and snowfree conditions occur (Ernakovich et al. 2014).

The influence of snow cover on plant phenology is less well understood, in part because temperature change due to climate change and experimental warming influence when an area becomes snowfree. Development of early season species may be closely synchronized with timing of snowmelt in Arctic and alpine ecosystems (Galen and Stanton 1995, Høye et al. 2007). However, few experiments have examined the isolated effects of early snowmelt and summer warming in the Arctic or alpine, and often these effects are confounded either by the use of warming treatments such as open-top chambers (OTCs) to accelerate snowmelt, or snow removal which reduces water inputs (Wipf and Rixen 2010).

Multifactor global change experiments have shown that plant production is sensitive to manipulations of abiotic factors, including air and soil warming, nutrients, CO_2, and precipitation (Fay et al. 2003, Dukes et al. 2005, Morgan et al. 2007, Dijkstra et al. 2008, Dawes et al. 2011).

Response to these factors is complex, with variation across plant communities due to differences in limiting factors (Smith et al. 2015), and variation within communities due to differences in functional group responses (Zavaleta et al. 2003, Wahren et al. 2005, Muldavin et al. 2008). In the Arctic, production is strongly limited by N availability, which in turn is sensitive to temperature and ongoing changes in the timing of seasonal climatic events such as snowmelt, soil thaw, the onset of freezing, and snowfall (Bliss 1956, Shaver and Kummerow 1992, Sturm et al. 2005, Weintraub and Schimel 2013). In recent years, both observational and experimental studies have linked increased production to warmer temperatures, with a prevailing trend in the Alaskan Arctic of expansion and increased biomass of woody shrubs (Graglia et al. 2001, Tape et al. 2006, Elmendorf et al. 2012a, Sistla et al. 2013). However, a number of experiments that have manipulated summer temperature in both Arctic and alpine regions did not find a consistent increase in community-level ANPP; rather, individual species or functional groups varied in their response and changes in ANPP canceled out at the community level (Chapin et al. 1995, Harte and Shaw 1995, Hobbie and Chapin 1998, Price and Waser 2000). For example, a meta-analysis of standardized warming experiments over the past three decades from the International Tundra Experiment (ITEX) showed that deciduous shrub growth and increased height and cover of graminoids is linked to warmer summer temperatures, while evergreen shrubs and forbs show both positive and negative responses (Walker et al. 2006).

Changes in plant production may also be expected to vary in relation to changes in the timing of growth; for example, earlier leaf expansion may lead to greater productivity (Richardson et al. 2010). There is evidence that phenological 'tracking' of climate change across biomes can result in positive growth responses, through increased abundance, production, or flowering effort (Cleland et al. 2012). However, physiological constraints and interactions of the

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affected species may prevent some plants from taking advantage of an earlier start to the growing season (Schwartz 1998, Richardson et al. 2010, 2013, Polgar and Primack 2011). One such constraint could be negative impacts of exposure to cold temperatures and freezing damage if snow melts early (Gorsuch and Oberbauer 2002, Wipf et al. 2009, Rixen et al. 2012). Differences in functional group response may also affect the relationship between phenology and production; for example, a community dominated by deciduous shrubs showed greater advance in phenology and positive production response than an evergreen dominated community in the same region (Sweet et al. 2014).

In the Arctic, climate is changing at a faster rate than in other regions, a trend that is expected to continue (Christensen et al. 2013). Rapidly increasing air temperature (~ 1°C/decade) (Christensen et al. 2013), earlier snowmelt (3-5 days/decade) and later snowfall (Serreze et al. 2000, Dye 2002, Hinzman et al. 2005, Zeng et al. 2011) are changing the seasonality of this ecosystem. The consequent impacts to ecosystem function are already being observed; for example, the amplitude increase of the seasonal CO_2 cycle in the northern hemisphere is highest at latitudes above 45° (Keeling et al. 1996, Zhao and Zeng 2014). Landscape-scale observations via remote sensing suggest that vegetation phenology in the Arctic is indeed advancing and plant production is increasing (Myneni et al. 1997, Jia et al. 2003). Furthermore, repeat photography has shown that deciduous shrub abundance has increased, through greater growth of this functional group relative to others since the 1950's (Sturm et al. 2001, Tape et al. 2006). Earlier snowmelt, especially in combination with warmer temperatures in early spring, should benefit plant growth, since it is the time of year with the greatest light and nutrient availability (Weintraub and Schimel 2013, Edwards and Jefferies 2013). However, experiments are needed to determine how shifts in seasonality will affect phenology of Arctic

species, and how consequent changes in phenology impact plant productivity and future community composition.

In an Arctic ecosystem, we established a three-year study in which we altered seasonality through the independent and combined manipulation of warming via open-top-chambers and snowmelt via accelerating snowmelt. We examined the response of spring phenology and plant production for key tundra species and hypothesized that:

(1) The timing of snowmelt and temperature are cues for initiating plant growth. We predicted that leaf appearance and expansion would advance due to early snowmelt and climate warming for all species.

(2) The timing of snowmelt and temperature affect plant production. We predicted that early snowmelt and warmer temperatures would increase biomass of deciduous shrub, graminoid and forb species, but would not change biomass of evergreen shrubs.

(3) The timing of plant growth affects plant production. We predicted that earlier leaf expansion would lead to greater biomass at peak season.

Methods

Site Description

The experiment was conducted near Imnavait Creek on the North Slope of Alaska, close to the Arctic Long-Term Ecological Research (LTER) site at Toolik Field Station. The plant community at Imnavait is moist acidic tussock tundra, characterized by the tussock forming sedge *Eriophorum vaginatum* and a high moss cover, including *Hylocomium spp., Aulacomnuim spp.,* and *Dicranum spp.*(Bliss and Matveyeva 1992). Plants associated with moist depressions in the inter-tussock spaces at this location include another sedge, *Carex bigelowii*, the deciduous

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shrubs *Betula nana* and *Salix pulchra*, the evergreen shrubs *Ledum palustre, Vaccinium vitis-idaea*, and *Cassiope tetragonum,* and a variety of forbs. The community composition specific to Imnavait Creek is shown in

Table **7**. The old (~120,000-600,000 years; (Whittinghill and Hobbie 2011)), acidic soil (mean pH of 4.5) at this site is underlain by continuous permafrost, with an uneven surface layer of organic material 0-20 cm thick (Shaver and Chapin 1991, Walker et al. 1994) and variable soil moisture.

Altered Seasonality

For three years (2010-2012), snowmelt was accelerated in five 8m x 12m plots using radiation-absorbing black 50% shade cloth that was placed over the snowpack in late April-early May. The dark fabric accelerated melt without decreasing snow-water inputs and allowed for minimal disturbance of the snowpack. The fabric was removed when plots became 80% snow-free (determined by daily visual estimates). As plots became snowfree, open-top chambers (OTC) were deployed as subplots within the accelerated snowmelt and control areas. The OTCs are hexagonal chambers with sloping sides, constructed of Plexiglas material that allows transmittance of wavelengths of light in the visible spectrum, enabling passive warming primarily through reducing heat loss by wind (Marion et al. 1997). The approximate area of both control and warming subplots was 1 m^2. Treatments were replicated five times in a full factorial, randomized split-plot design.

In 2012, we achieved a 10 day acceleration in the timing of snowmelt, with shade cloth being placed on April 28, early snowmelt plots becoming snow-free on May 16 and control plots snow-free on May 26. Colder temperatures and cloudy conditions contributed to a relatively long, slow melt period. OTCs warmed air temperatures by an average of 1.4°C in 2012.

Five individuals of seven species were marked in each plot and phenology events were monitored every two to three days from snowmelt through mid-August. Observations of 'leaf appearance' and 'leaf expansion' were recorded for each individual. Although definitions of events varied between functional groups, we generally considered leaf appearance to be the first observation of new green leaves and leaf expansion to be when an individual had a leaf that was fully expanded or had reached a previously determined size. For deciduous shrubs (*B. nana* and *S. pulchra*), leaf appearance was recorded at the first observed leaf bud burst (corresponds to ITEX protocol P2 event, (Molau and Edlund 1996)) and leaf expansion when an individual had at least one fully unfurled leaf. Similarly, evergreen shrub (*L. palustre* and *V. vitis-idaea*) leaf appearance was recorded when the first leaf bud was visible, and full leaf expansion occurred when at least one leaf bud was fully open and leaves unfurled. *E. vaginatum* retains green leaf material over winter and often begins growth of new leaves and re-greening of old leaves before snow is completely melted (Shaver and Kummerow 1992). Therefore, we recorded leaf appearance (new leaves > 1cm length) for *E. vaginatum* on the day of snowmelt, but did not consider this a treatment effect. Rather than continuously measuring leaf length to record full leaf expansion, we determined leaf expansion for *E. vaginatum* to have occurred when a new leaf reached > 4cm length. We only considered growth of new leaves, which were identified as those with no senescent material at the leaf tip. *C. bigelowii* followed similar protocol for leaf appearance (new leaf > 1 cm length) (corresponds to ITEX protocol P2 event, (Molau and Edlund 1996)) and leaf expansion (new leaf > 4 cm length), but leaf appearance was considered a treatment effect. First leaf appearance for the forb *P. bistorta* was marked when leaves were

visible (generally > 1 cm length) and leaf expansion when leaves were fully unrolled and > 5 cm length.

Plant Production

A destructive harvest to measure plant production, as characterized by individual biomass, was carried out on the same species for which phenology was observed. The seven species chosen represented four functional groups and comprised the majority of vascular plant cover at our site (Table 7). The harvest took place in the third year of treatments at peak growing season, which was determined by phenology observations and analysis of daily NDVI measurements showing that peak greenness (i.e. full canopy development) had occurred in each treatment (unpublished data). Randomly selected individuals were clipped in the field, and then taken back to the lab where old and new growth was separated and biomass measured. Eight individuals each of *B. nana, S. pulchra,* and *L. palustre,* and sixteen individuals each of *V. vitis-idea, E. vaginatum, C. bigelowii,* and *P. bistorta* were collected and pooled. Plant material was separated by tissue type, dried at 60°C for 48 hrs and weighed.

Mean individual biomass for each species was calculated as the sum of current years' biomass divided by the number of individuals collected. Current years' biomass included leaves, new stems and secondary growth for shrub species and all aboveground plant tissue for graminoid and forb species. We calculated current annual secondary stem growth for *B. nana, S. pulchra,* and *L. palustre* as a proportion of standing stem biomass, using previously determined annual growth rates of woody stems from the nearby Toolik Lake LTER site (Bret-Harte et al. 2002). For these species, leaf production contributed more to total biomass than the calculated secondary growth. Secondary growth for the remaining shrub species, *V. vitis-idaea*, is negligible, and therefore was left out of biomass calculation for this species (Shaver 1986).

Standing stem biomass, excluding current seasonal growth, for individual shrub stems varied among plots and likely is a result of variation prior to when the experiment was established. To control for this variation and better detect treatment effects, individual biomass data are presented in relation to standing stem biomass excluding current annual growth (i.e. g new production/g standing stem biomass).

Statistical Analyses

For all analyses, the experiment was treated as a blocked split-plot design, where a large early snowmelt plot paired with an equally sized control plot comprise a single block. Plant responses and environmental variables were analyzed using a mixed model analysis of variance (ANOVA; SAS v 9.2, SAS Institute, Inc., Cary, NC, USA), with early snowmelt as the main plot factor and warming as the within plot factor. A random effect of block was included to control for inherent variation between the five replicates. All data were checked for normality and were found to meet the assumptions of ANOVA. Linear regression was used to analyze the relationship between phenology and plant growth.

Results

Early snowmelt was a strong driver of change in both the timing and rate of leaf appearance and expansion. These events advanced due to early snowmelt for all species except the one forb, *P. bistorta* (Figure 1), and the amount of change in timing varied between events, species and functional groups. The largest change in timing was a 10 day advance in leaf expansion for *E. vaginatum* ($P = 0.0033$), corresponding to the 10 day advance in snowmelt through our snow manipulation. Leaf appearance and expansion of evergreen and deciduous shrubs was significantly earlier, advancing by 1 to 8 days for *B. nana*, *S. pulchra*, *L. palustre* and

V. vitis-idaea (Figure 1, Table 1). The advancement of leaf appearance versus expansion differed in magnitude for *S. pulchra*, *V. vitis-idaea*, *C. bigelowii*, by decreasing the number of days following leaf appearance prior to leaf expansion by 2 to 5 days. For example, leaves first appeared for *S. pulchra* 8 days earlier than the control (*P = 0.002*), while leaf expansion advanced by only 3 days (*P < 0.0001*). For deciduous shrubs, evergreen shrubs and the forb, the shift in phenology was less than the 10-day advance in snowmelt, increasing the number of days after snowmelt to when canopy development (i.e. leaf expansion) began; this effectively slowed the rate of plant production (Figure 2, Table 2). The sedges, *E. vaginatum* and *C. bigelowii* did not follow this pattern, with leaf appearance and expansion following snowmelt just as quickly when snow melted early (Figure 2).

Table 1: Results of mixed-model ANOVA on timing of early season phenology events. Leaf appearance for *E. vaginatum* was not considered a treatment effect and was excluded from the analysis. Bold values here and in following tables indicate a significant main effect of the treatment at $P \leq 0.05$.

	Leaf appearance								
	Warming			Early snowmelt			Warming x Early snowmelt		
	d.f.	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
B. nana	1, 85	0.88	0.3503	1, 4	9.46	**0.0373**	1, 85	1.49	0.2253
S. pulchra	1, 71	0.21	0.6501	1, 8	20.24	**0.0019**	1, 71	0.15	0.7045
L. palustre	1, 86	5.75	**0.0186**	1, 4	21.53	**0.0099**	1, 86	0.00	0.9775
V. vitis-idaea	1, 83	15.08	**0.0002**	1, 4	8.92	**0.0405**	1, 83	0.01	0.9241
C. bigelowii	1, 83	0.16	0.6910	1, 4	65.58	**0.0012**	1, 83	0.20	0.6533
P. bistorta	1, 65	0.13	0.7212	1, 7	1.34	0.2829	1, 65	0.25	0.6184
	Leaf expansion								
	Warming			Early snowmelt			Warming x Early snowmelt		
	d.f.	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
B. nana	1, 86	55.71	**<0.0001**	1, 4	79.28	**0.0008**	1, 86	2.33	0.1308
S. pulchra	1, 77	1.86	0.1766	1, 77	42.81	**<0.0001**	1, 77	0.04	0.8329
L. palustre	1, 86	3.26	0.0743	1, 8	30.97	**0.0006**	1, 86	3.95	0.0501
V. vitis-idaea	1, 88	1.59	0.2108	1, 88	19.73	**<0.0001**	1, 88	1.04	0.3100
E. vaginatum	1, 86	3.36	0.0702	1, 4	37.14	**0.0033**	1, 86	1.38	0.2436
C. bigelowii	1, 84	1.64	0.2037	1, 4	31.25	**0.0053**	1, 84	0.55	0.4599
P. bistorta	1, 70	0.13	0.7182	1, 70	0.30	0.5882	1, 70	1.33	0.2525

Table 2: Results of mixed-model ANOVA on duration of time since snowmelt for early season phenology events. Leaf appearance for *E. vaginatum* was not considered a treatment effect and was excluded from the analysis.

	Leaf appearance								
	Warming			Early snowmelt			Warming x Early snowmelt		
	d.f.	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
B. nana	1, 86	1.00	0.3210	1, 8	22.56	**0.0015**	1, 86	1.35	0.2479
S. pulchra	1, 74	0.14	0.7070	1, 7	1.25	0.2975	1, 74	0.26	0.6112
L. palustre	1, 86	5.73	**0.0188**	1, 4	33.32	**0.0047**	1, 86	0.00	0.9889
V. vitis-idaea	1, 83	15.03	**0.0002**	1, 4	30.73	**0.0057**	1, 83	0.01	0.9179
C. bigelowii	1, 87	0.16	0.6933	1, 87	1.81	0.1823	1, 87	0.19	0.6639
P. bistorta	1, 65	0.10	0.7576	1, 65	36.75	**<.0001**	1, 65	0.49	0.4859

	Leaf expansion								
	Warming			Early snowmelt			Warming x Early snowmelt		
	d.f.	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
B. nana	1, 85	55.48	**<.0001**	1, 4	40.62	**0.0030**	1, 85	2.36	0.1281
S. pulchra	1, 75	0.89	0.3475	1, 4	45.21	**0.0028**	1, 75	0.35	0.5537
L. palustre	1, 90	3.44	0.0669	1, 90	59.34	**<.0001**	1, 90	4.16	**0.0444**
V. vitis-idaea	1, 85	1.50	0.2234	1, 4	173.94	**0.0002**	1, 85	0.95	0.3323
E. vaginatum	1, 87	3.51	0.0645	1, 4	0.00	0.9497	1, 87	1.33	0.2526
C. bigelowii	1, 84	1.71	0.1951	1, 4	4.42	0.1025	1, 84	0.54	0.4635
P. bistorta	1, 70	0.26	0.6115	1, 70	51.99	**<.0001**	1, 73	1.66	0.2013

Warming also advanced the timing of leaf appearance and expansion for most species, but to a lesser extent than early snowmelt (Figure 1, Table 1). All of the deciduous shrub and graminoid species advanced leaf phenology with warming alone, but only by 1 or 2 days (*B. nana* leaf expansion, $P < 0.0001$). Evergreen shrubs showed contrasting responses to warming: leaf appearance for *V. vitis-idaea* advanced by 3 days ($P = 0.0002$), while *L. palustre* leaf expansion was delayed for 2 days ($P = 0.0743$). Warming did not often alter phenology in relation to the timing of snowmelt (Figure 2, Table 2). One exception is that warming led to faster leaf expansion following snowmelt for *B. nana* ($P < 0.0001$), effectively speeding plant growth.
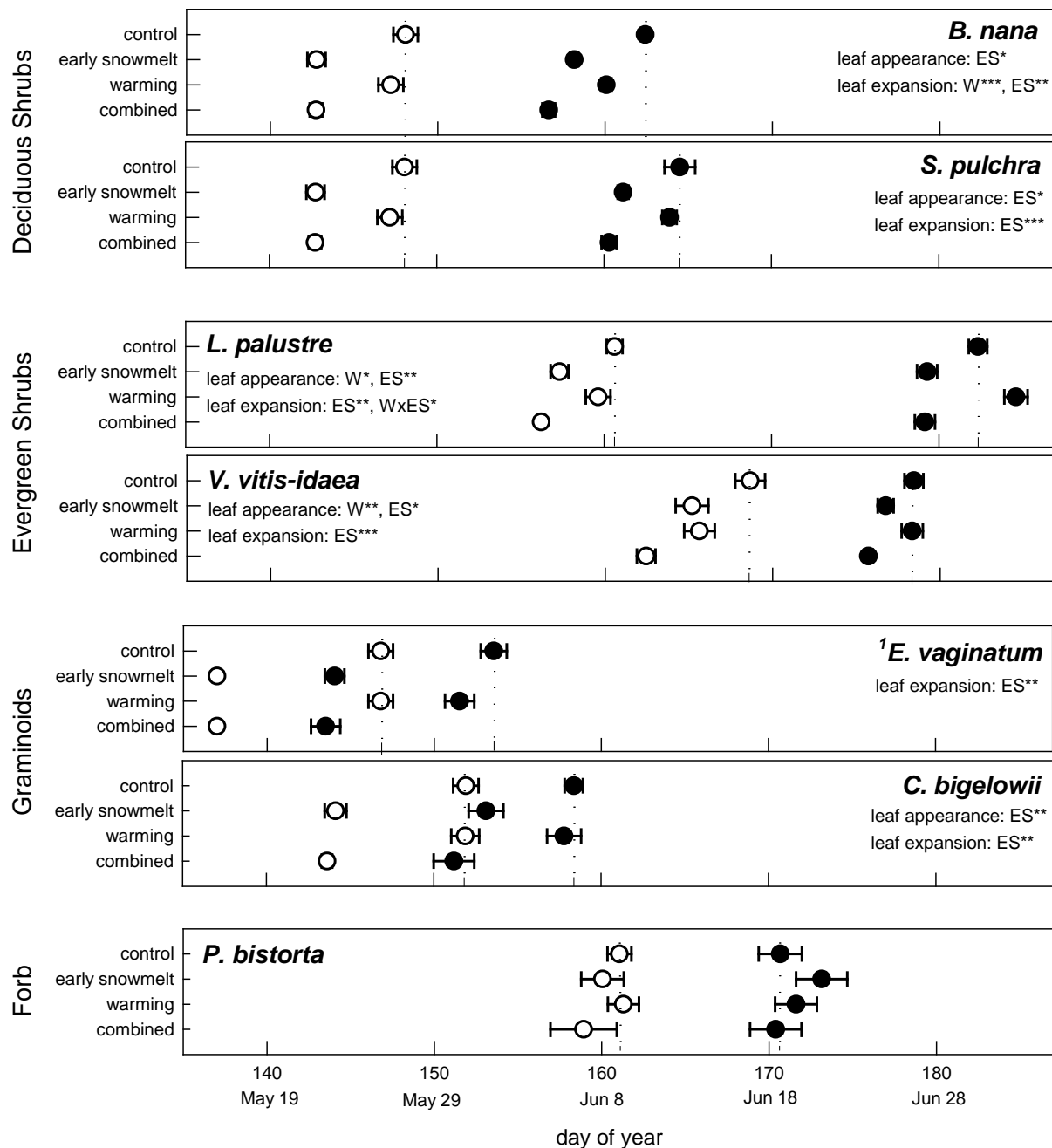
Figure 1: Dates of early season phenology events, where open circles represent leaf appearance and filled circles represent leaf expansion. Points are the mean date of event ± 1 s.e.m. Vertical dashed lines denote mean event date for control plots. The statistical significance of warming (W), early snowmelt (ES), and combined treatments (WxES) are shown in each species panel, where *P≤0.05, **P<0.01, ***P<0.0001. [1]*E. vaginatum* initiates growth underneath the snowpack so we did not consider leaf appearance to be a treatment effect; however, the event date is shown to signify the presence of new leaves at the time of snowmelt.
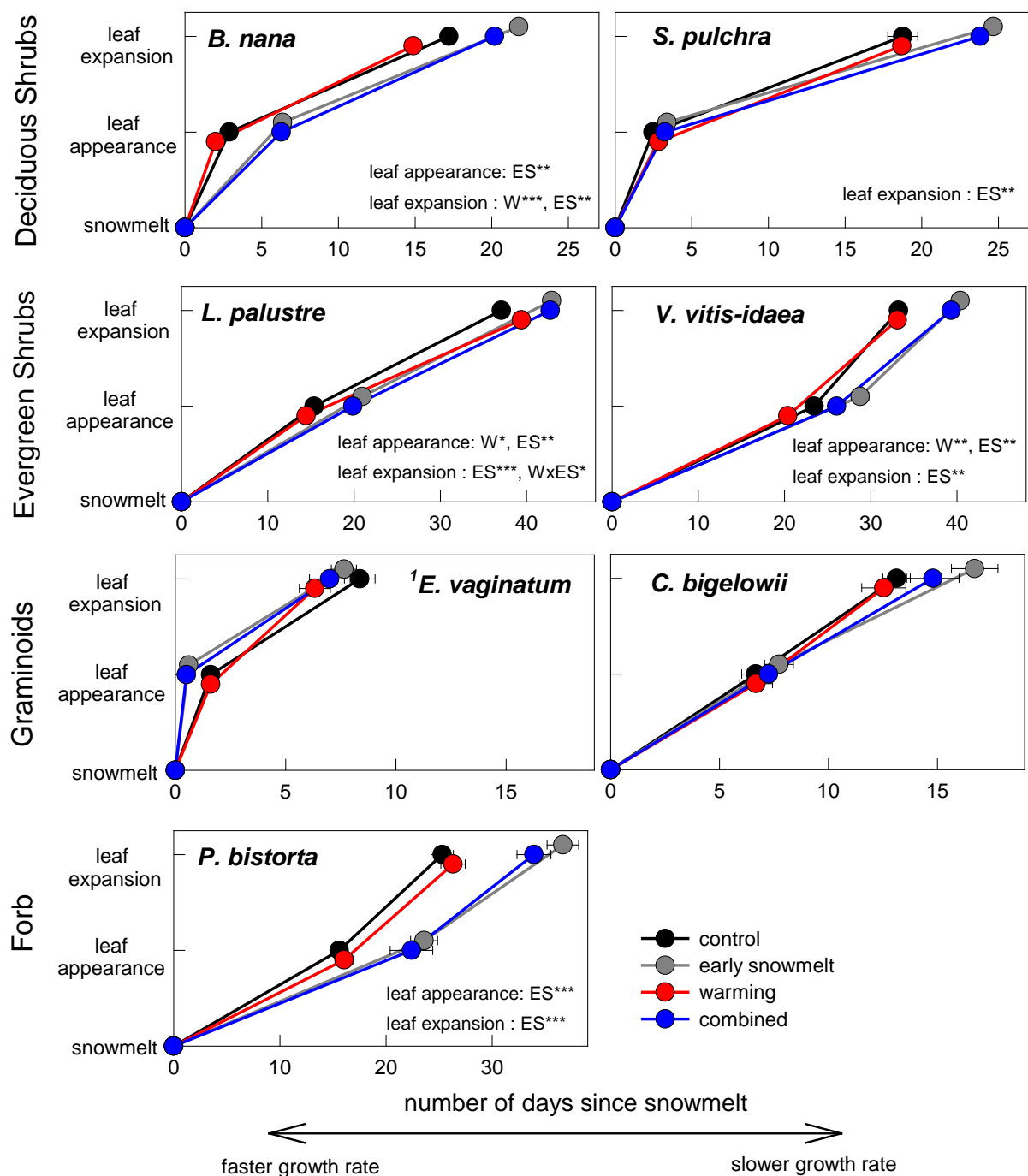
Figure 2: Number of days since snowmelt for early season phenology events. Points are average number of days since snowmelt and error bars are ±1 standard error of the mean. A greater number of days until full leaf expansion is interpreted as a slower growth rate. Note different scales on x-axes. Levels of statistical significance are noted as in Figure 1.

[1]Also as noted in Figure 1, leaf appearance of *E. vaginatum* is not considered a treatment effect but is shown for clarity.

Phenological responses to the combination of early snowmelt and warming most often were comparable to the response to early snowmelt alone (Figure 1, Figure 2). However, the interactive effect of warming x early snowmelt on timing of phenology was never significant (Table 1). For evergreen shrubs, leaf appearance occurred earliest with the combined treatment, which was 1 to 3 days earlier than in snowmelt and warming alone.

Although phenological events often occurred earlier in the year due to earlier snowmelt and warming, an increase in individual biomass was not often observed. For individual biomass, species' responses to early snowmelt and warming varied within and among growth forms. Differences were often not significant (Table 3), in part due to the challenge of quantifying plant production in an ecosystem with high spatial variation, but were a high proportion of production in this low productivity system. Deciduous shrub species differed in their response, with *S. pulchra* decreasing individual biomass by 6 (WxES: *P = 0.299*) to 11% (W: *P = 0.69;* ES: *P = 0.6783*) and *B. nana* showing little change across the three treatments. Evergreen shrub species increased individual biomass by 28 and 8% for *L. palustre* and *V. vitis-idaea*, respectively, due to early snowmelt (*P = 0.2782, P = 0.6686*). Individual biomass of *P. bistorta,* the forb, was highly variable within treatments; for example, biomass of control plants ranged from 36 to 297 mg. The most evident response for this species was a large decrease (36%) in biomass due to early snowmelt (*P = 0.7808*).

The effect of warming on growth was statistically significant for two species, and led to the largest proportional changes in individual biomass. Both graminoid species responded positively to warming. Mean individual biomass for *E. vaginatum* increased by 36% (*P = 0.0256*), which was the greatest proportional increase of any species. When early snowmelt and warming were combined, *E. vaginatum* increased individual biomass by 27% relative to the

control ($P = 0.1635$). The other graminoid, *C. bigelowii,* increased individual biomass by 17% with warming ($P = 0.2425$) and 24% with warming and early snowmelt ($P = 0.6926$). An evergreen shrub, *V. vitis-idaea*, had relatively large decreases relative to the control with warming (21%) and the combined treatment (42%), and the main effect of warming was significant ($P = 0.0338$).

Table 3: Results of mixed-model ANOVA on individual biomass.

	Individual biomass								
	Warming			Early snowmelt			Warming x Early snowmelt		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
B. nana	1, 16	0	0.9859	1, 16	0.22	0.6466	1, 16	1.02	0.3287
S. pulchra	1, 12	0.17	0.6900	1, 12	0.18	0.6783	1, 12	1.18	0.2990
L. palustre	1, 8	0.73	0.4185	1, 8	1.35	0.2782	1, 8	0.43	0.5283
V. vitis-idaea	1, 16	5.39	**0.0338**	1, 16	0.19	0.6686	1, 16	0.95	0.3454
E. vaginatum	1, 8	7.48	**0.0256**	1, 4	0.20	0.6757	1, 8	2.35	0.1635
C. bigelowii	1, 12	1.51	0.2425	1, 12	1.04	0.3277	1, 12	0.16	0.6926
P. bistorta	1, 16	0.85	0.3831	1, 16	0.08	0.7808	1, 16	0.28	0.6106

Across all species and for all treatments, earlier leaf expansion was associated with increased production (Figure 4, $R^2 = 0.09$, $P = 0.0021$). This relationship reflects differences in the timing of leaf expansion among growth forms and the response of individual biomass to early snowmelt and warming. Species varied in the timing of leaf expansion by 40 days, a range that was expanded by 14 days due to altered seasonality. Early greening species (*E. vaginatum, C. bigelowii*) had increases in biomass while later greening species (*L. palustre, V. vitis-idaea*) had some increases but also large decreases in biomass as a result of warming. Across functional groups, warming drove the relationship between timing of leaf expansion and individual biomass, as shown by significantly negative slopes within the warming and combined treatments (Figure 6; W: $R^2 = 0.13$, $P = 0.036$, WxES: $R^2 = 0.24$, $P = 0.005$). Within functional groups, there was no relationship between the timing of leaf expansion and individual biomass response, despite earlier leaf expansion due to early snowmelt and warming (Figure 5).
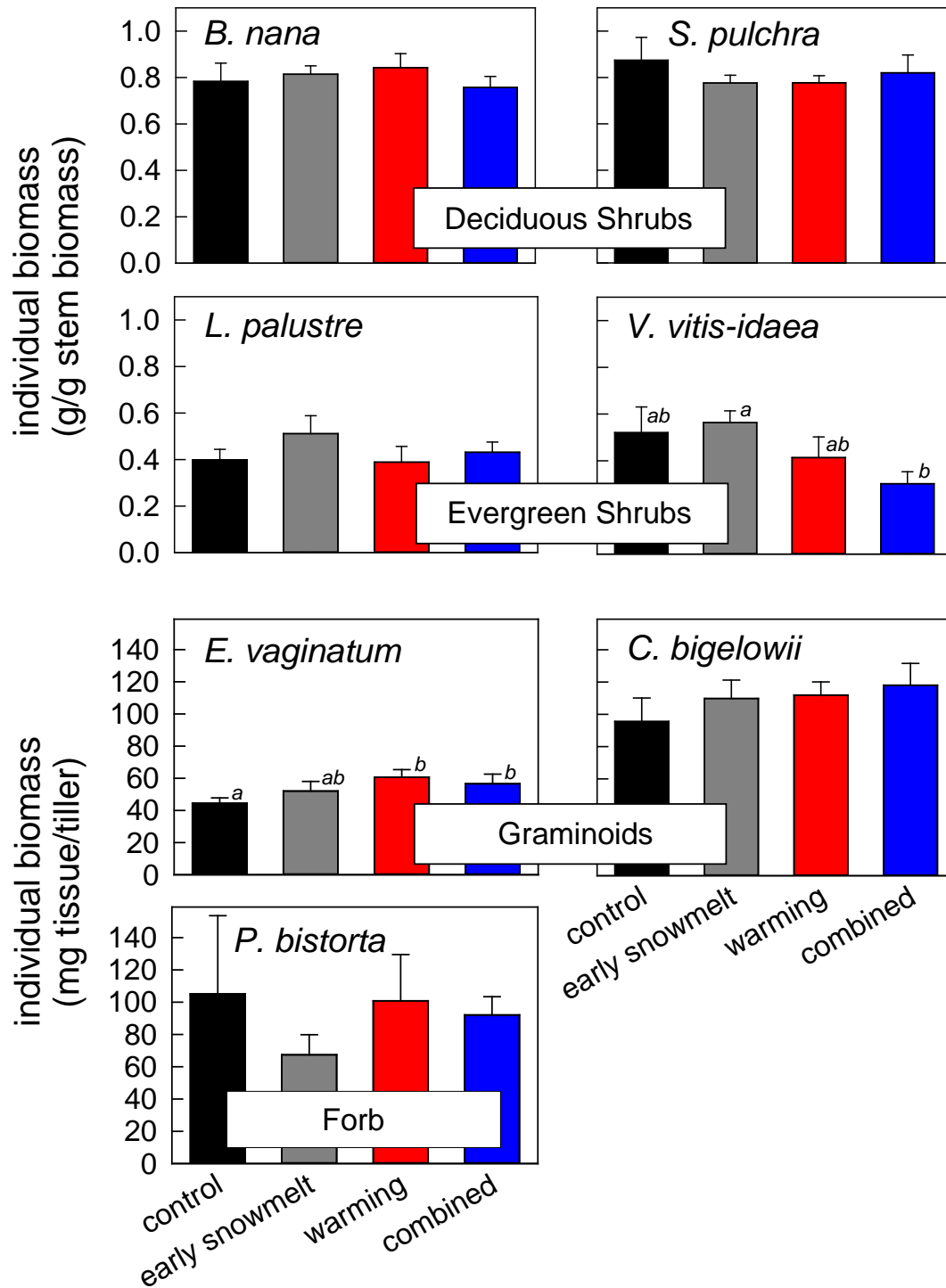
Figure 3: Biomass of individual species harvested at peak season in the third year of altered seasonality. For deciduous and evergreen shrubs, bars represent means of proportion of current annual growth to standing stem biomass of the individual, ± 1 s.e.m. For graminoids and a forb, bars represent means of aboveground biomass, ± 1 s.e.m. Letters (*a, b*) represent groupings based on least squares means of the ANOVA mixed model, where bars with the same letter are not statistically different at P ≤ 0.05.
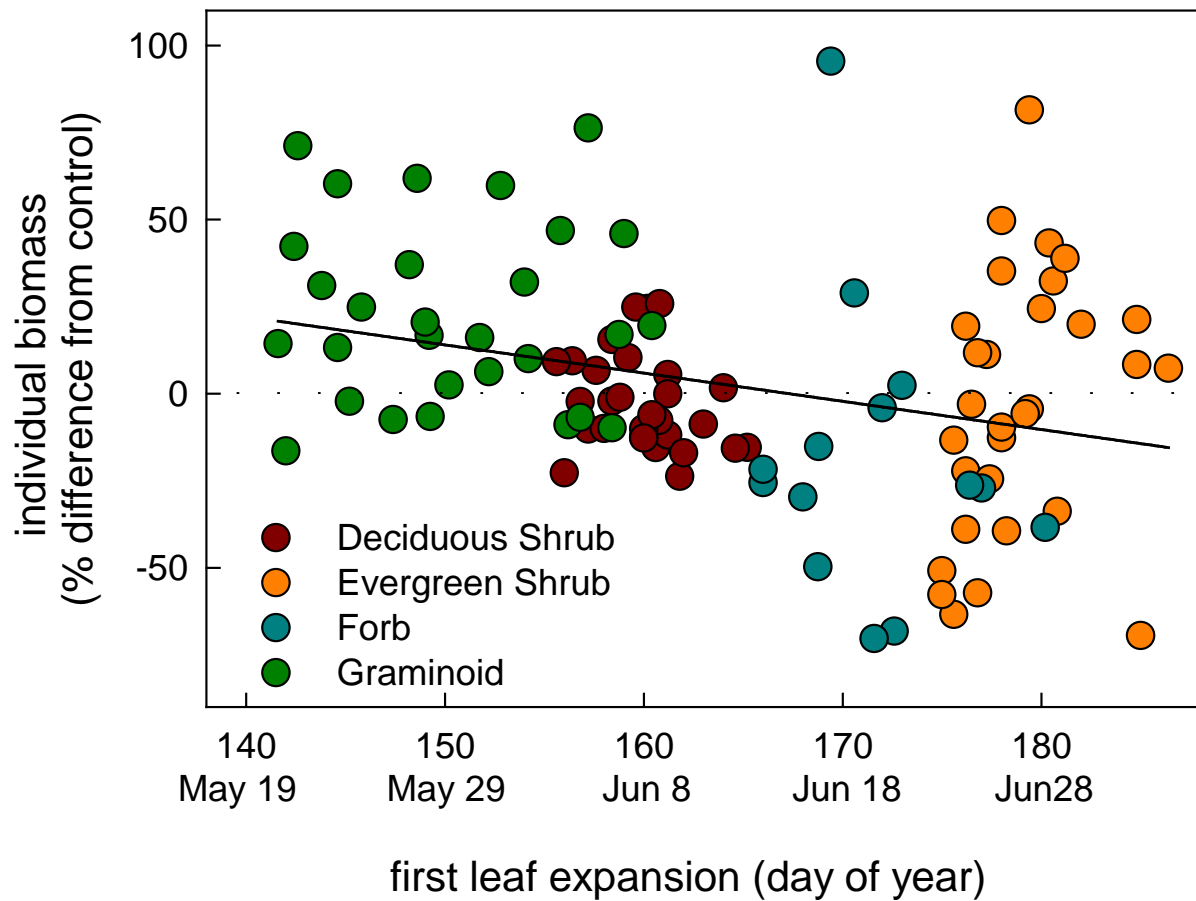
Figure 4: Relationship between phenology and production, with ANPP (y-axis) represented as the percent difference from the control mean ANPP for each species (100*_treatment-control mean/control_). Each point represents one species, treatment, and plot. The solid line is the linear regression (y = 135.52 – 0.81x) with slope significantly different than 0 (_P = 0.0021_).
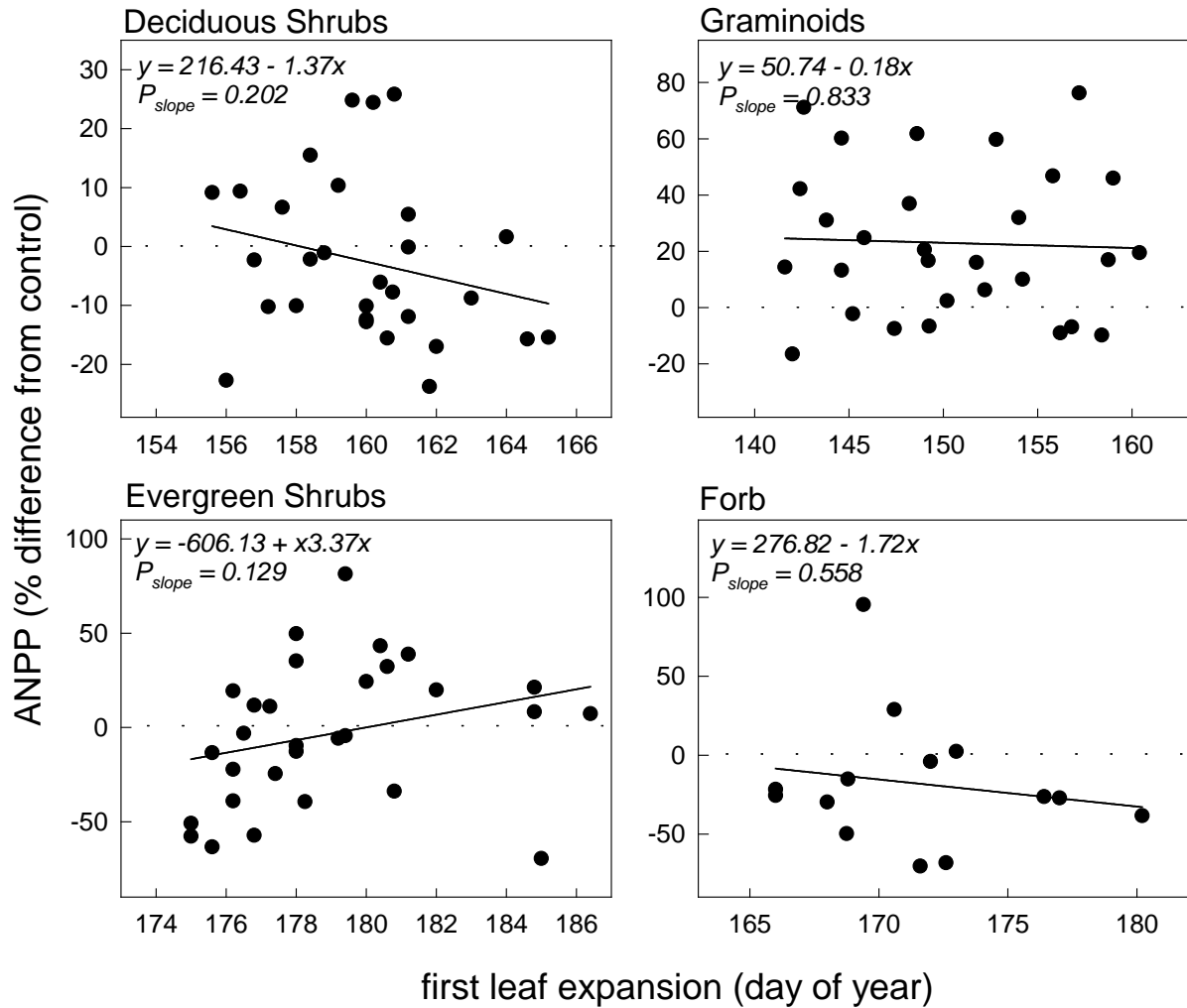
Figure 5: Relationship between phenology and production by functional group. Data follows Figure 4. Solid lines are linear regressions for each functional group, with the regression equation and significance level of slope shown in each panel.
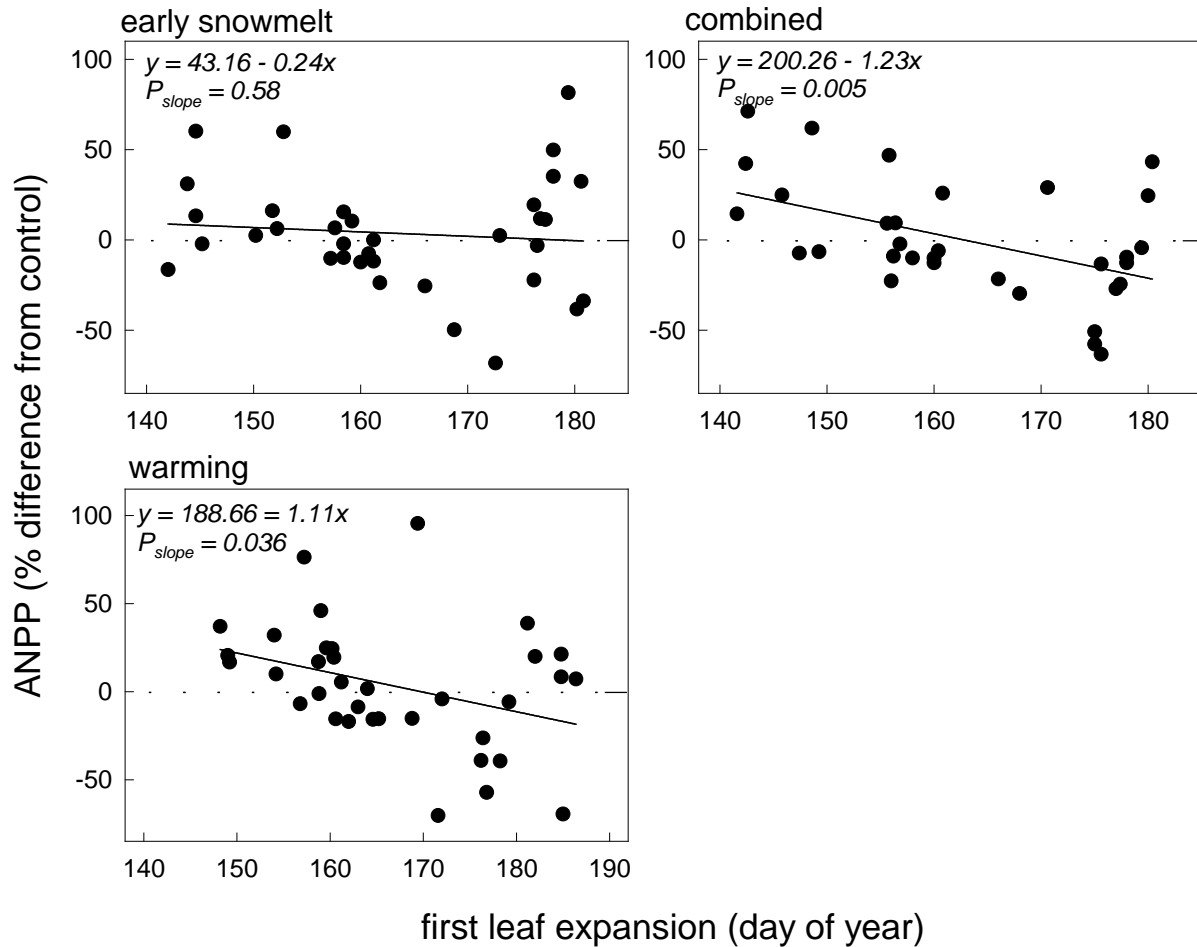
Figure 6: Relationship between phenology and production by treatment type. Data follows Figure 4. Solid lines are linear regressions for each functional group, with the regression equation and significance level of slope shown in each panel.

Discussion

Our results showed consistent advancement of leaf appearance and expansion, indicating that spring phenology of moist acidic tundra species is sensitive to early snowmelt and warming. Warmer temperatures have been shown to advance spring phenology in other systems, particularly for deciduous shrubs where budburst is well predicted by growing degree-days (Perry 1971, Polgar and Primack 2011). However, we found that species were more responsive to early snowmelt, by advancing timing of events to a greater extent than with warming alone. Timing of snowmelt has been shown to be a cue for spring phenology in Arctic and alpine

ecosystems (Arft et al. 1999, Steltzer et al. 2009), but experiments often confound the effects of warming and timing of snowmelt. Arctic species generally have a wide range of physiological tolerance, allowing spring growth to occur despite temperatures at or near freezing (Billings and Bliss 1959), and our experiment shows that early snowmelt can advance phenology independent of warming. Along with clear advances in spring phenology, we also observed slower rates of leaf expansion for many species in response to early snowmelt, supporting the conservative growth strategy demonstrated by many Arctic and alpine species to compensate for interannual variation in snowmelt timing (Billings and Mooney 1968). Species that expand leaves early may be susceptible to frost damage if temperatures remain cold or freezing events occur (Inouye 2008, Rixen et al. 2012).

Growth responses to warming and early snowmelt were dependent on growth form and individual species. Previous warming experiments have also shown interspecific variation in plant communities, with graminoids and deciduous shrubs showing rapid change relative to evergreen shrubs and forbs (Chapin and Shaver 1985, Chapin et al. 1995, Hobbie and Chapin 1998, Hollister et al. 2005b). The response of graminoids in our study was consistent with these experiments, with both *E. vaginatum* and *C. bigelowii* increasing biomass in response to warming and early snowmelt. While we measured biomass of individual tillers, new tiller recruitment is another likely mechanism by which either graminoid species could have increased total biomass (Chapin and Shaver 1985). If new tiller recruitment occurred along with increases in tiller biomass, we may have underestimated the overall change in graminoid production. Graminoids were the only functional group that maintained their growth rates when snow was melted early, which may confer an advantage in accessing early season nutrient pulses, and consequently increasing biomass in the same year (Shaver et al. 1986). They were also able to

advance timing of early season phenology to a greater extent than the other functional groups. This may be due to their ability to initiate growth underneath the snowpack and therefore have new leaves present at snowmelt in addition to green leaves that have overwintered (Chapin et al. 1979). Results of past work on *E. vaginatum* showed that early season air warming leads to accelerated leaf growth, greater light interception and earlier arrival at peak biomass (Sullivan and Welker 2005).

Warming resulted in a large decrease in biomass for the evergreen shrub, *V. vitis-idaea*, a species that has shown much variability in response to warming in previous experiments (Chapin et al. 1995, Hobbie and Chapin 1998, Arft et al. 1999, Zamin et al. 2014). A meta-analysis of warming experiments across the Arctic suggests that evergreen shrub response to warming depends on soil moisture regime, with plants in moist soils more often decreasing in abundance (Elmendorf et al. 2012b). Regardless, the large change in biomass that we observed was unexpected because evergreen shrubs have a conservative growth strategy, demonstrated by slower growth rates, lower specific leaf area, and lower photosynthetic capacity than other species in the tundra community (Shaver and Kummerow 1992, Chapin and Shaver 1996, Starr et al. 2008). A decrease in new leaf biomass by *V. vitis-idaea* could be related to conditions in previous years, since evergreen shrub growth relies in part on nutrients stored in old leaves (Billings and Mooney 1968). Evergreen shrubs also have the ability to access early-season nutrient pulses (McKane et al. 2002, Larsen et al. 2012) which may explain why both species increased biomass in response to early snowmelt, similar to graminoids. However, this does not explain why *V.vitis-idaea* would show the opposite response when early snowmelt was combined with warming.

Deciduous shrubs and a forb did not show clear responses to warming or early snowmelt. It may be that the 3-year duration of our study did not allow enough time for *B. nana* or *S. pulchra* to show significant changes in biomass. Short- and long-term responses to warming in the moist acidic tundra have been shown to vary, in part because of slow recruitment and establishment of new individuals (Hollister et al. 2005b). For example, observations from the ITEX experiments showed that community changes in deciduous shrubs did not become significant until after four years of warming (Walker et al. 2006). However, since we measured growth at an individual (rather than community) level in order to detect within-season changes of biomass accumulation, the response of deciduous shrubs may be more likely attributed to nutrient availability in that year. If evergreen shrubs were able to access nutrient pulses early in the season before deciduous shrubs, it may help explain why the latter showed little response, specifically when snow was melted early. The one forb tested in this experiment, *P. bistorta*, had highly variable results which may have obscured any treatment effects.

While the magnitude of temporal shifts is often a focus of phenological studies, our results suggest that evolved strategies within the plant community also play an important role in determining functional response to altered seasonality. Early greening species were able to advance phenology and increase biomass, while later greening species did not, demonstrating that temporal niche partitioning influences species' functional response to environmental change. A previous study (Cleland et al. 2012) examined plant responses to warming and found that phenologically flexible species (able to 'track' climate change) had positive performance responses (e.g., increased abundance, production). Our results are consistent with this hypothesis; however, changes in phenology alone did not result in a change in production. Rather, community patterns of greening, along with warming-driven increases and decreases in

ANPP, contributed to the relationship between spring phenology and production. Differences in species' ability to shift the timing and rate of leaf expansion may affect competitive interactions and subsequently influence future plant community composition (Richardson et al. 2010, Cleland et al. 2012). Specifically, *E. vaginatum*, which was able to green rapidly and maintain its growth rate, may have a competitive advantage.

Changes in vegetative phenology, regardless of changes in production, have important implications for the life history and productivity of vertebrate and invertebrate herbivores. Phenological shifts can affect competition among species, and differential responses of individual species may determine future plant community structure. Changes in Arctic plant communities have the potential to impact multiple aspects of ecosystem functioning, including: (1) carbon (C) cycling, by altering the balance between ecosystem-scale productivity and respiration (Shaver et al. 1992, Hobbie et al. 2000); (2) surface energy balance and feedbacks to the climate system, through change in albedo and seasonal changes in leaf area (Penuelas et al. 2009, Richardson et al. 2013); and (3) trophic relationships that may become decoupled if plant phenology responds to a changing climate differently than vertebrate and invertebrate herbivores (Post and Forchhammer 2008, Høye et al. 2013).

Our findings support the suggestion that satellite observations of earlier green-up across the Arctic may not be indicative of increased growth for all species (Gamon et al. 2013, Campioli et al. 2013). Rather, our study suggests that an earlier spring as indicated by satellite data is likely driven by early greening species such as *E. vaginatum* and *C. bigelowii*. These species have the advantage of being able to respond rapidly and positively to changes in seasonality, and may increase in abundance in tundra ecosystems as earlier snowmelt and warmer springs continue.

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CHAPTER THREE: MULTIPLE CLIMATE DRIVERS ACCELERATE ONSET OF

SENESCENCE IN ARCTIC PLANT COMMUNITY

Introduction

The timing and duration of peak season and the growing season are shifting due to altered seasonal cues for plant development (Sparks and Menzel 2002, Walther et al. 2002, Linderholm 2006). Growing season length for a plant community is determined by individual species' annual life cycles; it is characterized by the onset of greening for the first species, through leaf expansion and full canopy development, to the onset of leaf senescence and total leaf fall for the last species (Steltzer and Post 2009). Changes in the length of peak season, the time of full canopy development to the onset of senescence, or the entire growing season affect many aspects of ecosystem function, such as carbon balance (White et al. 1999, Richardson et al. 2012, Sweet et al. 2014), feedbacks to climate (Penuelas et al. 2009, Richardson et al. 2013), and trophic interactions (Visser and Holleman 2001, Clausen and Clausen 2013). Vegetative phenology is driven by multiple abiotic cues (Forrest and Miller-Rushing 2010, Polgar and Primack 2011). Some cues, like photoperiod, remain constant, whereas air and soil temperature, and water and nutrient availability are cues that are altered by climate change (Ernakovich et al. 2014). But, as climate change continues to increase temperatures and alter precipitation regimes (Christensen et al. 2013), how will plant communities alter their peak season and growing season length?

Extension of the growing season can be the result of earlier green-up and/or later onset or prolonged leaf senescence (Steltzer and Post 2009). Growing season changes have been documented through satellite observations of the Normalized Difference Vegetation Index (NDVI), which measures land surface greenness. However, varying definitions and methods for

extracting phenological events from remotely-sensed NDVI constrains our ability to detect overall trends (White et al. 2009). Nonetheless, earlier springs have been observed over the past three decades across temperate and northern latitudes (Zhou et al. 2001, Buitenwerf et al. 2015), with estimates of 2.7-11.5 days/decade depending on the region (Zeng et al. 2011). Delays in end of season phenology (i.e., leaf color change and leaf fall), with some estimates ranging from 2.5-5.5 days/decade, have also been detected (Jeong et al. 2011, Dragoni and Rahman 2012, Zhu et al. 2012). Remote sensing data indicate that later falls correlate to warmer temperatures (Jeong et al. 2011). But, remote sensing can only document emergent trends, and do not shed light on the mechanistic controls on end of season phenology. An improved mechanistic understanding is required to predict whether these trends will continue (Richardson et al. 2013, Gallinat et al. 2015), and causation can best be determined through experimentation.

Multiple abiotic drivers are known to exert control on the timing and duration of senescence, including photoperiod, temperature, and soil water and nutrient availability (Perry 1971, Estiarte and Peñuelas 2014). In addition, genetic control on leaf longevity can lead to periodic constraints (i.e., a set length for leaf lifespan), which may vary due to evolved life history strategies (Lam 2004, Kikuzawa et al. 2013). Response to these drivers varies across regions, latitudes, plant community types, and individual species (Menzel et al. 2006, Richardson et al. 2010, Buitenwerf et al. 2015). For example, experimental warming has led to delayed senescence in Arctic tundra communities (Marchand et al. 2004, Natali et al. 2012) and deciduous forest species (Gunderson et al. 2012, Marchin et al. 2015), while in a temperate grassland, the rate of community-level senescence was accelerated (Zavaleta et al. 2003). Further, multifactor global change experiments have shown that multiple drivers may interact to influence timing of senescence (Reyes-Fox et al. 2014).

Timing of changes in climatic cues (i.e., altered seasonality) may influence observed responses, and contribute important information to a mechanistic understanding of phenological events (Craine et al. 2012, Craine 2013, Clark et al. 2014). In addition to climate cues, recent studies have pointed to periodic control, where changes in start of season phenology (i.e., bud burst, canopy development) correspond to change in end of season phenology (Fu et al. 2014, Keenan and Richardson 2015).

The effects of changes in growing season length on ecosystem functioning may be especially important in regions with short growing seasons, such as the Arctic. In Arctic regions, favorable growing conditions are short and seasonal transitions are rapid. Theory suggests that these factors contribute to strong photoperiod control over leaf senescence due to conservative life history strategies that favor winter survival over competitive ability (Pau et al. 2011, Ernakovich et al. 2014, Estiarte and Peñuelas 2014). While photoperiod may be the ultimate cue that initiates senescence processes, observations and experiments in Arctic regions suggest that climate may also be responsible for variation in the timing of senescence. To understand the role of multiple climate cues, we investigated the influence of air temperature, soil temperature, and soil moisture on the onset and rate of senescence in an ecosystem characterized by extreme seasonality. We altered seasonal cues by advancing snowmelt and warming temperatures in moist acidic tundra, changing microclimate at a plot level. The following alternative hypotheses for mechanisms of control on timing of senescence were tested:

H1) Microclimate Conditions: Senescence is influenced by air temperature, soil temperature, and/or soil moisture. We predicted that the onset of senescence will be delayed by favorable growth conditions such as warmer air and soil temperatures and

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increased soil moisture, or accelerated by less favorable conditions (e.g., low soil moisture).

H2) Early Season Phenology: Senescence is controlled by periodic constraints on leaf longevity. We predicted that senescence will advance concurrent with timing of start of season phenology.

Methods

Snowmelt Project

The experiment took place at Imnavait Creek, located <20km from the Long-Term Ecological Research (LTER) site at Toolik Lake on the North Slope of Alaska. The plant community at Imnavait Creek is moist acidic tussock tundra, characterized by the tussock forming sedge *Eriophorum vaginatum* and high moss cover, including *Hylocomium spp., Aulacomnuim spp.,* and *Dicranum spp.*(Bliss and Matveyeva 1992). Plants associated with moist depressions in the inter-tussock spaces at this location include another sedge, *Carex bigelowii*, and the deciduous shrubs *Betula nana* and *Salix pulchra*. Other species common to moist acidic tundra include the evergreen shrubs *Ledum palustre, Vaccinium vitis-idaea*, and *Cassiope tetragonum,* and a variety of forbs. Detailed species composition data can be found in the Supplementary Information (Table **7**). The old (~120,000-600,000 years; (Whittinghill and Hobbie 2011)), acidic soil (mean pH of 4.5) at this site is underlain by continuous permafrost, with an uneven surface layer of organic material 0-20 cm thick (Shaver and Chapin 1991, Walker et al. 1994) and variable soil moisture. At Toolik Field Station, mean annual temperature is approximately -6°C and mean annual precipitation is 200-300 mm (Maxwell 1992).

The seasonality of moist acidic tundra was experimentally altered through a combination of early snowmelt and warming, using a randomized split-plot factorial design with five replicate blocks. Early snowmelt was achieved using 50% black shadecloth placed on the snowpack in late May, over five 8x12m plots. The dark, radiation absorbing fabric accelerated snowmelt with minimal disturbance to the snowpack and underlying vegetation, and was removed when plots were 80% snowfree, determined by daily visual estimates. Once plots were snowfree, passive open-top warming chambers (OTCs) were installed as subplots. OTCs are hexagonal plexiglass chambers that reduce heat loss by wind, enabling warming of approximately 1-2°C (Marion et al. 1997). The approximate area of both control and warming subplots was 1 m^2. Treatments were repeated over three years (2010-2012).

Table 4: Monitoring dates and control means ± 1 s.e.m. for 2010-2012 of microclimate variables.

Year	Monitoring Dates (DOY)	Seasonal Mean Air Temperature (°C)	Seasonal Mean Soil Temperature (°C)	Seasonal Mean Soil Moisture (VWC)
2010	135-244	9.5 ± 0.02	7.7 ± 0.4	0.22 ± 0.02
2011	135-245	9.3 ± 0.05	6.8 ± 0.18	0.19 ± 0.03
2012	141-229	10.9 ± 0.02	8.3 ± 1.03	0.21 ± 0.06

Microclimate and Surface Reflectance Measurements

Sensor arrays installed at each plot were used to monitor microclimate variables and surface reflectance. Arrays were equipped with HOBO® Weather Station data loggers (Onset Computer Corporation) and sensors for soil temperature (°C), soil water availability (volumetric water content (VWC)), air temperature (°C), and surface reflectance. Dates of monitoring and microclimate conditions varied between years (Table 4). Surface reflectance data were monitored and processed as described in Sweet et al. (2014) in order to generate daily plot-level Normalized Difference Vegetation Index (NDVI), from the time of snowmelt until after onset of plant community senescence. An abbreviated description follows here.

At each plot, two downward facing sensors recorded surface reflectance of (1) photosynthetically active radiation over the visible spectrum (PAR, 400-700 nm) (PAR Smart Sensor, Onset Computer Corporation) and (2) irradiance over the shortwave and visible spectrum (300-1100 nm) (Silicon Pyranometer Smart Sensor, Onset Computer Corporation). Upward facing light sensors at two reference site locations recorded incoming solar radiation, in order to calibrate and filter data. Data were filtered to only include measurements from the two hours surrounding solar noon (1200-1400 local time) on clear sky days. Based on the filtering criteria, some days had no useable data points (e.g., due to persistent cloud cover) and were excluded.

Following methods from Huemmrich et al. (1999), data from the two light sensors were used to calculate broadband NDVI. In short, reflectance values were calibrated with reference to the upward facing sensors in order to account for variable light conditions. Then, the difference between reflected PAR (ρPAR) and pyranometer sensors was used to determine optical infrared reflectance (ρOIR), and these reflectance values were used to calculate broadband NDVI as in Eqn (1).

$$NDVI = \frac{\rho OIR - \rho PAR}{\rho OIR + \rho PAR}$$

(1)

Determining Phenological Events from NDVI

Daily NDVI data was used to describe the seasonal development of the plant canopy. The following phenological events were determined: onset greening (OG), onset peak season (OPS), and onset senescence (OS). Determination of phenological metrics from remotely sensed NDVI can be accomplished by multiple methods (de Beurs and Henebry 2010, Klosterman et al. 2014); we chose to fit piecewise linear models. Piecewise linear regression models are an effective method to find inflection points in high temporal resolution data (Vieth 1989), and they

allow for day to day variation in the seasonal NDVI curves (Figure 7) (Sweet et al. 2014). To

account for differences in the seasonal canopy progression due to response to treatments, four

piecewise linear models were fit and compared for each NDVI curve: (1) immediate greening

following snowmelt to a plateau at maximum NDVI; (2) delay in greening following snowmelt

to a plateau at maximum NDVI; (3) immediate greening following snowmelt, plateau at

maximum NDVI, and decrease for senescence; and (4) delay in greening following senescence,

plateau at maximum NDVI, and decrease for senescence (see Figure 7). Models were fit using

proc nlmixed in SAS 9.4 (SAS Institute Inc., Cary, NC USA), and the best fit model selected by

lowest Akaike's Information Criterion (AIC) value. If the best fit model did not include a

decrease for senescence, no OS date was estimated and these plots were excluded from further

analysis. Rate of senescence (RS) was calculated as the slope of the line from OS to the end of

the observation period: $RS = \Delta NDVI / \Delta DOY$. RS is presented as % slope ($= RS*100$) throughout

this paper for ease of interpretation.

A mixed model analysis of variance (ANOVA) was used to examine differences between

years and treatments for onset and rate of senescence. The main effects and interactions of early

snowmelt, warming and year were tested, including block as a random factor. All data were

checked and found to meet the assumptions of ANOVA prior to analysis, and one outlier was

omitted from RS data.
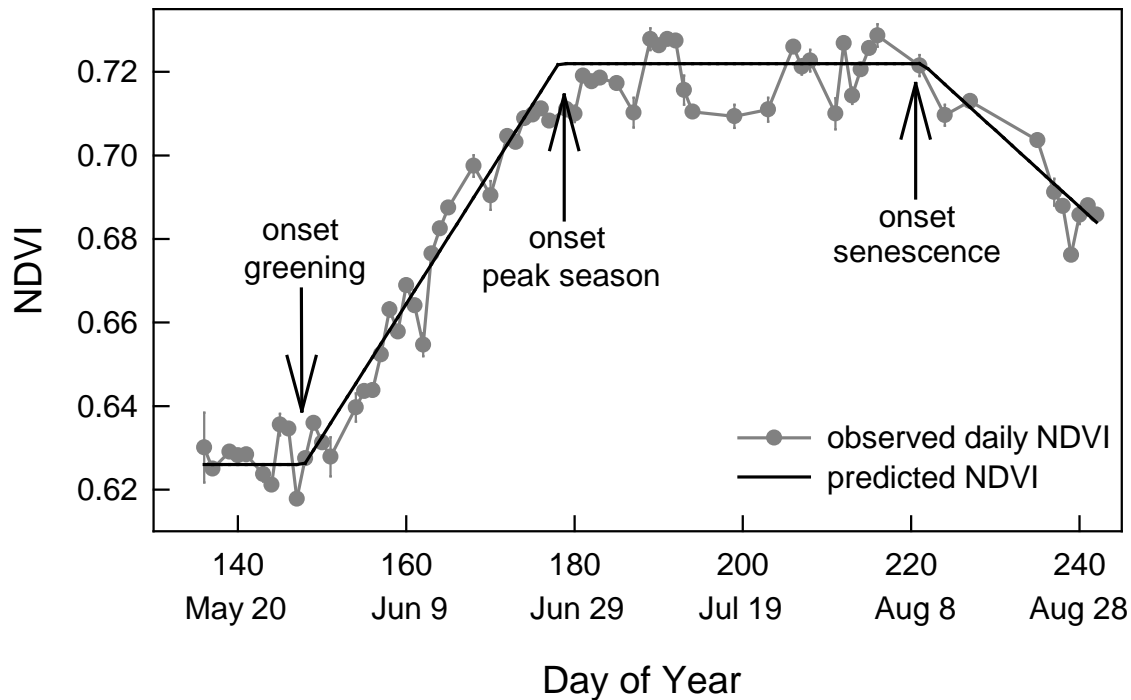
Figure 7: Example of fitted piecewise linear model (black line) showing estimated dates for onset of greening, peak season, and senescence. Dark gray points are daily means +/- 1 s.e.m. of observed NDVI.

Microclimate Influence on Senescence

A two-stage model approach was used to test alternative models of how microclimate influenced the onset and rate of senescence. In the first stage, multiple summaries of the three microclimate predictors (air temperature (AT), soil temperature (ST), and soil moisture (SM)) were compared and the top-ranked summaries were selected. Second, the alternative hypotheses were represented through linear multiple regression models and compared in a separate model set. In both stages, second-order AIC (AIC_c) was used to rank models, with the lowest AIC_c value indicating the top-ranked model. AIC_c is preferred for use with small sample sizes (Burnham and Anderson 2002). Due to the relatively small sample size (n=55), the maximum number of parameters (*K*) in any model was limited to five.

Stage 1: Selection of best microclimate summary.

Summaries of climate data over specific time periods may predict phenological events better than yearly or seasonal means. For example, bud burst in temperate deciduous forests is often modeled by thaw degree-days (TDD) over a variable period of time preceding the event (Chuine 2000, Polgar and Primack 2011). A critical period for predicting onset of senescence in the Arctic has not been determined; however, models of senescence in other systems have successfully used cold degree-days (CDD) (Delpierre et al. 2009, Archetti et al. 2013). We tested different summaries of the three microclimate predictors based on cumulative measures (TDD, CDD) and means over multiple time periods. TDD were calculated as the sum of days of daily mean temperature above a temperature threshold (0°C), and CDD were calculated as the difference between a temperature threshold (AT: 8°C, ST: 6°C) and the minimum daily temperature. The time periods considered included seasonal (entire observation period, see Table 4), monthly (June, July, August), and three phenological periods: (1) green-up (OG-OPS), (2) active growth (OG-OS), and (3) peak season (OPS-OS)).

The best summaries were determined by constructing a model set for each predictor (AT, ST, and SM), and comparing multiple linear regression models where two predictors were held at their seasonal mean value and the third predictor varied by each summary. Multiple linear regression models were used to control for potential interactions between predictors that would not be accounted for with univariate models of the different summaries. The top-ranked model was selected for the next stage.

Stage 2: Compare alternative hypotheses.

In the second stage, a model set was constructed to compare the microclimate conditions (H1) and early season phenology (H2) hypotheses. H1 was represented by multiple linear

regression models of AT, ST and SM using the previously selected best summaries of these three predictors. H2 was represented by linear regression models of onset of greening and onset of peak season. Additionally, a constant model was included in the model set to represent the null hypothesis that onset and/or rate of senescence do not vary with either microclimate or early season phenology. Separate model sets were tested for onset and rate of senescence. Multicollinearity of the microclimate predictors (AT, ST, SM) was assessed, and each variable was found to have variance inflation factor (VIF) < 2, which is below a standard cutoff value of 2.5 (corresponding to an R^2 of 0.6). As above, models were ranked using AIC_c.

Results

Timing and Rates of Senescence

Over the three years of the study period, onset of senescence (OS) for the plant community varied by 20 days in control plots (DOY 211-231) and this range was expanded by an additional 13 days due to experimentally altered seasonality (DOY 200-233). OS advanced significantly due to warming (W) by 2-8 days, and early snowmelt (ES) by 3-8 days (Table 5, Figure 8; W: *F = 4.66, P < 0.05*, ES: *F = 9.19, P < 0.01*). Since there was no significant interaction between the two treatments, combined warming and early snowmelt led to 5-18 days advance in OS (WxES: *F = 0.26, P = 0.61*). The main effect of year on OS was not significant, and did not interact significantly with either early snowmelt or warming.

Rates of senescence (RS) are presented as negative slopes, where a more negative number indicates a faster rate of senescence. Control plot slopes varied from -0.05 to -0.26%, and treatments expanded this range up to -0.37%. Treatments altered RS depending on year, leading to significant interactions of early snowmelt and warming with year (Table 5; YxES: *F =*

3.94, P < 0.05; YxW: *F = 4.01, P < 0.05*). Early snowmelt slowed RS in 2010 and 2011, by

0.03-0.05%, but accelerated it in 2012 by 0.1% (Figure 8). Conversely, warming accelerated RS

in 2010 and 2011, by 0.08 and 0.04%, respectively, and slowed it in 2012 by 0.05% (Figure 8).

The combination of early snowmelt and warming had consistent effects in all three years,

slowing RS by 0.01-0.03%.
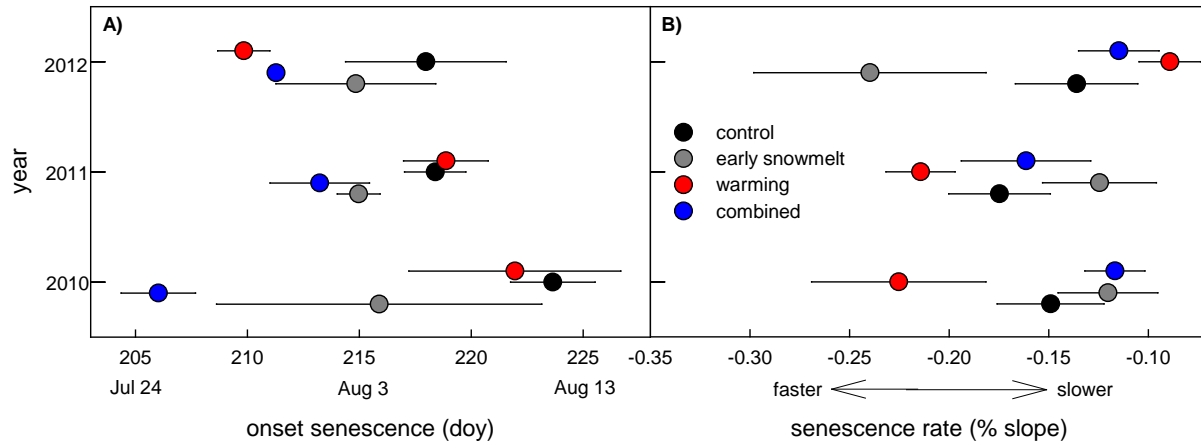
Figure 8: A) Mean +/- 1 s.e.m date of onset of senescence. B) Mean +/- 1 s.e.m. rate of senescence. Data was generated from piecewise linear model estimates for the seasonal NDVI curve. Points are offset along the y-axis for clarity.

Table 5: Results of mixed-model ANOVA on onset and rate of senescence showing main effects and interactions of early snowmelt (ES), warming (W), and year (Y). Values in bold indicate a significant (*P* ≤ 0.05) effect.

	Onset senescence		Rate senescence	
	F	*P*	*F*	*P*
ES	**9.19**	**0.0046**	1.01	0.3218
W	**4.66**	**0.0378**	0.05	0.8194
ES x W	0.26	0.6116	1.89	0.1778
Y	1.08	0.3500	0.60	0.5559
Y x ES	2.92	0.0671	**3.94**	**0.0288**
Y x W	0.92	0.4078	**4.01**	**0.0273**
Y x ES x W	0.88	0.4228	0.50	0.6106

Microclimate Conditions

The effects of early snowmelt and warming on microclimate conditions varied between years (Figure 9). Seasonal air temperature means always increased due to warming, by 1.4-1.7°C on average. TDDs over peak season reflect this pattern with 43-53°C more accumulated in the warming and combined treatments, but little change due to early snowmelt alone. Over the three years of this study, TDDs over peak season were similar, with accumulated air temperatures in the control plots ranging from 320 – 330°C on average. Similar to air temperature, soil temperature increased due to warming; however, it also increased due to early snowmelt in all years. Mean control plot soil temperature was 7.5°C, and warming and early snowmelt increased this by 0.8-1.1°C. Minimum soil temperatures similarly increased due to warming and early snowmelt, resulting in lower accumulated CDD compared to the control. Soil moisture decreased in response to warming and early snowmelt by 13-40% relative to the control, with the combined treatments having the largest effect. Seasonal patterns of air temperature, soil temperature and soil moisture are shown in Supplementary Figures 12, 13 and 14.

Comparison of different phenological periods and monthly summaries of microclimate predictors showed that peak season was the phenological period best supported for predicting OS. Further, cumulative summaries rather than means of air and soil temperature were favored. When comparing air temperature summaries, peak season CDD and peak season TDD were equally ranked as top models, therefore both summaries were used in the following stage. Comparison of soil temperature summaries showed that peak season CDD was clearly ranked as the top model, with 74% of model weights, and was used in the second model stage. Comparison of summaries of soil moisture revealed some model selection uncertainty; however, the equally ranked top models were all highly correlated means over monthly or phenological time periods.

Peak season mean soil moisture, which had the absolute lowest AIC$_c$ value, was used in the second model stage.

When comparing microclimate summaries for predicting RS, there was significant model selection uncertainty in each model set. All summaries were equally ranked for air temperature, soil temperature, and soil moisture. Consequently, seasonal means, as the most comprehensive microclimate summary, were used in the second model stage.
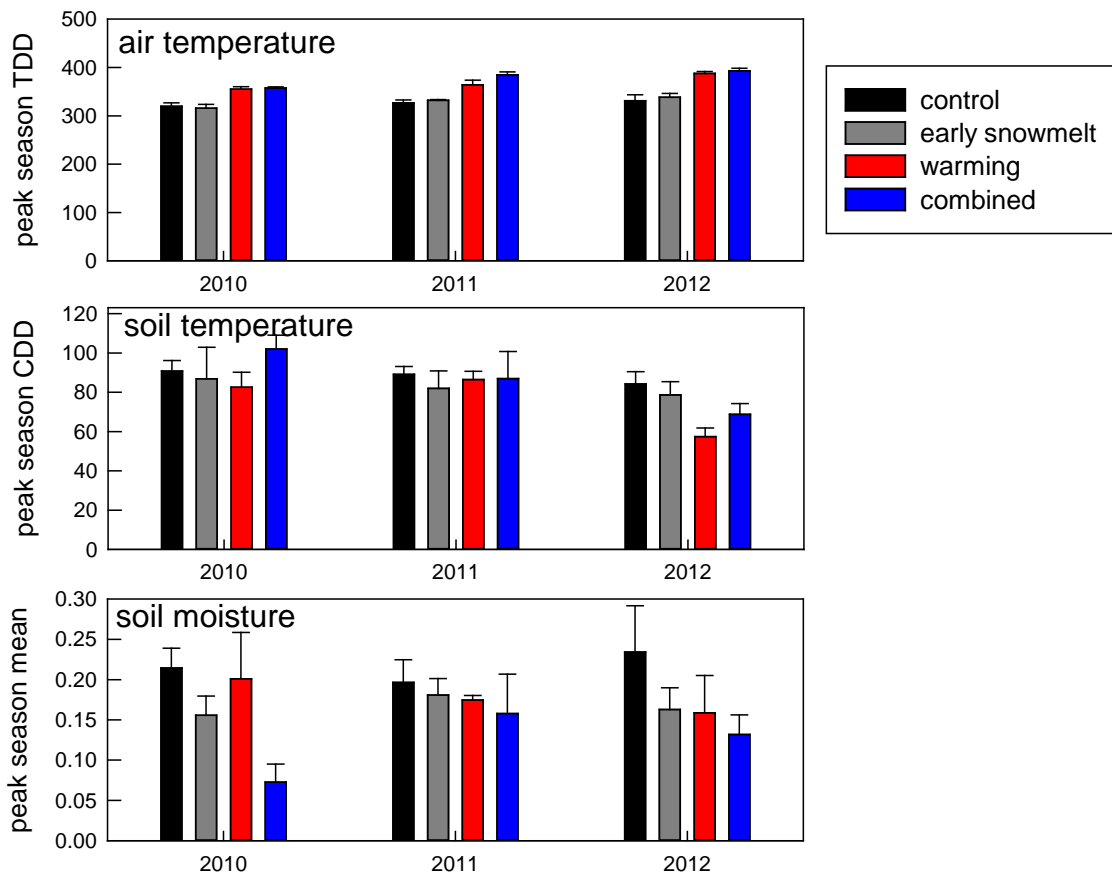
Figure 9: Year and treatment effects on microclimate. The best microclimate summaries of each predictor (AT, ST, SM) as determined by Stage 1 model results are presented, as means +/1 s.e.m across the replicate blocks.
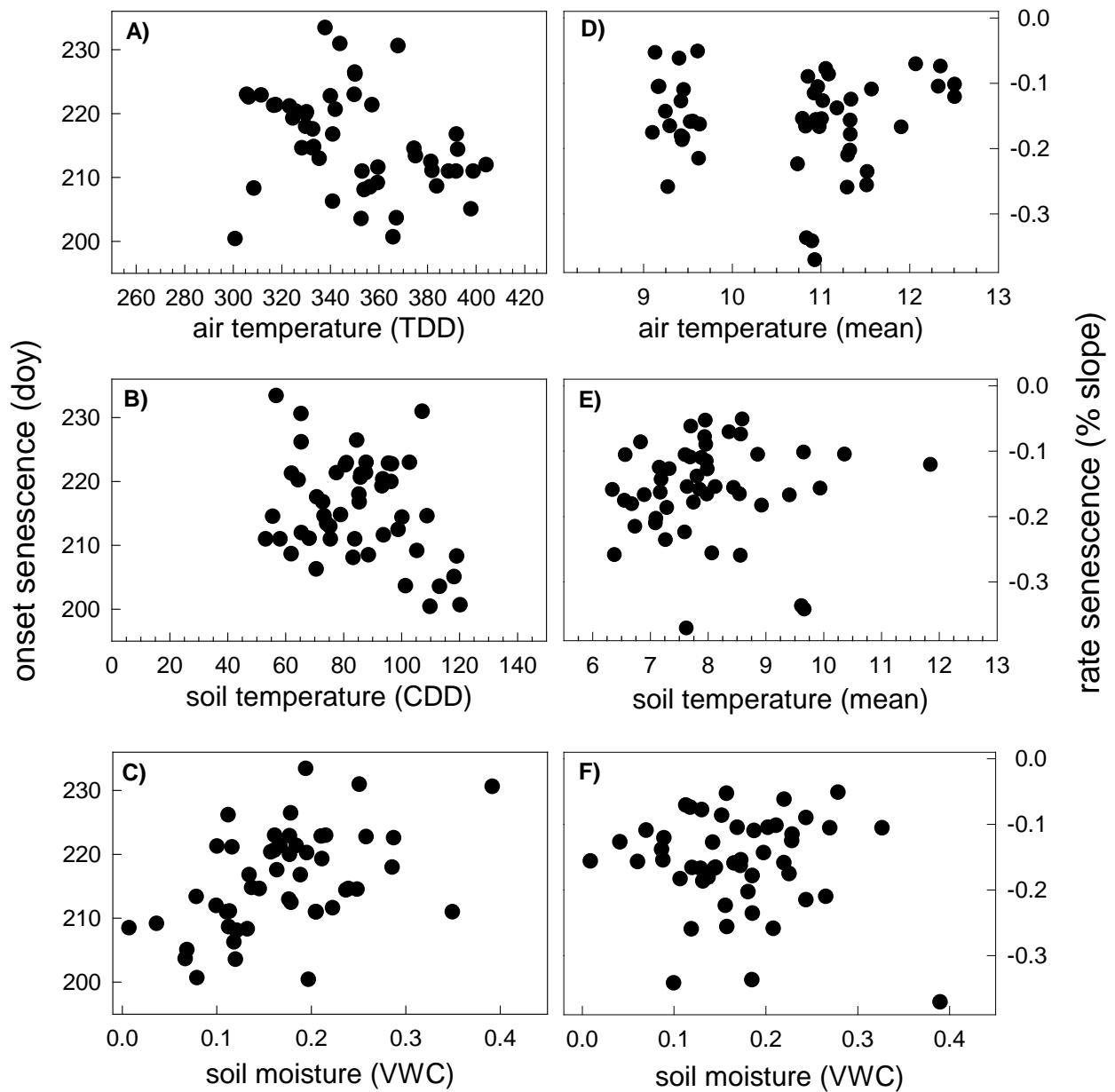
Figure 10: Relationship between onset and rate of senescence and microclimate summaries. Microclimate summaries along the x-axes are as follows: A) peak season TDD, B) peak season CDD, C) peak season mean, D), E), and F) seasonal mean.

Comparison of Alternative Hypotheses

Variation in onset of senescence was best explained by an additive model of air

temperature, soil temperature, and soil moisture (Table 6, $R^2 = 0.39$). Despite penalties for

greater number of parameters, this was clearly ranked as the top model for onset of senescence,

with 72% of model weights. Air and soil temperature summaries were poorly correlated (R^2 = -

0.23). Coefficients for each predictor in the model were significant (AT: β =- *0.095*, *P < 0.01*,

ST: β = *-0.145*, *P < 0.01*, SM: β = *37.91*, *P < 0.01*), and slopes differed in direction. A constant

model, representing the null hypothesis, had negligible support in the model set. Likewise,

models representing control by start of season phenology (onset greening and onset peak season)

were not supported.

Table 6: Comparison of multiple linear regression models predicting onset of senescence. AICc of the top model is 331.82. Subscripts for air temperature denote the two microclimate summaries compared in this model set: Air temperature$_1$ = peak season TDD, Air temperature$_2$ = peak season CDD

Model	K	Δ AICc	Cum.Wt	R^2
Air temperature$_1$ + Soil temperature + Soil moisture	5	0	0.718	0.39
Air temperature$_1$ +Soil moisture	4	5.38	0.766	0.29
Soil temperature + Soil moisture	4	5.73	0.807	0.28
Soil temperature x Soil moisture	5	5.74	0.848	0.32
Air temperature$_2$ + Soil moisture	4	6.18	0.881	0.27
Air temperature$_1$ + Soil temperature	4	6.94	0.903	0.26
Air temperature$_2$ + Soil temperature + Soil moisture	5	6.98	0.925	0.30
Air temperature$_1$ x Soil moisture	5	7.16	0.945	0.30
Soil moisture	3	7.54	0.961	0.22
Air temperature$_1$ x Soil temperature	5	7.79	0.976	0.29
Air temperature$_2$ x Soil moisture	5	8.17	0.988	0.28
Air temperature$_2$ x Soil temperature	5	8.67	0.997	0.27
Air temperature$_1$	3	13.63	0.998	0.12
Air temperature$_2$	3	13.77	0.999	0.11
Air temperature$_2$ + Soil temperature	4	14.79	0.999	0.14
Soil temperature	3	15.10	0.999	0.09
Constant	2	17.57	0.999	NA
Onset greening	3	18.03	0.999	0.04
Onset peak season	3	19.19	1	0.01

Rate of senescence was not well predicted by any of the alternative models (top model R^2

= 0.02), and there were four equally ranked top models, revealing high model uncertainty (not

shown). The model with the lowest AIC$_c$ was the constant model, but this had only 27% of

model weight. Univariate models of soil moisture, onset of greening and peak season were $\leq \Delta$ 2AICc from the constant model, indicating equal support for these models, but with similarly poor model fit ($R^2 \leq 0.02$).
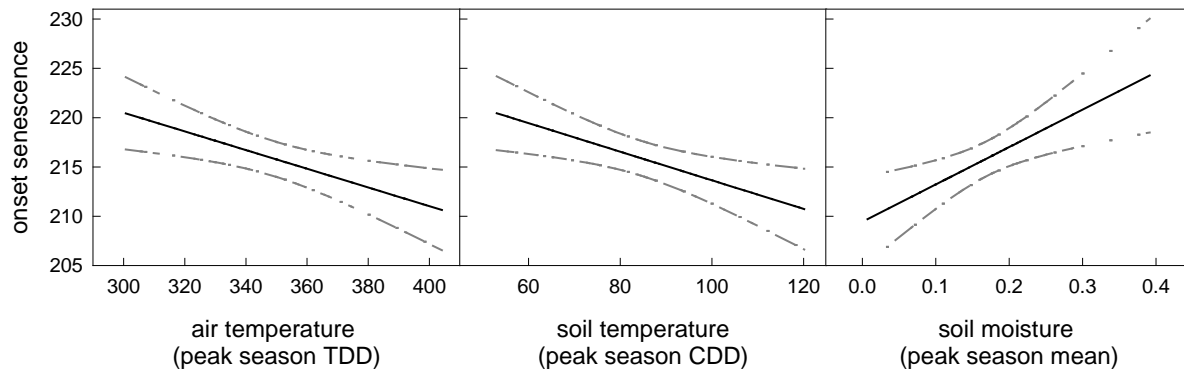

Figure 11: Model predictions of onset of senescence. Onset of senescence is predicted by a multiple linear regression model, so partial effects of each predictor are shown with the other two predictors held constant at their mean. Dashed lines indicate upper and lower 95% confidence intervals.

Discussion

We found that the onset of senescence in an ecosystem with extreme seasonality is influenced by multiple climate cues, rather than periodic constraints. When comparing alternative models of control on the onset of senescence, a model with three microclimate predictors was highly supported. This indicates that air temperature, soil temperature and soil moisture each contributed individually to explaining variation in the timing of senescence, and consequently the duration of peak season. While previous experiments in the Arctic have shown that community level senescence may be delayed in response to warming (Marchand et al. 2004, Natali et al. 2012), none have shown the simultaneous influence of multiple drivers.

As an ultimate control on onset of senescence, photoperiod may act as a threshold limit on climate-induced variation. Over a wider range of conditions than tested in this experiment, favorable conditions could allow senescence to be delayed to a point where photoperiod sharply

decreased. Models of senescence commonly rely on photoperiod modified by a single climate driver, usually air temperature (Richardson et al. 2012). However, temperature has been shown to explain less variation in autumn phenology compared to spring (Menzel 2003, Gallinat et al. 2015). Including soil temperature and moisture may improve models of autumn phenology.

Models relating start of season phenology to onset of senescence were unsupported. Evidence that timing of senescence is related to spring phenology has been previously shown for eastern deciduous forest, at a regional scale and for individual species (Fu et al. 2014, Keenan and Richardson 2015). Lack of support for this hypothesis in our study may be due to different species driving patterns in canopy greenness as detected by NDVI. In moist acidic tundra, the first species to green up are the sedges, *E. vaginatum* and *C. bigelowii*, whereas color change in leafy canopy species such as *B. nana* and *S. pulchra* are more likely to be indicative of onset of senescence dates.

Low soil moisture as a result of early snowmelt and warming led to accelerated onset of senescence. The predicted effects of our model supported the ANOVA results indicating that early snowmelt and warming significantly advanced timing of senescence (Figure 9, Figure 8, Figure 11). Further, they showed that reduced soil moisture as an indirect effect of early snowmelt and warming were a key component of the observed results. Although warmer conditions often result in delayed senescence, the opposite may occur if water stress occurs simultaneously (Hwang et al. 2014, Estiarte and Peñuelas 2014).

The timing and characterization of climate cues was critical in detecting relationships of microclimate with timing of senescence. While seasonal or monthly mean air and soil temperatures had weak correlations with onset of senescence, cumulative measures were better predictors. Further, summaries over the thirty days preceding onset of senescence (roughly

corresponding to the duration of peak season) were selected over cumulative summaries during other time periods. Thermal degree-day models have long been used to successfully predict budburst for individual species, and cold degree-day models more recently are being used to predict senescence (Delpierre et al. 2009, Dragoni and Rahman 2012, Archetti et al. 2013). We found that cold degree-days of soil temperature were selected in the final model, which may indicate that nighttime soil temperatures may be a stronger cue to plants to induce dormancy than air temperature, which is more variable.

Although rate of senescence varied among years and treatments, we did not find evidence of a relationship with single or multiple microclimate cues. The response of rate of senescence to early snowmelt and warming was mixed among years, but consistently slowed in response to the combined treatment. However, it is unclear what conditions contributed to slower senescence rates. Warming is hypothesized to slow senescence in order to facilitate more efficient resorption of nutrients (Estiarte and Peñuelas 2014); however, we did not find a clear relationship between warmer temperatures and rates of senescence. It may be that different microclimate summaries or time periods are needed to explain variation in rate of senescence; for example, we did not have microclimate data for the entire duration of the senescence period.

An earlier onset of senescence in an Arctic plant community changes the duration of peak season length, which corresponds to the period of maximum carbon uptake (Richardson et al. 2009, Mbufong et al. 2014). The length of peak season as well as the entire growing season are linked to various metrics of productivity in deciduous forests (Dragoni et al 2011, Garrity et al 2011, White et al 1999), and Euskirchen et al (2006) equate growing season extension of one day in tundra ecosystems to a gain of 5.3g C m^{-2} yr^{-1}. Ecosystem models where senescence processes

are misrepresented or have high uncertainty can result in poor prediction of CO2 flux at an

ecosystem scale (van Wijk et al. 2003, Richardson et al. 2012).

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CHAPTER FOUR: CONCLUSIONS

We found that altered seasonality in moist acidic tundra led to shifts in species phenology at an individual and community level. Shifts in species' phenology were not surprising, given that temperature and timing of snowmelt are known phenological cues for Arctic plants. However, we expected that earlier green-up would lead to increased production, given that this is a commonly held paradigm. Instead, we found evidence that differences species' temporal niche was related to changes in production. While nitrogen availability is the primary limiting factor of Arctic plant production, how plants respond as N limitations are alleviated under warmer temperatures may be related to evolved life history strategies. Under this framework, early-greening species such as *E. vaginatum* may benefit most under warmer temperatures. Deciduous shrubs also green early relative to other species, and in patches where deciduous shrubs already dominate, they may benefit from early season nutrient pulses as well. We may not have seen this result in our experiment because deciduous shrubs were not the first functional group to green up.

Given overall trends in delayed senescence at temperate and northern latitudes, it was surprising that we saw consistent advance in plant community senescence due to warmer temperatures. This highlights the complexity of phenological cues; while warmer temperatures may often be considered favorable, when they were associated with decreased soil moisture in our experiment (along with early snowmelt) the cue became an environmental stressor. Senescence responses of plant communities across the Arctic may be more dependent on the indirect effects of warming than previously thought, and heterogeneity across the landscape in soil moisture may play an important role in determining response. While we showed that

microclimate conditions explain some variation in timing of senescence, further experiments are needed to more clearly define the mechanisms controlling senescence processes in the Arctic. Specifically, testing senescence processes over a wider range of temperature and soil moisture conditions would be useful.

APPENDIX A: SUPPLEMENTARY MATERIAL

Table 7: Species composition at Imnavait Creek. Percent cover estimates are averaged over plots for the entire experimental site.

| Species	% Cover
Moss	52.00
Betula nana	8.14
Vaccinium vitis-idaea	7.06
Lichen	4.47
Eriophorum vaginatum	4.03
Salix pulchra	3.92
Ledum palustre	3.70
Carex bigelowii	3.12
Cassiope tetragona	2.11
Polygonum spp.	0.96
Pedicularis oederi	0.93
Petasites frigida	0.57
Salix phlebophylla	0.35
Vaccinium uliginosum	0.30
Pedicularis lapponica	0.27
Rubus chamaemorus	0.23
Pyrola grandiflora	0.22
Hierachum spp.	0.10
Andromeda polifolia	0.07
Empetrum nigrum	0.05
Oxycoccus microcarpus	0.03
Saxifraga punctate	0.03
Calamagrostis lapponica	0.02
Poa arctica	0.01
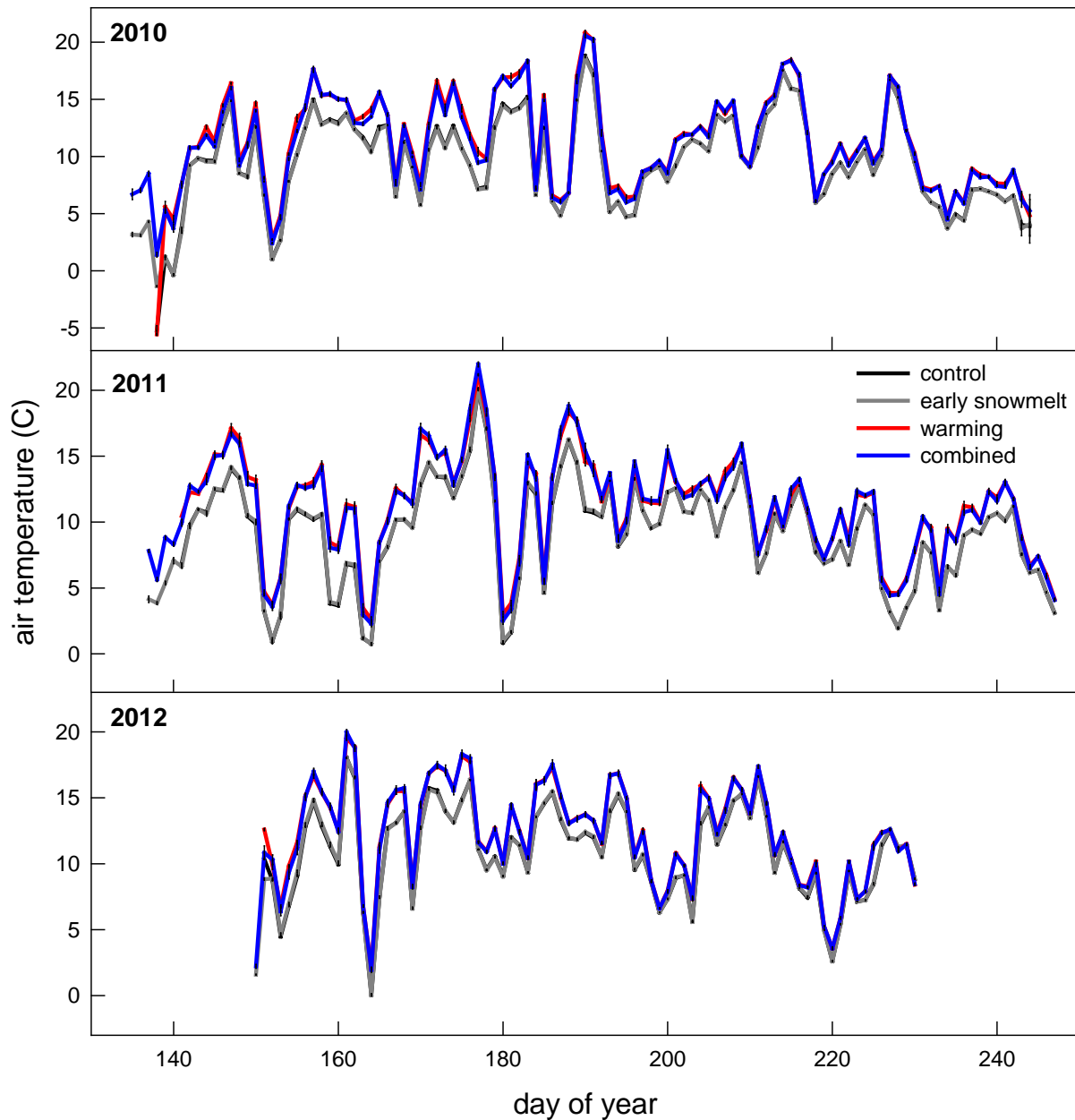
Figure 12: Seasonal patterns of air temperature at Imnavait Creek. Lines show mean air temperature across blocks. ±1 s.e.m. are plotted but often not visible.
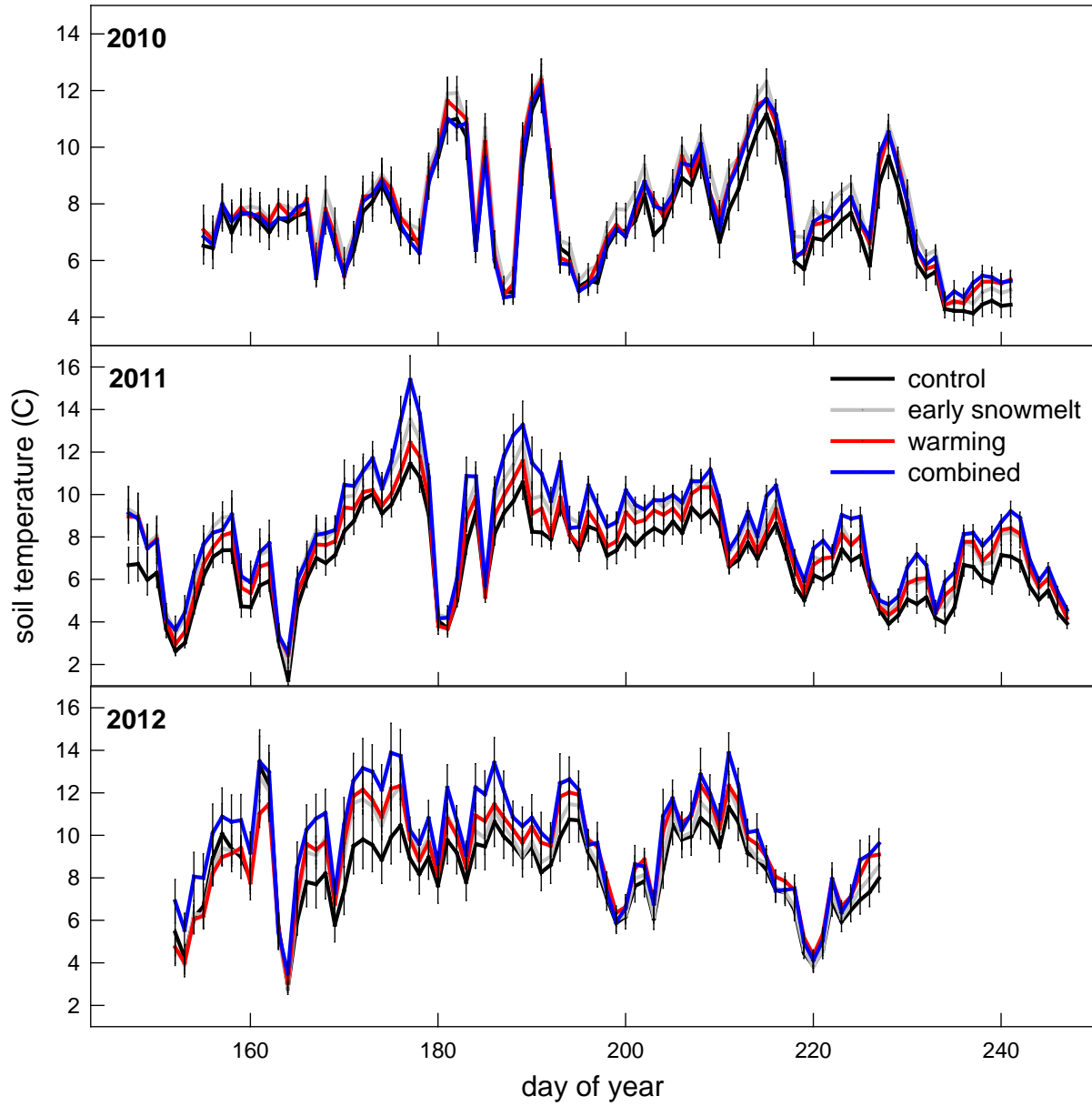
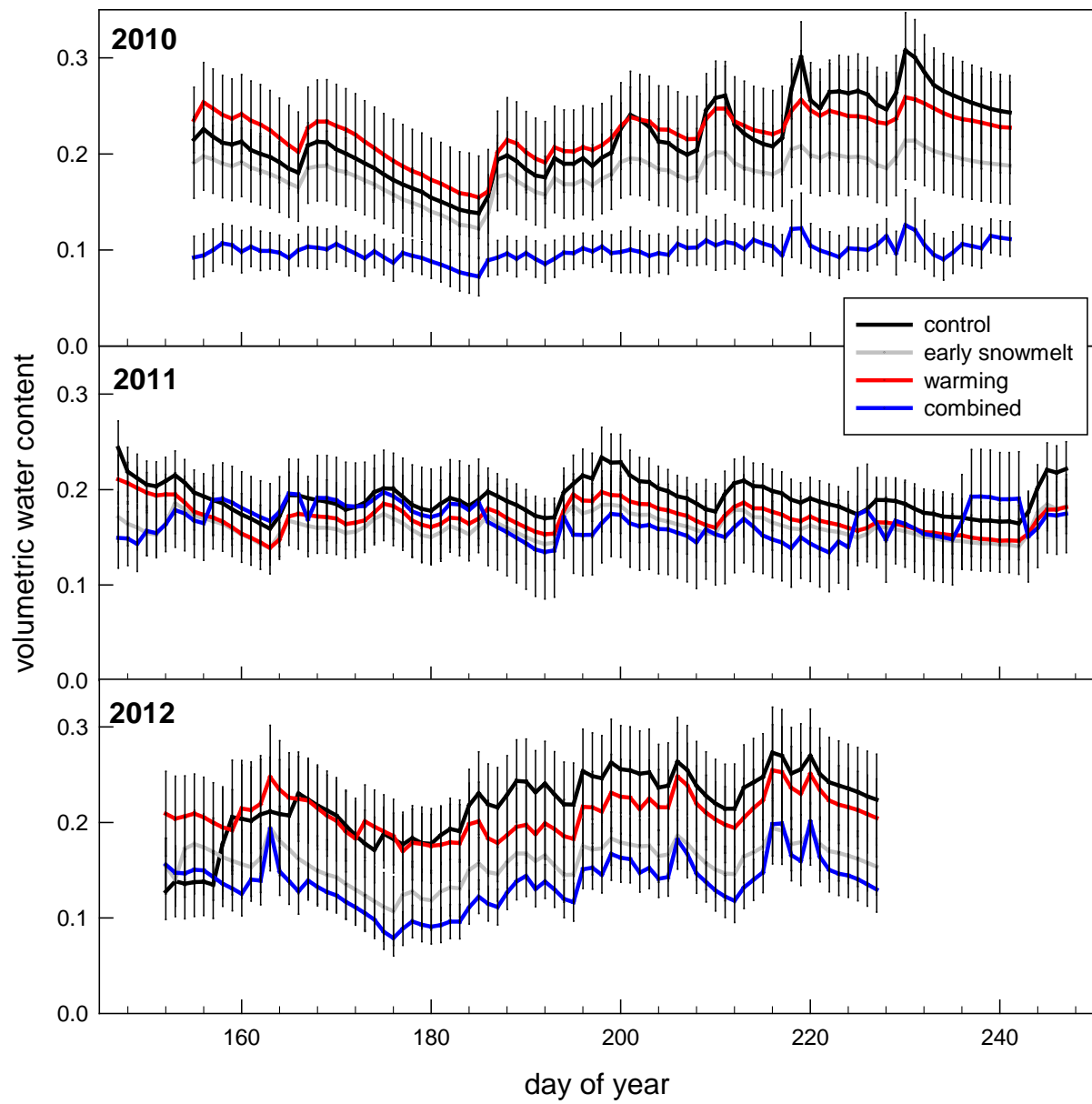**Figure 13:** Seasonal patterns of soil temperature. Lines show daily means ± 1 s.e.m.

Figure 14: Seasonal patterns of soil moisture. Lines show daily means ± 1 s.e.m.