THE IMPACT OF DECIDUOUS SHRUB DOMINANCE ON PHENOLOGY, CARBON FLUX, AND ARTHROPOD BIOMASS IN THE ALASKAN ARCTIC TUNDRA

by Shannan Kathlyn Sweet

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY OF THE
GRADUATE SCHOOL OF ARTS AND SCIENCES

COLUMBIA UNIVERSITY

2015

ABSTRACT

The Impact of Deciduous Shrub Dominance on Phenology, Carbon Flux,
and Arthropod Biomass in the Alaskan Arctic Tundra

Shannan Kathlyn Sweet

Arctic air temperatures have increased at two to three times the global rate over the past century. As a result, abiotic and biotic responses to climate change are more rapid and pronounced in the Arctic compared to other biomes. One important change detected over the past several decades by satellite studies is a lengthening of the arctic growing season, which is due to earlier onsets and/or delayed ends to growing seasons. A handful of studies also suggest the peak green season (i.e. when the tundra is at maximum leaf-out and maximum carbon uptake potential) is starting earlier in the arctic tundra. The vast majority of studies detecting shifts in the growing season suggest this is due to increasing spring and fall air temperatures, which lead to earlier spring snowmelt and later fall snowfall. Less well understood is how indirect consequences of arctic warming, such as ongoing changes in plant community composition, may also be contributing to these satellite signals. For instance, there is mounting evidence that deciduous shrubs are expanding into previously non-shrub dominated tundra in several parts of the Arctic. Deciduous shrubs may alter tundra canopy phenology and contribute to the regional shifts in timing of phenological events being detected by satellites.

Concurrently, in many areas where deciduous shrubs are expanding they are also becoming taller. As taller shrubs become increasingly dominant, arctic landscapes may retain more snow, which could lengthen spring snow cover duration, and offset advances in the start of the growing season that are expected as a result of earlier spring snowmelt. As a consequence, deeper snow and later snowmelt in taller shrub tundra could delay plant emergence, and shorten the period of annual carbon uptake. Thus greater dominance of taller stature deciduous shrubs in the Arctic may actually delay the onset of the growing season, which would suggest that increasing deciduous shrub dominance may not be contributing to satellite signals of an earlier start to the growing season. To contribute to satellite-detected shifts in the onset of the growing and peak seasons, tall deciduous shrubs would need to have accelerated leaf development to compensate for deeper snow packs and later spring snowmelt relative to surrounding tundra.

Understanding the drivers of shifts in tundra phenology is important since longer (or shorter) growing and peak green seasons would increase (or decrease) productivity and the period of carbon uptake, which will have implications for landscape-level carbon exchange, and ultimately global carbon balances.

Given the rate and magnitude of changes occurring in the face of acute arctic warming, there is a need to monitor, understand, and predict ecological responses over large spatial and temporal scales. However, compared to more southern environments, the arctic tundra is characterized by considerable heterogeneity in vegetation distribution, as well as a short and rapid growing season. In addition, the arctic tundra is relatively vast and inaccessible. These characteristics can make it difficult to monitor and study changes in the Arctic, and make it difficult to develop landscape-level models able to predict changes in ecosystem dynamics and tundra vegetation. The use of airborne and satellite sensors has at least partially fulfilled these needs to monitor, understand, and predict change in the Arctic. The normalized difference vegetation index (NDVI) acquired from these sensors, for instance, has become a widely adopted tool for detecting and quantifying spatial-temporal dynamics in tundra vegetation cover, productivity, and phenology. This suggests that remote sensing technology and vegetation indices may be similarly applied to characterizing patterns of primary and secondary consumers (e.g. arthropods), which would be enormously useful in a region as vast and remote as the Arctic.

The research presented in this dissertation provides useful insight into the influence vegetation community composition, particularly increasing deciduous shrub dominance, has on phenology, carbon flux, and canopy arthropod biomass in the arctic foothills region of the Brooks Range, Alaska. Findings in Chapter one suggest that delayed snowmelt in areas dominated by taller shrubs may have a short-lived impact on the timing of leaf development, likely resulting in no difference in duration of peak photosynthetic period between tall and short-stature shrubs. Findings in Chapter two suggest that greater deciduous shrub dominance not only increases carbon uptake due to higher leaf area relative to surrounding tundra, but may also be causing an earlier onset of, and ultimately a net extension of, the period of maximum tundra greenness and further increasing peak season carbon sequestration. Findings in Chapter three suggest that measurements of the NDVI made from air and spaceborne sensors may be able to quantify spatial and temporal variation in canopy arthropod biomass at landscape to regional scales in the arctic tundra.

Table of Contents

NOMENCLATURE AND ACRONYMS

α	empirical model parameter	LAI	leaf area index (m^2 leaf m^{-2} ground)
ß	empirical model parameter		
C	carbon	m	meter
CO_2	carbon dioxide	mg	milligram
df	degrees of freedom	MTT	moist tussock tundra
DOY	day of year	NEE	net ecosystem exchange (μmol CO_2 m^{-2} s^{-1})
DS	deciduous shrub		
DST	dwarf/deciduous shrub tundra	NDVI	normalized difference vegetation index
E_0	initial slope of light response curve; 'quantum yield' (μmol CO_2 fixed μmol^{-1} photons absorbed)		
		nm	nanometer
		NPP	net primary production
		P	P-value
EG	evergreen/graminoid	PAR	photosynthetically active radiation (μmol m^{-2} s^{-1})
EST	erect shrub tundra		
F	F-ratio	P_{maxL}	light saturated photosynthetic rate (μmol m^{-2} leaf s^{-1})
FLB	first leaf bud		
FLE	first leaf expanded	R_E	total (autotrophic + heterotrophic) respiration (μmol CO_2 m^{-2} s^{-1})
FLO	first leaf opening		
FLV	first leaf visible		
g	gram	R_0	basal respiration rate (μmol CO_2 m^{-2} leaf s^{-1})
GPP	gross primary production (μmol CO_2 m^{-2} s^{-1})		
		R_X	soil respiration (μmol CO_2 m^{-2} ground s^{-1})
I	irradiance (W m^{-2}, μmol PAR m^{-2} ground s^{-1})		
		RST	riparian shrub tundra
k	Beer's law extinction coefficient (m^{-2} ground m^{-2} leaf)	s	second
		SEM	standard error of the mean
		T	air temperature (°C)
		μmol	micromole

LIST OF TABLES

LIST OF FIGURES

LIST OF EQUATIONS

ACKNOWLEDGEMENTS

First and foremost I want to thank my advisor Natalie Boelman, to whom I am eternally grateful. It has been an honor to be her first Ph.D. student. Without Natalie I would never have had the opportunity to attend Columbia University, to work in the arctic tundra, nor would I be writing this dissertation. I appreciate her contributions of time, ideas, and funding to make my experience productive and stimulating. She taught me how good scientific research is done, and how to present ideas coherently and concisely. Natalie has been more than just an academic advisor; she has been a mentor and a confidant, which was especially important during rough times in the Ph.D. pursuit. I am grateful for the countless hours she dedicated to guiding me through the sometimes dizzying realm of graduate school, and for flawlessly and seamlessly keeping me on track through thick and thin. Thank you Natalie!

Laura Gough has also been an integral part of my endeavors. Her statistical expertise and knowledge of the arctic tundra have been invaluable. I am indebted to Laura for her continued patience and help in writing my dissertation, as well as for her practical and wise advice, which helped me maintain a healthy work-life balance. Both Natalie and Laura have shown me that it is possible to simultaneously be a mother, a teacher, a mentor, a wife, a research scientist, a grant writer extraordinaire, a friend and more. I am thankful for the amazing examples they have been of successful women researching and teaching in science. The dedication and drive Natalie and Laura have for their research is inspirational and motivational.

Kevin Griffin has also contributed immensely to my professional and personal time at Columbia, both practically and theoretically. His wealth of knowledge and lab space have been invaluable assets, and I truly appreciate all of the time and ideas he has given me over the years. Kevin's unbridled enthusiasm for the world of plants and ecophysiology is inspirational to say the least. I am thankful for having had such a great mentor who was able to teach me without me even knowing I was being taught, and who has shown me the meaning of the term 'humble genius'.

John Rowden has been yet another source of inspiration for me in graduate school. His Ornithology class was one of the first courses I took at and from the moment I stepped into his classroom I was enthralled by how excited someone could be about what they do for a living. John's sincere zeal and zest made me realize a career can be more than just making a living; it can be a passion and a love. I am grateful to John for never hesitating to take time out of his busy

schedule to offer guidance and advice. I would also like to thank Natalie, Kevin and John for being such supportive and helpful committee members. And I thank the other two members of my oral defense committee, Chris Small and Arnold Gordon, for their time and insightful questions and comments. It has been a privilege to work with such talented people who helped exponentially expand my intellectual horizons.

This dissertation would not have been possible without the collaborative effort of Team Bird. We had some incredible experiences and accomplished so much, and I cannot thank everyone enough for all the help in the field and beyond. Working in the vast and remote arctic tundra can take a toll on a person, and I am grateful to the other graduate students on Team Bird whom I worked with closely. Thank you Jesse Krause for sticking out the entire five years and teaching me the relaxation of gold panning. Thank you Ashley Asmus for showing me that even when experiments flop it's possible to move on with a smile. Thank you Jonathan Perez for never hesitating to help even in treacherous arctic conditions. And thank you Helen Chmura for inspiring me with your dedication, motivation, and enthusiasm. Thank you all for helping to keep me in one piece, mentally and physically, and for making blizzards in July and grizzly bears on our plots seem like reasonably ordinary events!

I am also grateful for the amazing undergraduate research assistants I worked alongside. We had a lot of fun and got everything done, and I truly appreciate your dedication. Thank you Adam Formica for your boundless energy and musical serenades. Thank you Jess Gersony for your very special friendship, scarily positive attitude and incredible dedication. And thank you Marley Tran for your invaluable help and for stepping (and excelling) way outside your comfort zone. I was incredibly lucky to work with such brilliant, quick-witted and all around great individuals and would never have made it through without your help, so thank you!

Thank you also to John Wingfield for always finding the time he didn't actually have to lend an ear and give advice. And thanks to the numerous people in John's lab group who never hesitated to lend a helping hand, including Kathleen Hunt, Simone Meddle, Karen Lizars, Jake Schas, Michaela McGuigan, Lisa Quach, and Shae Bowman. Searching the tundra for nests in vain would not have been the same without all of you!

Thanks also to Team Laser, including Lee Vierling, Jan Eitel, Heather Greaves and Troy Magney. Aside from being incredibly supportive and collaborative researchers, Team Laser

Finally, I would like to thank all of my friends and family for love, support and encouragement. Thank you especially to my brothers, Zac Rood and Josh Sweet, and sister-in-laws, Jasmine Peters and Kelly Sweet, for believing in me and not letting me lose my way! You truly helped me maintain lucidity and stay the course. Most of all I thank my parents, Mary Ruth Sweet-Rood and Marvin Rood, who raised me to believe in unthinkable things and pursue grandiose dreams. My parents have been more inspirational and motivational than they will ever know, possibly more than I will ever know. Besides the obvious fact that without them there would be no me, there is the less obvious fact that everything I have done and accomplished could (and should) be attributed to my parents. I am eternally grateful for the love of science, common sense, independence, patience, determination, and hardworking grit they instilled in me. Thank you! Thank you! Thank you mom and dad!

Shannan Kathlyn Sweet
May 2015

INTRODUCTION

Earth's surface temperatures have increased by about 0.72°C since 1950, primarily as a result of industrialization and anthropogenic greenhouse gas emissions (e.g. carbon dioxide, methane, and nitrous oxide) (IPCC 2013). Chlorofluorocarbons and other industrial heat retaining chemicals as well as agriculture and deforestation further promote climate change (IPCC 2013). According to IPCC (2013) model predictions, the planet could warm an additional 1 to 4°C by the end of the century.

Arctic air temperatures have been increasing at two to three times the global rate (~ 2°C) over the same time period (ACIA 2004, McBean et al. 2006), resulting in a particularly strong warming trend in arctic environments (Chapin et al. 2005, Serreze & Francis 2006) (Figure 1). Summer temperatures in Arctic Alaska, for instance, increased by about 1.5°C from 1961 to 2004 (Chapin et al. 2005). According to ACIA (2004), the Arctic could warm an additional 4 to 7°C by the end of the century.
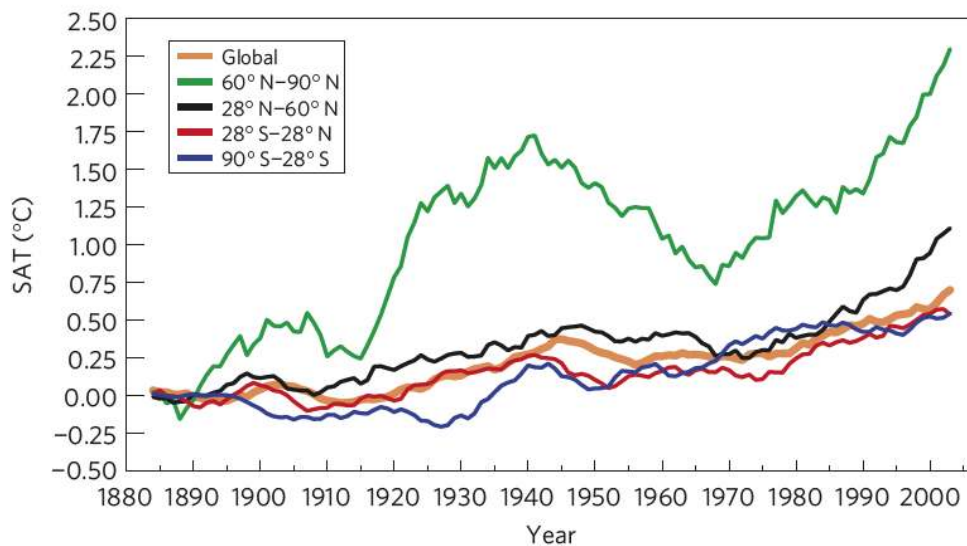
Figure 1. From Shindell & Faluvegi (2009) Figure 2: Area-weighted mean observed surface temperatures over the indicated latitude bands. The values are nine-year running means relative to the 1880–1890 mean. Correlations (R^2) with the global mean over 1931–2007 by region are: 0.94 tropics, 0.61 SHext, 0.86 NHml and 0.53 Arctic.

Such drastic increases in temperature could have significant implications for abiotic and biotic components of the arctic ecosystem, especially since life in this region has adapted to

extreme environments (Coulson et al. 1992, Hodkinson et al. 1998), and plant and insect communities have evolved to survive low temperatures, long winters, late springs, and short summers (Danks 2004, Wingfield et al. 2004).

Biotic responses to these upward temperature trends in the arctic tundra have already become apparent (Walther et al. 2002, Callaghan et al. 2004, McBean et al. 2006, ACIA 2004, AMAP 2012). One response is the expansion of deciduous shrubs (Hinzman et al. 2005, Walker et al. 2006). Over the last several decades, remote sensing data and satellite imagery have detected a 'greening' of the arctic tundra (Stow et al. 2004, Bunn et al. 2007, Verbyla 2008, Jia et al. 2009), as measured by changes in the normalized difference vegetation index (NDVI) (Figure 2). This 'greening' has been attributed to the expansion of deciduous shrubs (primarily birch, willow, and alder) into non-shrub tundra (typically dominated by evergreens, graminoids,
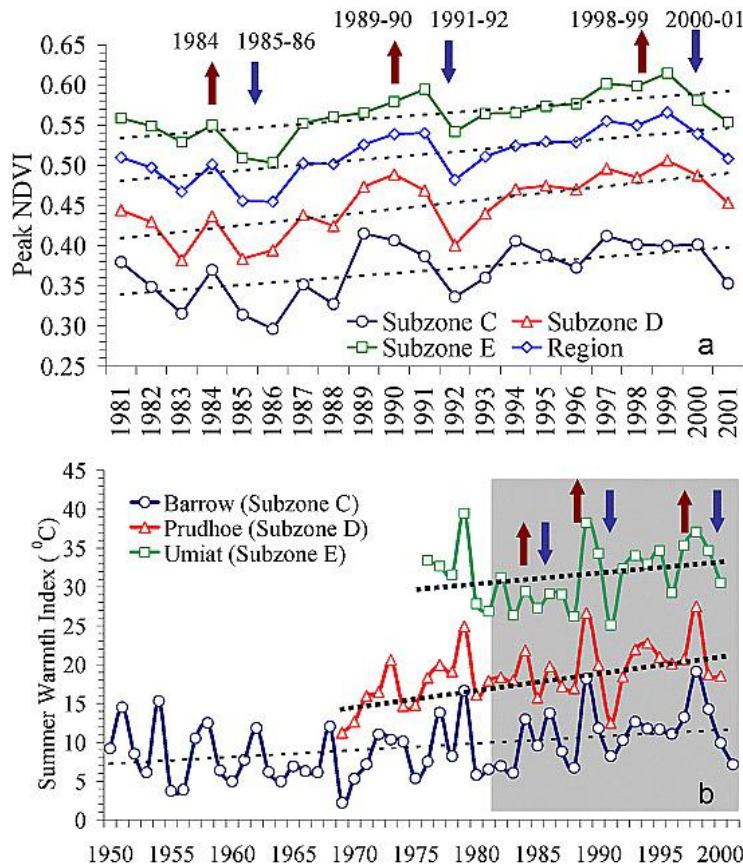
Figure 2. From Jia et al. (2003) Figure 2: Time series of (a) peak NDVI derived from 8-km resolution AVHRR data from 1981 to 2001 and (b) Summer Warmth Index (SWI) over the past 22-50 years among bioclimatic subzones. Dashed lines are linear regressions. The shaded area highlights the period of SWI covered by NDVI data

and cryptogams) (Jia et al. 2003, Olthof et al. 2008, Forbes et al. 2010, Fraser et al. 2011) (Figures 3, 4, & 5). Expansion of deciduous shrub tundra into non-shrub tundra is also evident in comparative photo interpretation (Sturm et al. 2001b, Tape et al. 2006) (Figure 6) and has been quantified in field surveys (Sturm et al. 2001a, Hinzman et al. 2005, Hallinger et al. 2010).
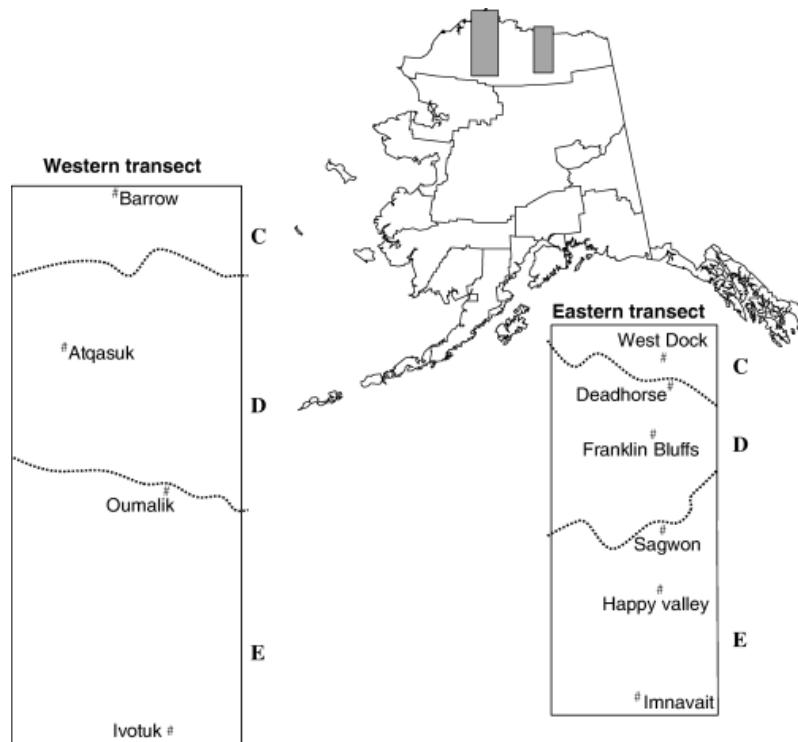
Figure 3. (NOTE: in combination with Figures 4 & 5). From Jia et al. (2006) Figure 1: Location of the study sites with respect to bioclimate subzones and vegetation transects. The dotted lines show the boundaries of bioclimate subzones, C, prostrate dwarf shrub subzone (north), D, erect dwarf shrub subzone (middle), and E, low shrub subzone (south). The solid polygons are the boundaries of transects used in our study. Black points represent the study sites.
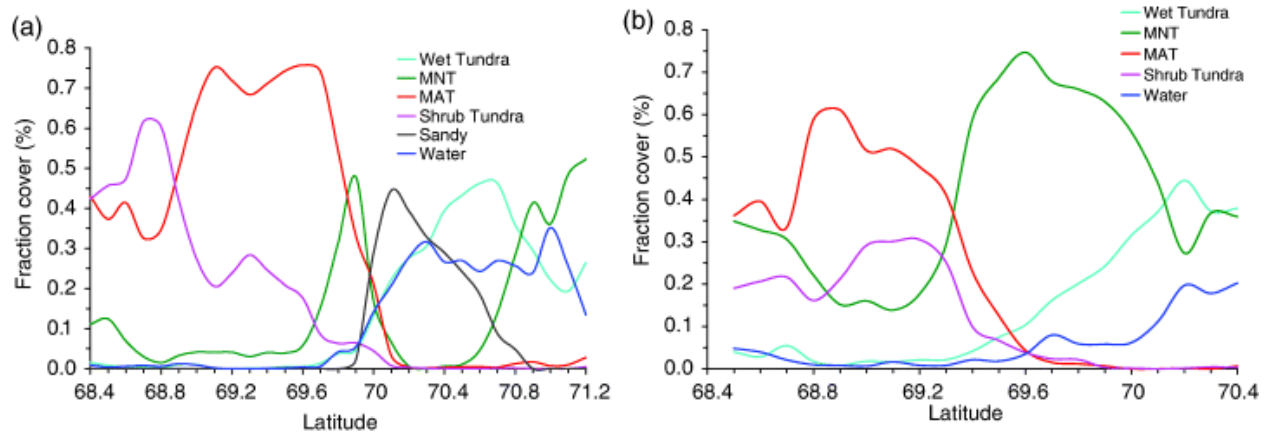
Figure 4. (NOTE: in combination with Figures 3 & 5). From Jia et al. (2006) Figure 2: Fractional covers of tundra vegetation along the latitudinal gradients for each transect (Figure 3). The fractional covers were summarized for 0.1° latitude intervals over a vegetation map of the (a) Western Transect and (b) Eastern Transect. [MNT, moist nonacidic tundra; MAT moist acidic tundra].

3
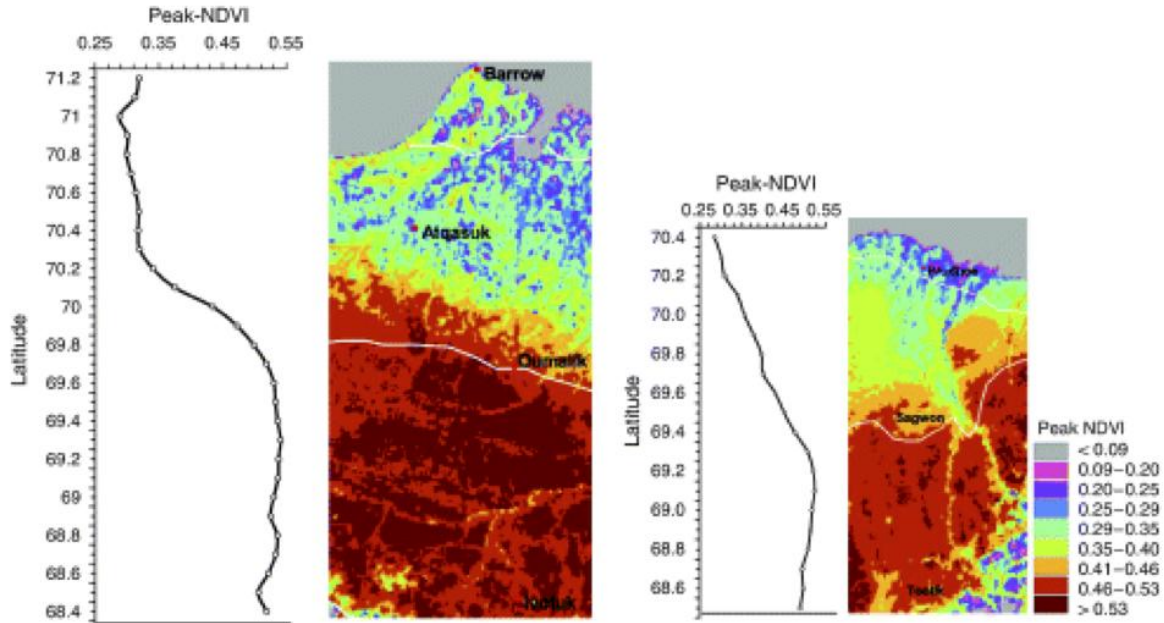
Figure 5. (NOTE: in combination with Figures 3 & 4). From Jia et al. (2006) Figure 3: Spatial patterns of decadal mean Peak- NDVI shown as images and summarized for 0.1° latitude intervals along latitudinal gradients for each transect (Figure 3).
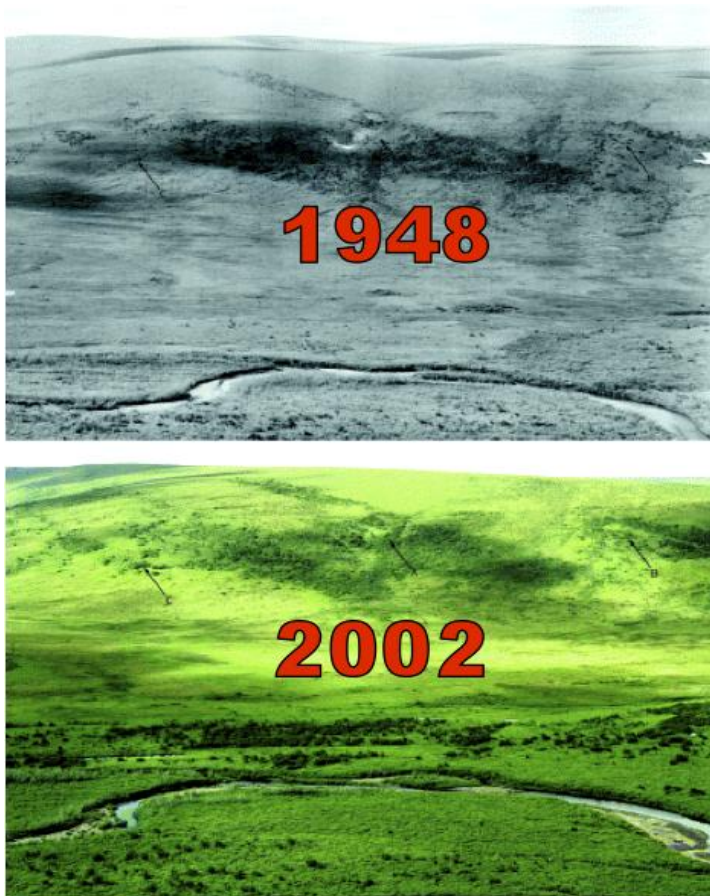
Figure 6. From Tape et al. (2006) Figure 5: Shrub expansion along the Oolamnagavik River located at 68°N 52.00′, 154°W 08.36′: 8/11/1948 and 7/27/2002.

Because deciduous shrubs are predicted to continue to expand their range and grow larger (Bret-Harte et al. 2001, Wookey et al. 2009, Myers-Smith et al. 2011, Pearson et al. 2013), numerous studies have examined the impact increasing shrub cover has in terms of changing plant community composition and potential positive feedback mechanisms that might facilitate shrub encroachment (Chapin et al. 1995, Wahren et al. 2005, Wookey et al. 2009, Hinzman et al. 2005, Jia et al. 2003, Tape et al. 2006). For instance, spread of shrubs into regions of tundra now occupied primarily by graminoids and cryptogams has been shown to reduce albedo (Sturm et al. 2005a, Chapin et al. 2005). This reduction in arctic albedo is most pronounced in winter and early spring when woody stems emerge through the snow and reduce the high albedo of pure white snow (Sturm et al. 2005a). Reduced albedo will further enhance warming temperature trends, which will likely lead to continued shrub expansion (Hinzman et al. 2005, Sturm et al. 2005a, Chapin et al. 2005, Wookey et al. 2009) (Figure 7).
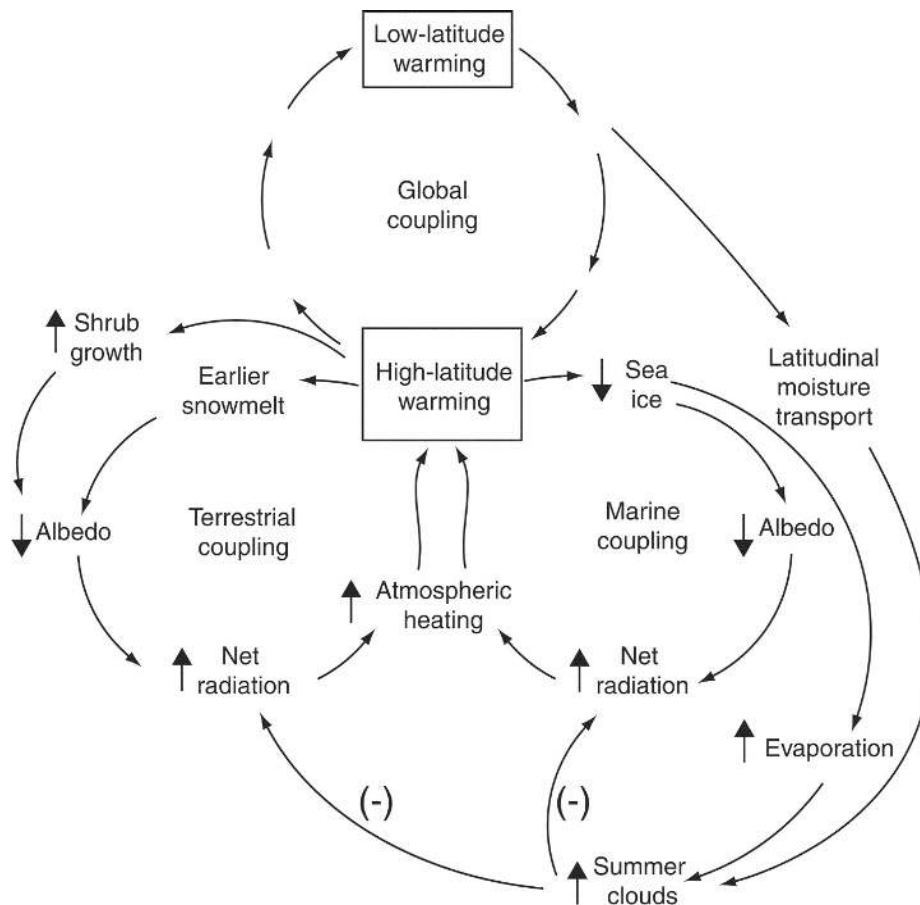
Figure 7. From Chapin et al. (2005) Figure 2: Diagram of feedback loops that couple climatic processes in arctic Alaska. Arrows linking processes indicate a positive effect of one process on another unless otherwise indicated (by minus signs).

Also, shrubs more efficiently trap snow, creating deeper drifts in shrubby tundra (Sturm et al. 2001a, Sturm et al. 2005b) (Figure 8), which leads to increased soil temperatures during winter and early spring (Schimel et al. 2004, Wahren et al. 2005, Wookey et al. 2009). Research has shown that higher soil temperatures under this deep, insulating blanket of snow leads to increased microbial activity, which leads to increased nutrient mineralization (Sturm et al. 2005b, Wookey et al. 2009, Wahren et al. 2005). Not only are these nutrients being released directly under shrubs, but also deciduous shrubs are generally more efficient than many other arctic plants at taking up nitrogen and other nutrients, giving them an advantage in the nutrient limited tundra (Chapin et al. 1995, Bret-Harte et al. 2001, Tape et al. 2006, Wookey et al. 2009). Shrubs are essentially playing a key role in the positive feedback loop of their own expansion: shrubs encroach and grow larger, effectively trapping more snow, which increases winter and spring soil nutrient mineralization, further promoting shrub expansion (Sturm et al. 2001a, Sturm et al. 2005b, Wahren et al. 2005) (Figure 9).

Increasing deciduous shrub cover may further influence the arctic ecosystem in a number of unpredictable ways (Figure 10). For instance, if height and density of arctic tundra shrubs continue to increase as predicted (Myers-Smith et al. 2011), overall canopy height would increase, increasing shading, and reducing shade-intolerant cryptogams (Walker et al. 2006, Cornelissen et al. 2001) (Figure 11).

Figure 8. (a) From Sturm et al. (2005b) Figure 5: A shrub patch that has created a snowdrift in and downwind of the patch. The snow on the tundra behind the patch was about one-fifth as deep as the drift. Photograph: Matthew Sturm.
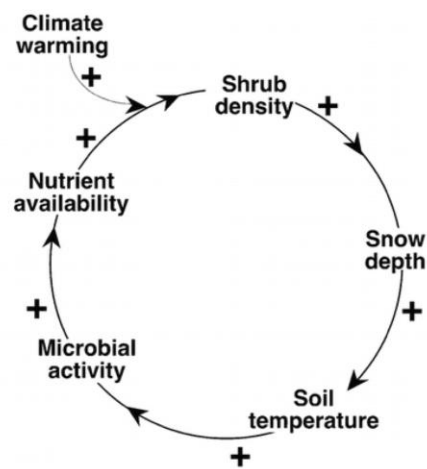
Figure 9. From Sturm et al. (2005b) Figure 9: The snow-shrub-soil-microbe feedback loop.
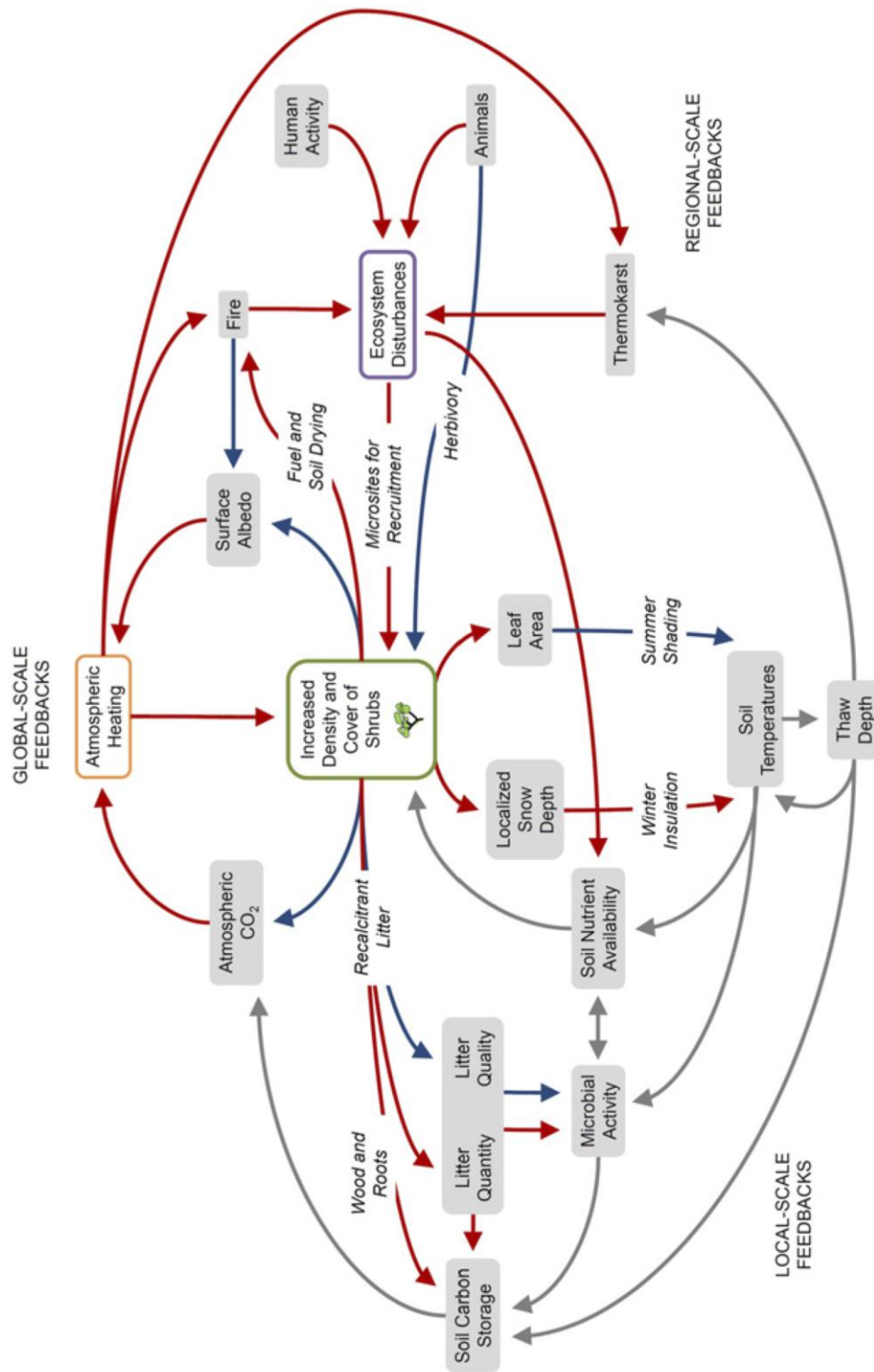
Figure 10. From Myer-Smith et al. (2011) Figure 3: Potential feedbacks from increased density and cover of shrubs to ecosystems processes and properties. Red arrows indicate positive relationships, and blue arrows indicate negative relationships between the two connecting factors, gray arrows indicate as yet undetermined influences.
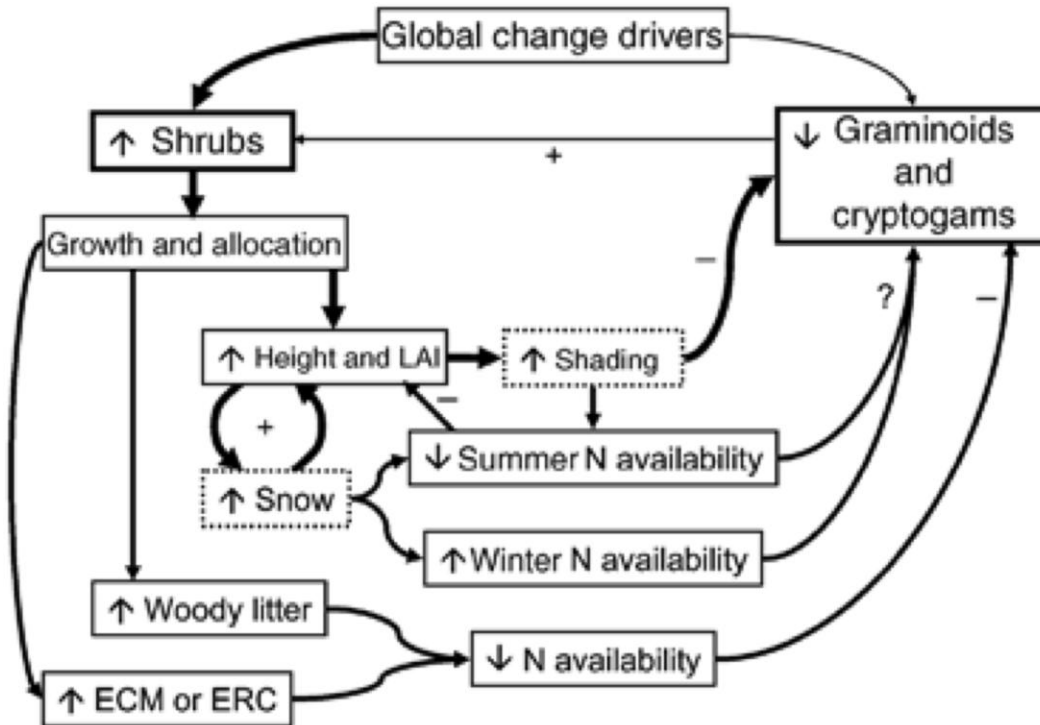
Figure 11. From Wookey et al. (2009) Figure 2: Ecosystem cascades and feedbacks resulting in an increase in deciduous shrubs and a decline in graminoids and cryptogams in response to increasing warmth and duration of the growing season in Arctic tundra. Note that stronger responses to climate drivers among deciduous shrub species (denoted by the thicker line from 'Global Change Drivers' to shrubs than to graminoids and cryptogams) result in a positive feedback between increasing height and leaf area index (LAI) and increased trapping of snow. Changes in the depth, duration, and properties of snow pack can have positive or negative impacts on nitrogen (N) availability through altering soil thermal and moisture regime. Increased height and LAI of shrubs will likely have a negative impact on graminoids and cryptogams through shading effects. Furthermore, increased prevalence of species with ectomycorrhizas (ECM) or ericoid mycorrhizas (ERC) will likely decrease nutrient availability to other species, with further negative consequences. Increases in the proportion of low N, but high lignin, woody litter (leaf and stem litter of woody species associated with increasing shrub dominance) will also tend to reduce N availability.

For instance, a long-term manipulative experiment done by Chapin et al. (1995) in the Alaskan arctic tundra showed that with increased temperature and nutrients (a likely climate change scenario) deciduous shrubs became dominant (e.g. became larger and denser), while the biomass of graminoids, evergreens, and cryptogams declined (Figure 12). Deciduous shrubs outcompeted other species via more efficient nutrient utilization, increased shading of understory, and increased smothering of understory through increased litter (Chapin et al. 1995). After nine years, Chapin et al. (1995) found a 30-40% decline in species richness, where *Betula nana* (dwarf birch) became the most dominant species, and entire functional groups, such as mosses, lichens, and forbs, were essentially eliminated, and other typically dominant non-shrub tundra species, such as *Eriophorum* spp. (cottongrass), declined sharply (Chapin et al. 1995). Not only

did deciduous shrubs respond most positively to increases in temperature and nutrient availability, but evergreen shrub species' growth was actually inhibited by these environmental changes (Chapin et al. 1995).
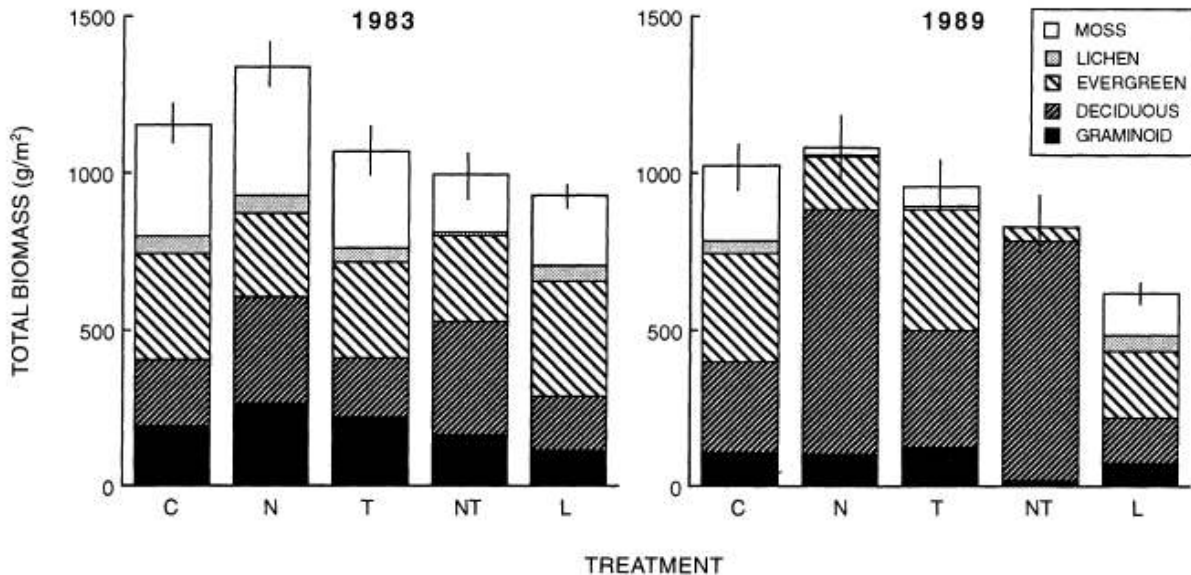
Figure 12. From Chapin et al. (1995) Figure 2: Total peak-season biomass (excluding roots) of tussock-tundra vegetation by growth form in response to environmental manipulations measured 3 and 9 yr after initiation of treatments. Data are means and SE, n =4 blocks, 5 quadrats per plot. Treatments are control (C), nutrient (N), temperature (T), nutrient-temperature (NT), and light attenuation (L).

Wahren et al. (2005) found similar results in their manipulative experiments in the Alaskan arctic tundra. In this study, sites were subjected to snow addition and summer warming to mimic potential climate change scenarios in the arctic tundra. They found altered snow and temperature dynamics led to increased mean canopy height of deciduous shrub species and a decrease in evergreen canopy height (Wahren et al. 2005). As with other studies (e.g. Cornelissen et al. 2001, Chapin et al. 1995), increased shading resulted in a dramatic decline of cryptogams (Wahren et al. 2005). Similar to what Chapin et al. (1995) found, Wahren et al. (2005) found that increased deciduous shrub dominance decreased species evenness and changed the plant community dynamics, with fewer species producing a larger proportion of cover.

Changes in plant community composition, biomass, production, and species evenness that occurs with increasing deciduous shrub dominance (Chapin et al. 1995, Cornelissen et al.

2001, Wahren et al. 2005) may impact arctic herbivores, and have cascading consequences for higher trophic levels. It has already been found that increased deciduous shrub cover negatively effects caribou (Joly et al. 2007, Gilg et al. 2009) through reduced availability of important food resources (Person 1975, White & Trudell 1980, Ferguson et al. 2001, Storeheier et al. 2002, Joly et al. 2009) and increasing snow depth that inhibits their mobility and access to forage (Adamczewski et al. 1987, Collins & Smith 1991). Research also suggests that changes in plant community composition and structure will likely lead to changes in arctic arthropod diversity (Muff et al. 2009, Bowden & Buddle 2010,) and abundance (Haddad et al. 2001, Richardson et al. 2002, Rich et al. 2013). Further, the reduction of specific plant species (e.g. *Carex*, *Eriophorum*, and *Pedicularis* spp.) that characteristically occurs with increases in deciduous shrub cover (Chapin et al. 1995) could decrease the success of small mammals such as lemmings (Batzli 1993, Oksanen et al. 2008), arctic ground squirrels (Batzli & Sobaski 1980, Karels et al. 2000), and voles (Galindo & Krebs 1985, Batzli & Lesieutre 1991). In turn, changes in herbivore communities may have unforeseen and potentially far-reaching implications for tundra carnivores (Finke & Denno 2006, Post et al. 2009, Usher et al. 2010), such as arctic fox (Angerbjörn et al. 1999), wolves (Dale et al. 1994), and snowy owls (Boxall & Lein 1982).

The strong warming trend in many arctic tundra regions has also been correlated with earlier spring snowmelt and later fall snow accumulation (Stow et al. 2004, Foster et al. 2008, AMAP 2012) (Figure 13). Satellite data since the 1960s, for example, has revealed a 10% decrease in snow cover as well as lengthening of freeze-free periods in high-latitude regions (Walther et al. 2002). As a result, many regions have experienced an earlier start and/or a later end to the growing season, and a lengthening of the overall growing season (Tucker et al. 2001, Zhou et al. 2001, Jia et al. 2004, Jeong et al. 2011, Zeng et al. 2011, Barichivich et al. 2013) (Figure 14). Some studies suggest an increase in growing season length of approximately 12 to 14 days per decade in North American high latitudes (Myneni et al. 1997, Zeng et al. 2011), and approximately 6 to 7 days per decade in northern Eurasia (Zhou et al. 2001, Jeong et al. 2011, Zeng et al. 2011). Research also suggests that some arctic regions are experiencing shifts toward an earlier peak green season (Goetz et al. 2005, Tagesson et al. 2012), resulting in an earlier, and potentially longer, period of maximum tundra greenness, but not necessarily a longer overall growing season (Jia et al. 2009) (Figure 15).
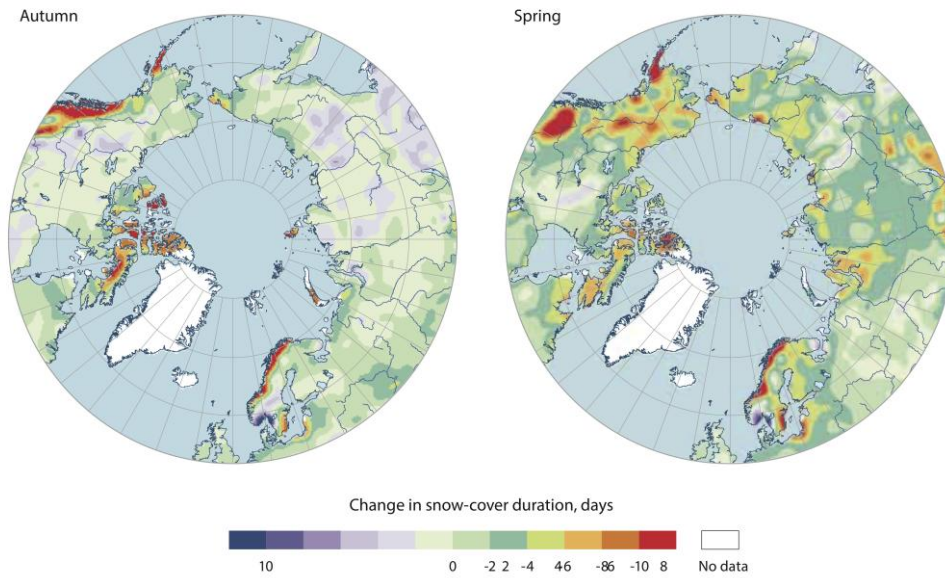
Figure 13. From AMAP (2012) Change in snow-cover cover duration for autumn (snow-cover onset period) and spring (snow-cover melt period) between 1973/72 and 2008/09.
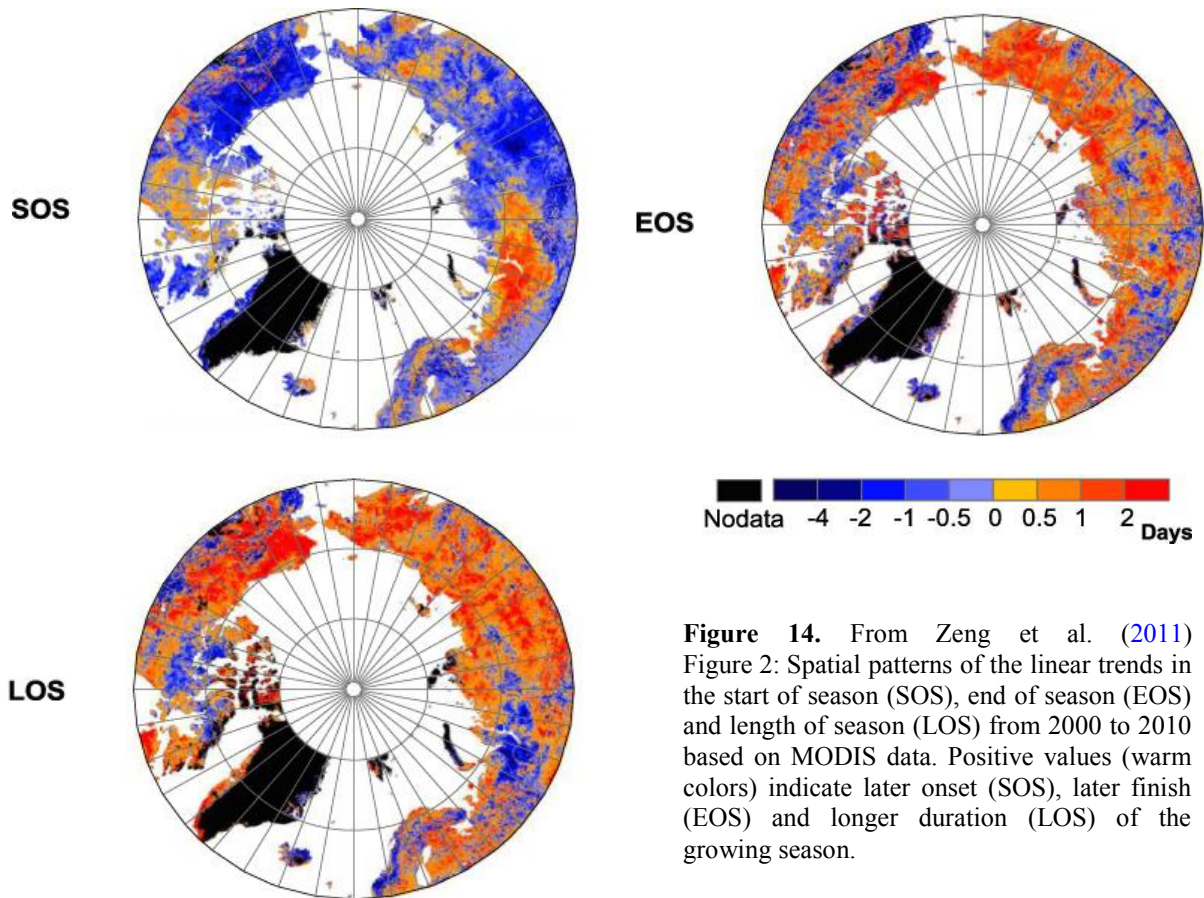
Figure 14. From Zeng et al. (2011) Figure 2: Spatial patterns of the linear trends in the start of season (SOS), end of season (EOS) and length of season (LOS) from 2000 to 2010 based on MODIS data. Positive values (warm colors) indicate later onset (SOS), later finish (EOS) and longer duration (LOS) of the growing season.

11
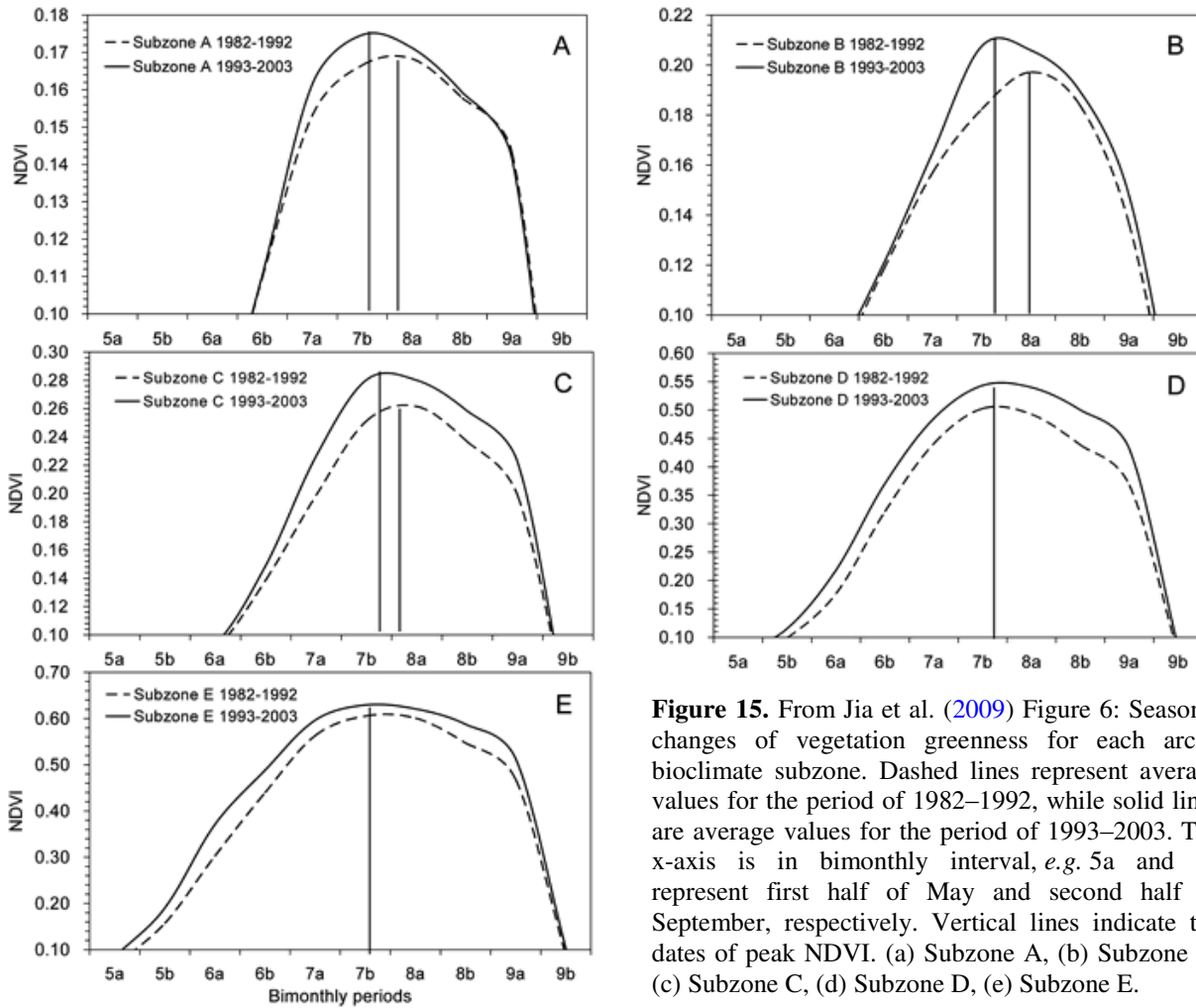
Figure 15. From Jia et al. (2009) Figure 6: Seasonal changes of vegetation greenness for each arctic bioclimate subzone. Dashed lines represent average values for the period of 1982–1992, while solid lines are average values for the period of 1993–2003. The x-axis is in bimonthly interval, *e.g.* 5a and 9b represent first half of May and second half of September, respectively. Vertical lines indicate the dates of peak NDVI. (a) Subzone A, (b) Subzone B, (c) Subzone C, (d) Subzone D, (e) Subzone E.

Because the arctic growing season begins in spring with increases in temperature and light, snowmelt, soil thaw, and the onset of photosynthesis, and ends in fall with decreases in temperatures and light, snowfall, soil refreezing, and the cessation of photosynthesis (Euskirchen et al. 2006), shifts in the onset and end of the growing season could have unforeseen consequences for arctic ecosystems and carbon (C) balances. Longer growing seasons, for example, could reduce the rate of atmospheric CO_2 accumulation in arctic regions (McDonald et al. 2004, Barichivich et al. 2013, Graven et al. 2013). Additionally, important factors in the terrestrial C budget, such as net ecosystem production (NEP) and gross primary production (GPP) and are closely linked with growing season length (Piao et al. 2007). For instance, an advance in start of the growing season in the Northern Hemisphere could increase spring NEP by 2-4 g C m^{-2} day^{-1} (Richardson et al. 2009), and increase annual GPP by 5.8 g C m^{-2} yr^{-1} (Piao et al. 2007). Further, because the arctic growing season is notoriously short, starting the growing season only a few days earlier could significantly enhance the carbon sink potential of the arctic

12

tundra, which covers a large portion of the terrestrial biosphere (Nemani et al. 2002, van Wijk et al. 2003, Euskirchen et al. 2006).

Post et al. (2009) suggests the low functional redundancy of the Arctic necessitates greater conservation attention, because extinction or range shifts here may have more significant ecological impacts compared to more diverse temperate or tropical ecosystems. Also, a majority of studies conducted in the Arctic suggest the rate and magnitude of current and expected abiotic changes (Post & Høye 2013) and subsequent biotic changes (Callaghan et al. 2004, McBean et al. 2006, Wookey et al. 2009) in arctic tundra environments has amplified the need to better monitor, understand, and predict the arctic tundra's ecological responses to climate change over large spatial and temporal scales (Gauthier et al. 2013, Nielsen & Wall 2013). In light of these needs, the research presented in this dissertation provides useful insight into the influence vegetation community composition has on phenology, carbon flux, and canopy arthropod biomass in the arctic foothills region of the Brooks Range, Alaska. Our findings in Chapter one suggest that delayed snowmelt in areas dominated by taller deciduous shrubs may have a short-lived impact on the timing of leaf development, likely resulting in no difference in duration of peak photosynthetic period between tall and short-stature shrubs. Our findings in Chapter two suggest that greater deciduous shrub dominance not only increases carbon uptake due to higher leaf area relative to surrounding tundra, but may also be causing a net extension in the period of maximum tundra greenness and further increasing peak season carbon sequestration. Our findings in Chapter three suggest that measurements of the NDVI made from air and spaceborne sensors may be able to quantify spatial and temporal variation in canopy arthropod biomass at landscape to regional scales, and across diverse tundra vegetation communities.

CHAPTER ONE:

Tall Deciduous Shrubs Offset Delayed Start of Growing Season Through Rapid Leaf Development in the Alaskan Arctic Tundra

Abstract. Increasing temperatures in arctic regions are causing earlier spring snowmelt, leading to earlier plant emergence, which could lengthen the period of carbon uptake. Warming is also leading to a shift from graminoid to deciduous shrub-dominated tundra, and in many areas deciduous shrubs are becoming taller. As taller shrubs become increasingly dominant, arctic landscapes may retain more snow, which could lengthen spring snow cover duration and offset advances in the start of the growing season that are expected as a result of earlier spring snowmelt. As a consequence, deeper snow and later snowmelt in taller shrub tundra could delay plant emergence and shorten the period of carbon uptake. This study tracked leaf development of two abundant deciduous shrubs, Betula nana and Salix pulchra, and compared individuals along a natural shrub height gradient on the North Slope of Alaska. We measured spring snow depth and snow cover duration, bud and developing leaf nitrogen content, as well as the timing of budburst and leaf expansion. Taller deciduous shrubs in shrub-dominated communities had deeper snow surrounding them, and became snow-free 1 to 6 days later, delaying budburst by 2 to 12 days relative to shorter deciduous shrubs in graminoid-dominated communities. However, leaf development of tall shrubs caught up to that of short shrubs; occasionally, tall shrubs reached full leaf expansion 1 to 4 days before short shrubs, indicating more rapid leaf development. This convergence in the timing of later leaf development stages is potentially enabled by approximately 16% to 25% greater nitrogen in buds and developing leaves of taller shrubs compared with shorter shrubs. Our findings suggest that delayed snowmelt in areas dominated by taller shrubs may have a short-lived impact on the timing of leaf development, likely resulting in no difference in duration of peak photosynthetic period between tall and short stature shrubs.

1.1 Introduction

Climate change has caused a particularly strong warming trend in the Arctic (Chapin et al. 2005, Serreze & Francis 2006, IPCC 2007), and spring snowmelt is occurring earlier in many arctic tundra regions (Stow et al. 2004, AMAP 2012). Meta-analyses in northern ecosystems correlate increasing temperatures and earlier spring snowmelt with earlier plant emergence (Arft et al. 1999, Root et al. 2003, Wipf & Rixen 2010). This phenomenon has been observed via field- (Starr et al. 2000, Wipf et al. 2009) and satellite-based studies (Myneni et al. 1997, Zhou et al. 2001, Zeng et al. 2011). The implication of a shift toward earlier plant emergence in arctic tundra ecosystems is not fully understood, but it could lengthen the period of maximum leaf area (Oberbauer et al. 1998), potentially increasing the amount of carbon sequestered by arctic plants within a given year (Euskirchen et al. 2006, Graven et al. 2013, Richardson et al. 2013).

In addition to an earlier start to the growing season, satellite studies suggest the Arctic has been "greening" over the past several decades (Bunn et al. 2007, Verbyla 2008, Jia et al. 2009), which is likely due in part to the expansion and increasing dominance of deciduous shrubs (Jia et al. 2003). Expansion of deciduous shrubs into primarily graminoid-dominated tundra in the Alaskan Arctic is evident in comparative historical photo interpretation (Tape et al. 2006) and has been quantified in field surveys (Hinzman et al. 2005). Deciduous shrub expansion has been attributed to increases in air temperature (Walker et al. 2006), subsurface water flow (Naito & Cairns 2011, Tape et al. 2012), and soil nutrient mineralization (Sturm et al. 2005b). Findings from experimental manipulation studies suggest that deciduous shrubs will continue to expand and grow taller as arctic warming continues (Chapin et al. 1995, Wahren et al. 2005).

Many arctic tundra studies have focused on the impacts of increasing deciduous shrub dominance on snow and nutrient cycling dynamics. For example, tall stature deciduous shrubs are more efficient at trapping snow, deeper drifts surround them compared to shorter stature shrubs (Sturm et al. 2001a, Sturm et al. 2005b, Myers-Smith & Hik 2013). Deeper snowdrifts increase soil insulation, which increases winter microbial activity and nutrient mineralization (Schimel et al. 2004, Wahren et al. 2005, DeMarco et al. 2011). Because deciduous shrubs have been shown to be more efficient than many other arctic plants at taking up nutrients (Shaver & Chapin 1991, Bret-Harte et al. 2001, Wookey et al. 2009), increased mineralization in this strongly nitrogen limited ecosystem allows deciduous shrubs to outcompete other plants (Chapin et al. 1995, Cornelissen et al. 2001, Shaver et al. 2001), creating a potential positive feedback for

increasing deciduous shrub dominance (Sturm et al. 2005b, Myers-Smith et al. 2011).

Further, it has been suggested that winter precipitation is also increasing in arctic regions (Serreze et al. 2000), contributing to deeper snowdrifts. Deeper snowdrifts lead to later snowmelt dates (Liston et al. 2002), which can delay timing of plant emergence (Borner et al. 2008), potentially shortening the growing season and delaying the period of photosynthetic activity. Thus, due to their tendency to increase spring snow cover duration, the increasing dominance of tall deciduous shrubs could delay plant emergence, thereby offsetting, at least to some extent, the earlier start to the growing season expected to continue with spring warming and earlier snowmelt.

Although several studies have explored how changing snow depth and spring snowmelt dates may affect plant phenology, most have been experimental, relying on snow removal (Oberbauer et al. 1998, Starr et al. 2000, Wipf et al. 2009) or artificial warming to simulate the impacts of early snowmelt (Wookey et al. 1993, Hartley et al. 1999, Aerts et al. 2006), and snow fences to simulate the impacts of greater snow depth and later snowmelt (Walker et al. 1999, Wahren et al. 2005). While snow manipulation studies are important for understanding potential implications of climate change on plant phenology, Wipf & Rixen (2010) suggested that such experimental techniques may deviate from natural scenarios by altering snow composition and compaction. Therefore, it is important to also include observations of how natural gradients in vegetation stature, and consequently snow depth, impact tundra plant phenology (Dunne et al. 2004, Hollister et al. 2005). Also, most plant phenological studies monitor the date on which some or all of the following life history events occur – snow-free, leaf budburst, flowering, and/or senescence dates (e.g. Molau & Molgaard 1996) – yet intermediate leaf development stages, such as leaf expansion, can also be important from a carbon gain perspective (Johnson & Tieszen 1976).

In this study, we monitored snow depth, timing of snowmelt, timing of leaf bud appearance, leaf budburst, leaf opening, and leaf expansion, as well as nitrogen contents of buds and emerging leaves for two species of deciduous shrubs (*Betula nana* and *Salix pulchra*, hereafter *B. nana* and *S. pulchra*) along a natural gradient of increasing shrub dominance (i.e. increasing aerial cover and stature) on the North Slope of Alaska. Because the rate of leaf development may affect timing of maximum photosynthetic capacity (Constable & Rawson 1980) and thus carbon sequestration (Street et al. 2007), we quantified sequential leaf stages

closely throughout the period of leaf development. Our goal was to gain an understanding of how shrub stature and associated snow dynamics impact the timing of leaf bud break and leaf development. Based on findings from previous studies (Sturm et al. 2001a, Liston et al. 2002), we hypothesized that taller stature deciduous shrubs would undergo a delay in leaf development as a result of deeper snow and a delayed snow-free date.

1.2 Methods

1.2.1 Study Sites and Study Areas

Data sets were collected in early May through the end of July in 2011 and 2012 at three field sites (Figure 1.1) within ~30 km of the Arctic Long Term Ecological Research (ARC LTER) site at Toolik Field Station in the northern foothills of the Brooks Range, Alaska (68'38N, 149'34W). Annual precipitation at Toolik is 200 – 400 mm, with 45% falling as snow; annual average air temperature is -10ºC (van Wijk et al. 2005) and average growing season air temperature is 7ºC (Johnson et al. 2000). We defined the growing season as the period from snow-free until senescence, which near Toolik extends from approximately late May/early June until mid to late August. Daily air temperature during the 2011 and 2012 growing seasons at our sites (Figure 1.2) were within the long-term average range of growing season air temperatures at Toolik (Johnson et al. 2000).

Sites were chosen in May 2010 to represent the most common shrub tundra types in the foothills of the Brooks Range (Hanson 1953) as part of a larger research effort investigating the effects of shrub vegetation on associated arthropod and migratory songbird reproductive success (Rich et al. 2013). The three sites used in this study were: Toolik Lake Field Station (TLFS), Sagavanirktok River-Department of Transportation camp (SDOT), and Imnavait Creek (IMVT) (Figure 1.1). Each of the three sites included two study areas dominated by different vegetation cover; one study area dominated by graminoids that also contained short deciduous shrubs (hereafter referred to as Open) and one study area dominated by deciduous shrubs (hereafter referred to as Shrub) (Figure 1.3). Within each Open or Shrub study area, two 100 m transects were established, for a total of 12 transects (6 Open and 6 Shrub). Ten 1-m^2 quadrats were established at 10 m intervals along each transect. In early 2012, along each transect, wooden 2x6 inch boardwalks were installed low to the ground and a reasonable distance from quadrats. In this study, five 1-m^2 quadrats were randomly chosen along each transect, for a total of 60

quadrats (30 Open and 30 Shrub). In all 60 quadrats, individual *B. nana* and *S. pulchra* plants closest to the lower left corner of each quadrat were selected and an individual branch at the top of the canopy of each plant was labeled with an identification (ID) tag in the spring of 2011.
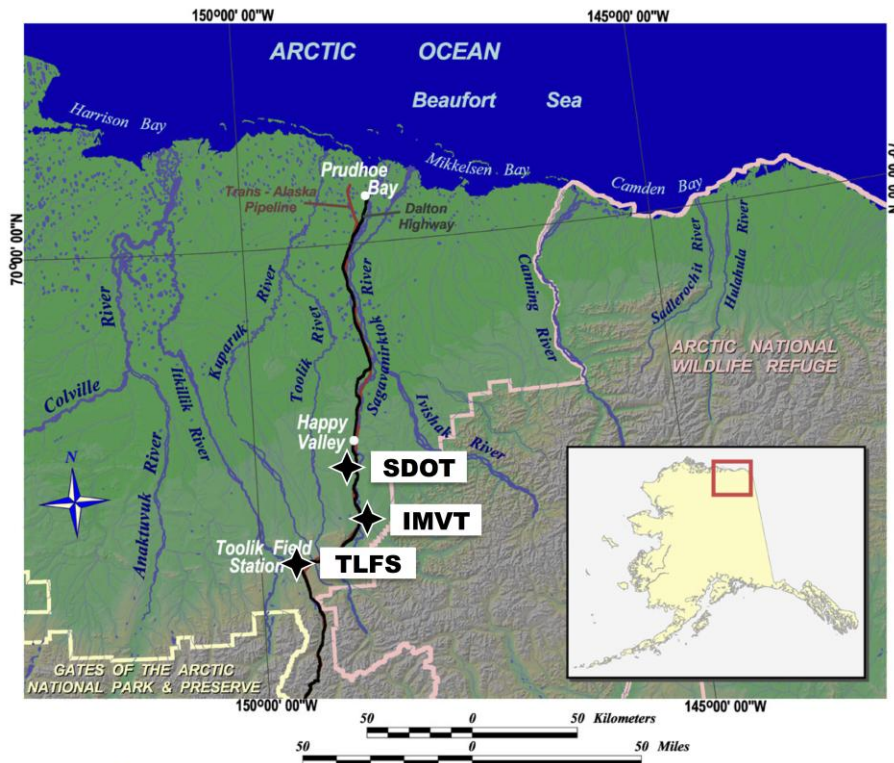
Figure 1.1. Map of Alaska and the North Slope of the Brooks Range (inset) showing the location of the three field sites near the Toolik Lake field station used in this study. TLFS = Toolik Lake Field Station; IMVT = Imnavait Creek; and SDOT = Sagavanirktok River–Department of Transportation.

Together, the Open and Shrub areas represent a natural gradient of increasing shrub dominance, because the same deciduous shrubs (*B. nana* and *S. pulchra*) are found in all study areas, however, their percent cover and stature increase from low percent cover (~ 20%– 30%) and short stature (< 30 cm) in Open areas to higher percent cover (~ 40%–55%) and taller stature (ranging from 30 to 105 cm) in Shrub areas. Although there is topographical variation between sites (TLFS, IMVT, and SDOT), the study areas within each site (Open and Shrub) are not topographically different enough (Table 1.1) to cause significant differences in snow depths, thus differences in snow depth between Open and Shrub areas at each site are primarily caused by differences in vegetation height.

18
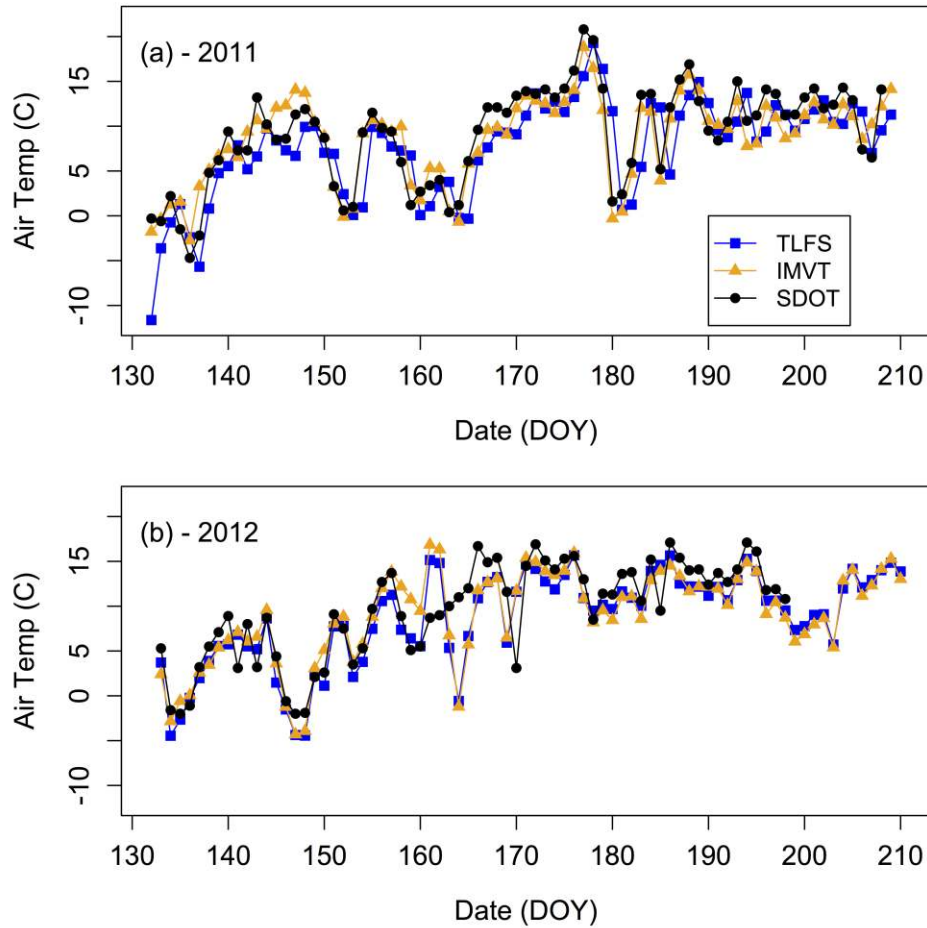
Figure 1.2. Average daily air temperature (Celsius) from 2 May to 28 July (DOY: 132 to 210) during the (a) 2011 and (b) 2012 field season at three sites used in this study.

The Open areas at all three sites are similar to one another and are characterized by tussock-forming sedges interspersed with a variety of dwarf shrubs, forbs, and mosses, with average maximum deciduous shrub heights of approximately 16 cm (IMVT), 23 cm (TLFS), and 28 cm (SDOT). The three Shrub areas differ from one another and represent a gradient of shrub statures, with average maximum deciduous shrub heights of approximately 22 cm (IMVT), 35 cm (TLFS), and 84 cm (SDOT). The IMVT Shrub area is located in water tracks and represents vegetation typical of water track tundra as described in Chapin et al. (1988). The TLFS Shrub area is located near the Toolik Lake outlet (~ 200 m from the outlet) and represents vegetation typical of shrub tundra described in Shaver & Chapin (1991). The SDOT Shrub area is a riparian community (~ 200 m from the Oksrukuyik Creek), has tall and structurally complex shrubs, and represents vegetation typical of riverside shrub tundra as described in Giblin et al. (1991).
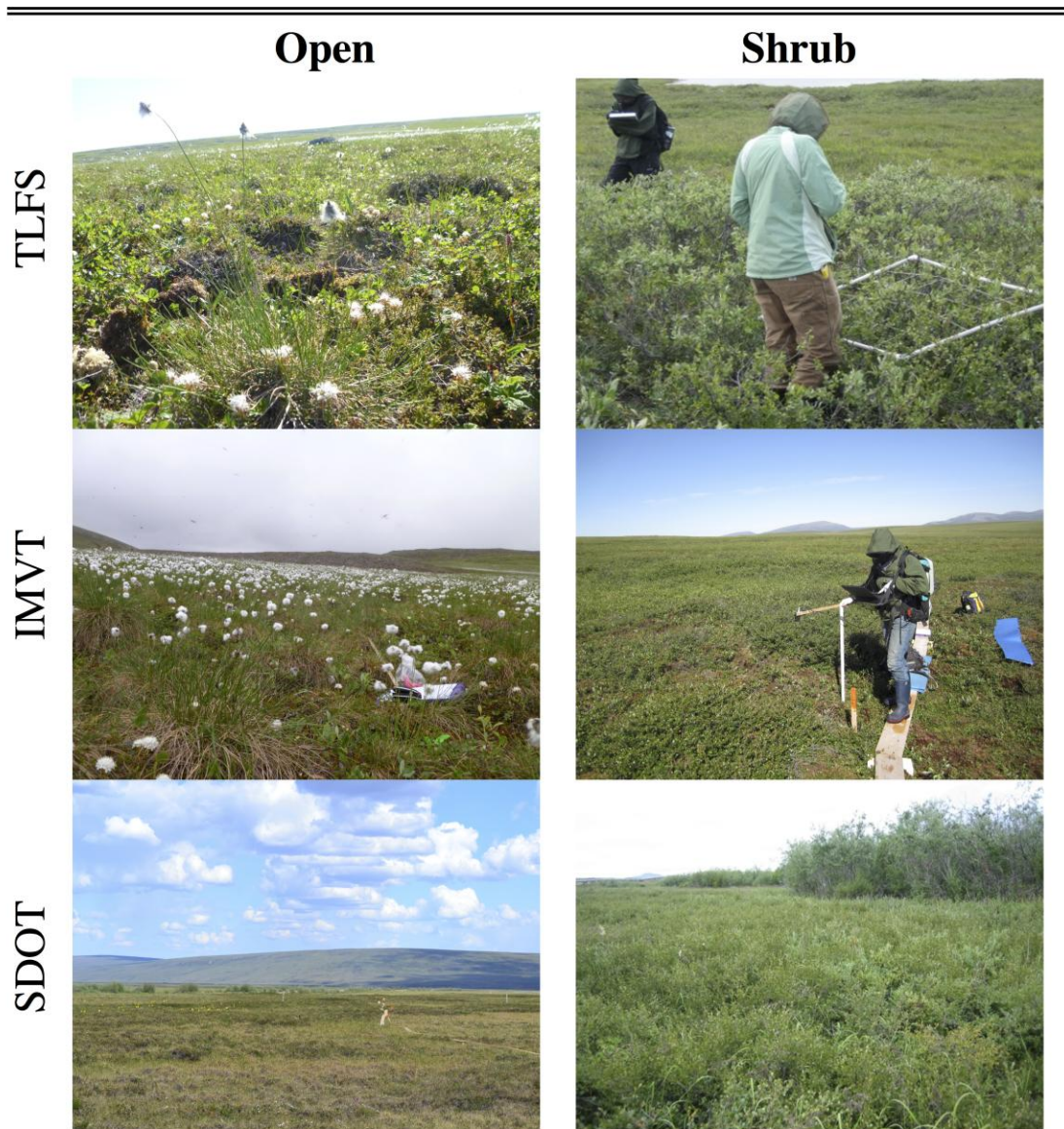
Figure 1.3. Examples of graminoid-dominated (Open – left panels) and deciduous shrub-dominated (Shrub – right panels) areas used in this study in the Northern foothills of the Brooks Range, Alaska.

Site	TLFS		IMVT		SDOT	
Area	Open	Shrub	Open	Shrub	Open	Shrub
Average elevation	747 m	722 m	918 m	910 m	508 m	504 m
Minimum elevation	735 m	716 m	913 m	902 m	503 m	500 m
Maximum elevation	755 m	725 m	923 m	919 m	510 m	509 m

Table 1.1. Average, minimum, and maximum topographic elevation (in meters) at each site and study area used in this study. Additional maps at [http://toolik.alaska.edu/gis/index.php]

1.2.2 Snow Depth and Melt

The day of year (DOY) on which each individual plant being monitored for leaf development (see Timing of Leaf Development) was snow-free (snow-free date) was recorded in 2011 and 2012. In addition to individual plant snow-free dates, in 2012 snow depth was measured every four to six days in each of the quadrats where individual plants were monitored, from 11 May until snow depth reached 0 cm (ca. 24 May to 5 June, depending on the site). Snow depth was measured at the center and four corners in all sixty 1-m^2 quadrats by pushing a 1 cm diameter aluminum pole into the snow until soil or moss surface was reached (for a total of 25 measurements per transect, per sampling date). The five snow depth values associated with each quadrat were averaged to give a mean quadrat value.

1.2.3 Timing of Leaf Development

In 2011 and 2012, the timing of leaf development stages (described below and in Figure 1.4) of individuals labeled with ID tags (see Study Sites) were monitored every two days, from the time each individual was snow-free until leaves were fully expanded (ca. 6 June to 30 June, depending on the species, site, and year) for a total of 60 *B. nana* and 60 *S. pulchra* monitored (n = 30 *B. nana* Open, 30 *B. nana* Shrub, 30 *S. pulchra* Open, and 30 *S. pulchra* Shrub). A modified version of the International Tundra Experiment (ITEX) phenology protocol (Molau & Molgaard 1996) for *Salix* spp. was used, with the modification being that two additional leaf development stages (first leaf opening and first leaf expanded) were added to the existing ITEX protocol. For each *B. nana* and *S. pulchra* individual, the date on which the following four leaf development stages were reached for the first leaf on an individual labeled branch was recorded: (1) the appearance of the first leaf bud (first leaf bud, FLB), (2) when the first leaf became visibly distinct with green tissue splitting through bud scales (first leaf visible, FLV), (3) when the first leaf separated from the bud and individual leaves became apparent (first leaf opening, FLO), and (4) when the first leaf completely separated from the bud and expanded (first leaf expanded, FLE) (Figure 1.4). This may not have always been the same leaf monitored at each stage, but the date the *first* leaf on the same branch reached each stage.

	Betula nana	*Salix pulchra*

FLB:
First leaf bud

FLV:
First leaf visible

FLO:
First leaf opening

FLE:
First leaf expanded
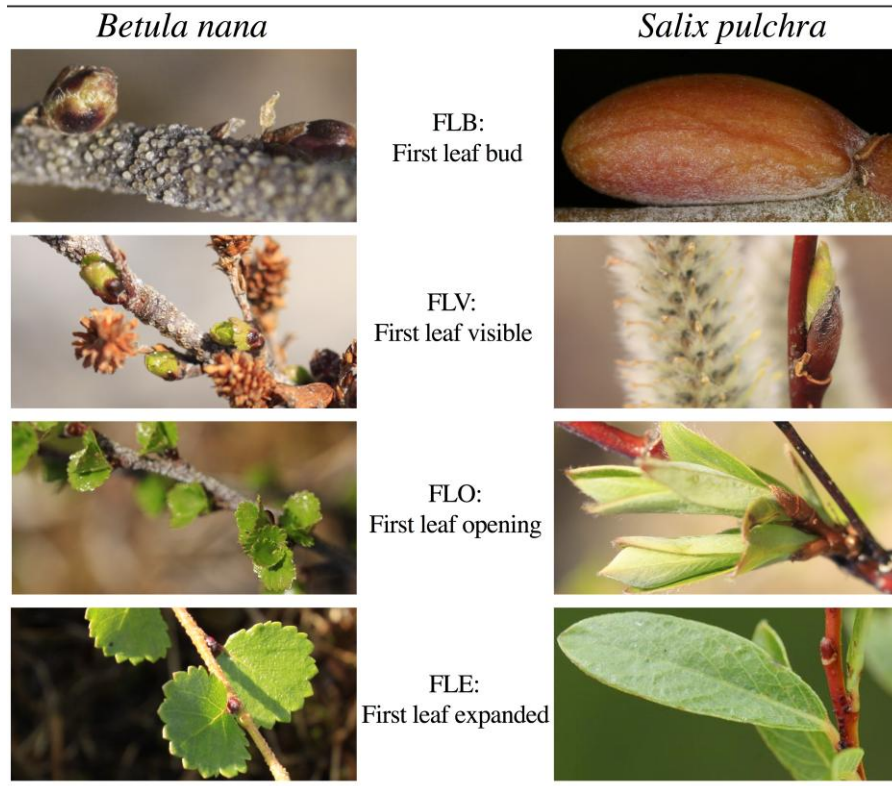
Figure 1.4. Examples of *Betula nana* (left panels) and *Salix pulchra* (right panels) leaf development stages.

1.2.4 Leaf Nutrient Content

Buds and leaves were collected for nutrient content analysis in 2012 from 25 May to 9 June at three times (corresponding to three leaf development stages: FLB, FLV, and FLO) from one *B. nana* and one *S. pulchra* individual located directly adjacent to each plant being monitored for timing of leaf development. A total of five bud or leaf samples per species, per leaf development stage, per transect were collected (n = 30 for each species, in each vegetation type, at each leaf development stage; for a total of 60 *B. nana* and 60 *S. pulchra* samples for each leaf development stage). Samples were placed in paper coin envelopes, air dried, and later dried in an oven at 60 °C for 24 hours. Samples were ground into a powder using a Mini-Beadbeater-16 ball mill (Bio Spec Products, Oklahoma, U.S.A.). Subsamples of approximately 10 mg were weighed into tin capsules, combusted at 950 °C, and analyzed for nitrogen content using a Thermo Scientific Flash 2000 CHN Analyzer (CE Elantech, New Jersey, U.S.A.). Because of equipment failure, there was only one sample available for data analysis for the FLB stage for *S. pulchra* from the IMVT Open area, thus data for IMVT Open *S. pulchra* were not included in statistical analysis.

1.2.5 Statistical Analysis

Because the same individual plants were tracked for leaf development and used for sample collection for nutrient analysis, repeated measures MANOVA was used with timing of leaf developmental stages or leaf nutrient content as the dependent variables and vegetation cover type (Shrub and Open) and site (TLFS, IMVT, and SDOT) as the main effects. For repeated measures multivariate between subject tests, we report Wilks's Lambda results. Because snow depth was measured repeatedly throughout 2012, and because snow-free date was monitored in both 2011 and 2012, a repeated measures analysis was performed on each data set separately, using a linear mixed-effects model, which included vegetation cover and site as the main effects. Quadrats were used as replicates for all data sets (n = 60; 30 Open and 30 Shrub). If the repeated model depicted a significant effect, means were compared using Tukey's honestly significant differences (Tukey's HSD) criterion. Statistical analysis was done in R (R Core Team 2011) and SAS (SAS Software, v. 9.2, SAS Institute, Cary, North Carolina, U.S.A.).

1.3 Results

1.3.1 Snow Depth and Melt

Depending on the site (i.e. TLFS, IMVT, and SDOT), snow depth (Figure 1.5) ranged from 6 to 30 cm deeper in Shrub areas compared to Open areas from DOY 132 to 136 (12 May 2012 to 15 May 2012), and remained significantly deeper until the end of May (effect of cover: $F_{1,54} = 20.24$, $P < 0.0001$). The pattern of snow depth over time varied between site and cover type (i.e. Open and Shrub), driving a significant three-way interaction for the overall data set (effect of day*site*cover: $F_{10,100} = 1.94$, $P = 0.05$). The pattern of snow depth also differed over time and across sites (effect of day: $F_{5,50} = 128.84$, $P < 0.0001$; effect of day*site: $F_{10,100} = 9.98$, $P < 0.0001$) and cover type (effect of day*cover: $F_{5,50} = 4.69$, $P = 0.001$). These significant interaction effects were driven by the differences in snow depth over time between sites and cover type. As can be seen in Figure 1.5, snow depth appears to have decreased at a fairly constant rate at TLFS, decreased more rapidly at SDOT after the second measurement date, and decreased even more rapidly at IMVT after the third measurement. There was also a significant interaction between site and cover type for the first two sample dates, driving a significant interaction for the overall data set (effect of site*cover: $F_{2,54} = 4.06$, $P = 0.02$). The significant

interaction of site*cover disappeared over time because, as snow melted, the magnitude of difference between sites and cover types decreased. Because the IMVT Open area actually had greater snow depths than TLFS or SDOT Shrub areas, there was also an effect of site on snow depth (effect of site: $F_{2,54} = 16.5$, $P < 0.0001$).
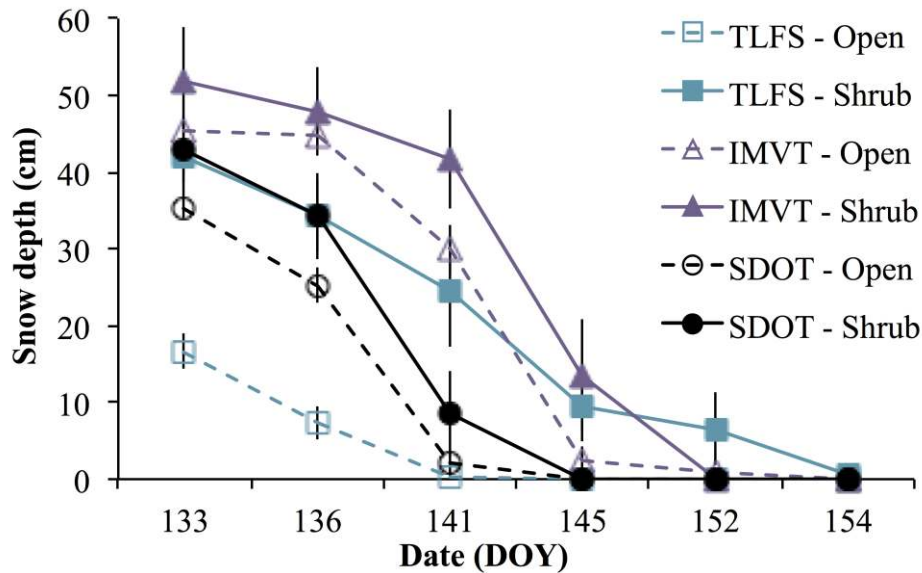
Figure 1.5. Average snow depth (cm) in 2012 throughout measurement period in Open (dashed lines and open symbols) and Shrub (solid lines and filled symbols) areas by site (TLFS = teal squares; IMVT = purple triangles; SDOT = black circles). Error bars represent 1 SEM.

Although there was variation from year to year and among the sites and cover types, the snow-free date for *B. nana* (Table 1.2) was approximately 1 to 6 days later in Shrub areas (depending on the site and year) as compared to Open areas (effect of year*site*cover: $F_{2,54} = 4.15$, $P = 0.02$), which corresponds with deeper snow of Shrub areas (Figure 1.5). This three-way interaction of year*site*cover was driven by the fact that there was no statistically significant difference in snow-free date between Shrub and Open cover type at SDOT in either year, nor at IMVT in 2012; but there were significant differences between cover types at TLFS in both years and at IMVT in 2011. There were also significant effects of year*site ($F_{2,54} = 19.63$, $P < 0.0001$) and year ($F_{1,54} = 37.07$, $P < 0.0001$), because *B. nana* was snow-free earlier in 2012 compared to 2011 at SDOT and TLFS, but later in 2012 at IMVT. Also, *B. nana* at IMVT was snow-free last compared to TLFS and SDOT, and whether TLFS or SDOT melted out first varied from year to year and between cover types. There was a significant interaction between site and cover type for *B. nana* in 2012 ($F_{2,54} = 4.31$, $P = 0.02$), because in 2012 there was a significant difference in

24

snow-free date between cover types at TLFS only. Although Shrub areas were snow-free later than Open areas in both years (effect of cover: $F_{1,54}$ = 25.69, P < 0.0001), the magnitude of difference between snow-free dates in Open and Shrub areas was greater at TLFS compared to IMVT or SDOT (effect of site: $F_{2,54}$ = 68.82, P < 0.0001).

Table 1.2. Average snow free dates (DOY) in 2011 and 2012 for *B. nana* and *S. pulchra*. Means are listed (± 1 SEM) for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Different letters in parentheses next to mean indicate means within the row are significantly different (P < 0.05) from each other.

Site		TLFS		IMVT		SDOT	
	Area	**Open**	**Shrub**	**Open**	**Shrub**	**Open**	**Shrub**
Year	**Species**						
2011	*B. nana*	142 ± 0 (a)	144 ± 0.6 (b)	144 ± 0.4 (b)	148 ± 0 (c)	141 ± 0 (a)	142 ± 1 (a)
2012	*B. nana*	136 ± 0.6 (a)	141 ± 1.1 (b)	146 ± 0.8 (c)	148 ± 1.1 (c)	140 ± 0.5 (b)	140 ± 0.5 (b)
2011	*S. pulchra*	142 ± 0 (a)	145 ± 0.6 (b)	144 ± 0.4 (b)	148 ± 0.3 (c)	141 ± 0 (a)	142 ± 1 (a)
2012	*S. pulchra*	136 ± 0.9 (a)	141 ± 1.3 (b)	145 ± 0.7 (b)	148 ± 1.3 (bc)	139 ± 0 (ab)	140 ± 0.6 (ab)

As with *B. nana*, snow-free date for *S. pulchra* was later in Shrub areas compared to Open areas (Table 1.2), but this trend differed across sites and years (effect of year*site: $F_{2,54}$ = 10.68, P = 0.0001; effect of year: $F_{1,54}$ = 29.59, P < 0.0001). As with *B. nana*, this was driven by the fact that *S. pulchra* was snow-free earlier in 2012 compared to 2011 at SDOT and TLFS, but later in 2012 at IMVT. There was also a significant interaction between site and cover type for *S. pulchra* in 2011 (effect of site*cover 2011: $F_{2,54}$ = 3.4, P = 0.04), because there was a smaller magnitude of difference in snow-free date between cover type and sites for *S. pulchra* in 2012. Although the *S. pulchra* individuals in Shrub areas melted out later than Open areas in both years (effect of cover: $F_{1,54}$ = 41.21, P < 0.0001), as with B. nana, the magnitude of difference between snow-free dates for S. pulchra in Open and Shrub areas differed from site to site (effect of site: $F_{2,54}$ = 67.34, P < 0.0001). *S. pulchra* at IMVT were snow-free last compared to TLFS and SDOT, and whether TLFS or SDOT melted out first varied from year to year and between cover types.

1.3.2 Timing of Leaf Development

Although there were differences among sites, years, and species, because *B. nana* and *S. pulchra* in Open areas were snow-free earlier (Table 1.2) due to shallower snow (Figure 1.5),

initial leaf development stages (e.g. first leaf visible [FLV] and first leaf opening [FLO]) occurred 2 to 12 days earlier (depending on the site) in Open areas as compared to Shrub areas (Figures 1.6a & 1.7a). However, individuals located in Shrub areas accelerated leaf development to such an extent that they reached the last leaf development stage (i.e. first leaf expanded [FLE]) only 2 days later or even 4 days *earlier* than those in Open areas. For instance, at TLFS in 2011, *B. nana* and *S. pulchra* reached FLO 12 and 10 days later (respectively) in Shrub areas compared to Open areas, but reached FLE 0 and 1 day later (respectively) (Figures 1.6b & 1.7b). And at SDOT in 2011, *B. nana* and *S. pulchra* reached FLV 2 and 5 days later (respectively) in Shrub areas compared to Open areas, but reached FLE 1 and 5 days *earlier* (respectively) (Figures 1.6d & 1.7d).
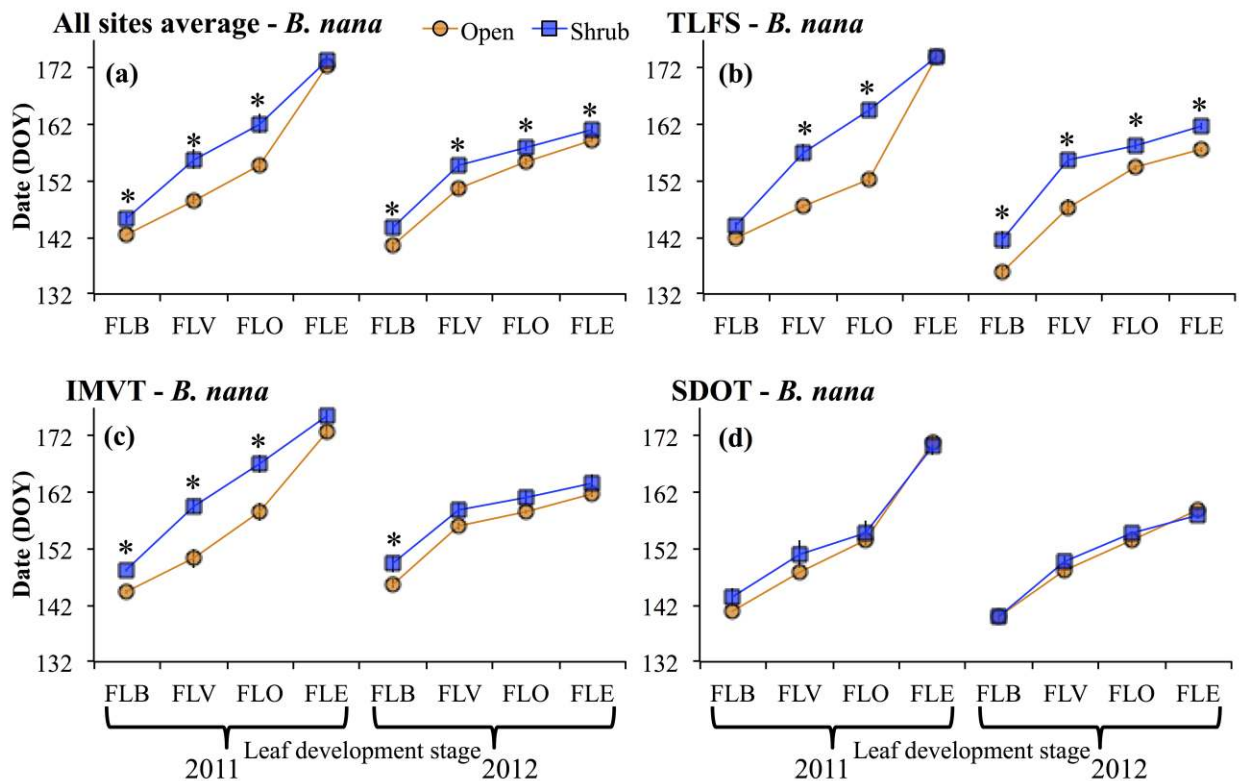
Figure 1.6. Average relative timing of leaf development stages (FLB = first leaf bud; FLV = first leaf visible; FLO = first leaf opening; and FLE = first leaf expanded) for *B. nana* in Open (orange circles) and Shrub (blue squares) areas in 2011 and 2012 for (a) all three sites averaged; and at (b) TLFS, (c) IMVT, and (SDOT). Error bars represent 1 SEM. Asterisks (*) above symbols indicate a significant difference (*P* < 0.05) in time when leaf development was reached between Open and Shrub areas.

In both 2011 and 2012, the pattern of leaf development of *B. nana* over time differed between site and cover type, driving a significant three-way interaction for the overall data set (effect of leaf stage*site*cover: 2011, $F_{6,104} = 4.83$, $P < 0.0002$; 2012, $F_{6,104} = 4.83$, $P < 0.0002$). In 2012, only the pattern of leaf development of *B. nana* differed between site and cover type (effect of site*cover: 2012, $F_{2,54} = 7.91$, $P = 0.001$) because shrubs at IMVT reached all leaf development stages in both Open and Shrub areas later than SDOT or TLFS in 2012 (Figure 1.6), which corresponds with the later snow-free date at IMVT (Table 1.2). Differences between timing of leaf development stages FLV and FLO for *B. nana* between Shrub and Open areas were greatest at TLFS and IMVT in 2011 and at TLFS in 2012; and there was no significant difference in timing between cover types at SDOT in either year. Overall, in both 2011 and 2012, *B. nana* in Shrub areas reached the first three leaf development stages later than in Open areas (effect of cover: 2011, $F_{1,54} = 27.86$, $P < 0.0001$; 2012, $F_{1,54} = 28.70$, $P < 0.0001$) (Figure 1.6a). For individual leaf development stages, in both years, *B. nana* in Shrub areas reached FLB, FLV, and FLO significantly later (2 to 12 days later depending on the site) than in Open areas, but there was a significant difference in timing at FLE in 2012 only (Table 1.3). In 2011, the effect of site was driven mostly by TLFS and IMVT (effect of site: 2011, $F_{2,54} = 13.11$, $P < 0.0001$), and by TLFS in 2012 (effect of site: 2012, $F_{2,54} = 55.75$, $P < 0.0001$). Differences between sites and years could also be affected by differences in air temperatures (Figure 1.2). Although the difference in timing when leaf development stages were reached was not significant at SDOT, it is notable that although Open areas reached FLB and FLV leaf development stages 2 to 3 days earlier than Shrub areas, *B. nana* in SDOT Shrub areas reached FLE 1 day *before* those in Open areas, indicating an accelerated rate of leaf development (Figure 1.6d).

For *S. pulchra*, there was a significant three-way interaction effect in 2011 only (effect of leaf stage*site*cover: 2011, $F_{6,104} = 2.53$, $P = 0.03$), because in 2011 there were significant differences in timing of leaf development stages being reached between Open and Shrub areas, but the stage at which the differences were significant differed among sites (Figure 1.7). Overall, in both years, *S. pulchra* individuals in Shrub areas reached the first three leaf development stages later than *S. pulchra* in Open areas (effect of cover: 2011, $F_{1,54} = 11.17$, $P < 0.002$; 2012, $F_{1,54} = 6.45$, $P = 0.01$) (Figure 1.7a). For individual leaf development in 2011, *S. pulchra* in Shrub areas reached FLV and FLO significantly later (4 to 10 days later depending on the site)

than in Open areas, but there was no significant difference in timing at FLB or FLE (Table 1.3). For individual leaf development in 2012, *S. pulchra* in Shrub areas reached FLB and FLV significantly later (2 to 6 days later depending on the site) than in Open areas, but there was no significant difference in timing of FLO or FLE. Effect of site in 2012 was driven by the fact that the only significant difference in timing of leaf development stages was at TLFS at FLB and FLV (effect of site: 2012, $F_{2,54}$ = 37.47, P < 0.0001) (Figure 1.7b). Similar to *B. nana*, differences between sites and years could also be due to differences in air temperature (Figure 1.2). As with *B. nana*, *S. pulchra* in Open areas reached FLB and FLV leaf development stages earlier than Shrub areas at SDOT, but *S. pulchra* in SDOT Shrub areas reached FLE *before* those in Open areas – 5 days in 2011 and 3 days in 2012 – indicating an accelerated leaf development (Figure 1.7d). *S. pulchra* in IMVT Shrub areas also reached FLE 2 days *before* those in Open areas in 2012 (Figure 1.7c).
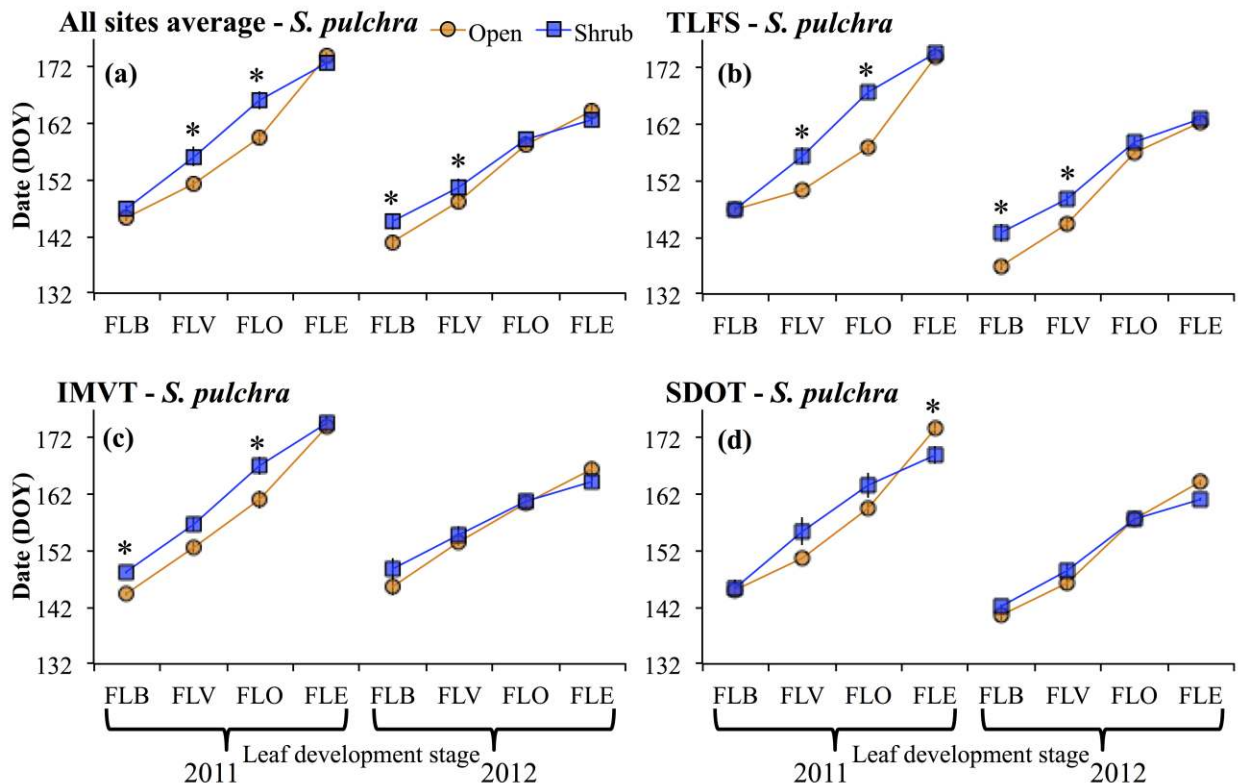
Figure 1.7. Average relative timing of leaf development stages (FLB = first leaf bud; FLV = first leaf visible; FLO = first leaf opening; and FLE = first leaf expanded) for *S. pulchra* in Open (orange circles) and Shrub (blue squares) areas in 2011 and 2012 for (a) all three sites averaged; and at (b) TLFS, (c) IMVT, and (SDOT). Error bars represent 1 SEM. Asterisks (*) above symbols indicate a significant difference (P < 0.05) in time when leaf development was reached between Open and Shrub areas.

28

Table 1.3. Repeated measures MANOVA *P*- and *F*-values for main effects (Site and Cover) as well as their interaction comparing dates (DOY) when leaf development stages (FLB, FLV, FLO, and FLE) were reached for *B. nana* and *S. pulchra* in 2011 and 2012 for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Direction of significant effects (S = Shrub and O = Open) are noted for means comparisons significant at *P* < 0.05. Any effect with a *P*-value > 0.05 is listed as NS. Degrees of freedom for leaf development stage = Cover: 1, 54; Site and Interaction: 2, 54.

Source			Cover		Site			Interaction	
			P : effect	*F*	*P* : effect	*F*		*P*	*F*
Species	**Year**	**Leaf Stage**							
B. nana	2011	FLB	< 0.0001 : S > O	22	< 0.0001 : IMVT > TLFS = SDOT	16.71		NS	
B. nana	2011	FLV	< 0.0001 : S > O	36.16	0.0027 : IMVT > TLFS = SDOT	6.6		0.0606	2.95
B. nana	2011	FLO	< 0.0001 : S > O	37.15	< 0.0001 : IMVT > TLFS > SDOT	16.79		0.0015	7.37
B. nana	2011	FLE	NS		0.003 : IMVT = TLFS > SDOT	6.48		NS	
B. nana	2012	FLB	0.0001 : S > O	16.75	< 0.0001 : IMVT > TLFS = SDOT	58.82		0.0038	6.19
B. nana	2012	FLV	< 0.0001 : S > O	31.23	< 0.0001 : IMVT > TLFS > SDOT	45.33		0.0013	7.57
B. nana	2012	FLO	< 0.0001 : S > O	19.11	< 0.0001 : IMVT > TLFS > SDOT	30		NS	
B. nana	2012	FLE	0.0066 : S > O	7.98	< 0.0001 : IMVT > TLFS = SDOT	17.36		0.0029	6.53
S. pulchra	2011	FLB	NS		NS			NS	
S. pulchra	2011	FLV	0.0002 : S > O	16.49	NS			NS	
S. pulchra	2011	FLO	< 0.0001 : S > O	29.5	NS			NS	
S. pulchra	2011	FLE	NS		0.0111 : IMVT = TLFS > SDOT	4.89		0.0278	3.83
S. pulchra	2012	FLB	< 0.0001 : S > O	19.33	< 0.0001 : IMVT > TLFS = SDOT	31.44		NS	
S. pulchra	2012	FLV	0.0038 : S > O	9.14	< 0.0001 : IMVT > TLFS = SDOT	30.22		NS	
S. pulchra	2012	FLO	NS		< 0.0001 : IMVT > TLFS = SDOT	13.84		NS	
S. pulchra	2012	FLE	NS		0.0065 : IMVT > TLFS = SDOT	5.54		NS	

Figure 1.8, which depicts the relationship across species, sites, and years between the difference in snow-free dates and the difference in FLV and FLE dates (Shrub dates minus Open dates), shows that later snow-free dates for *B. nana* and *S. pulchra* in Shrub areas led to a later budburst relative to Open areas (FLV: $R^2 = 0.6$, $P < 0.01$), but did not significantly affect the date of leaf expansion (FLE: $R^2 = 0.21$, $P = 0.2$). Occasionally, even when snowmelt and budburst were delayed, taller shrubs in Shrub areas reached the leaf expansion stage before shorter shrubs in Open areas (Figure 1.8).

1.3.3 Leaf Nutrient Content

Although there were differences among sites, and at each leaf development stage, Shrub areas overall had higher percentage of nitrogen (%N) in developing leaves (e.g. first leaf visible [FLV] and first leaf opening [FLO]) of *B. nana* and *S. pulchra* as compared to Open areas (Figure 1.9a). For instance, percentage of nitrogen in *B. nana* buds (measured at FLB) and leaves
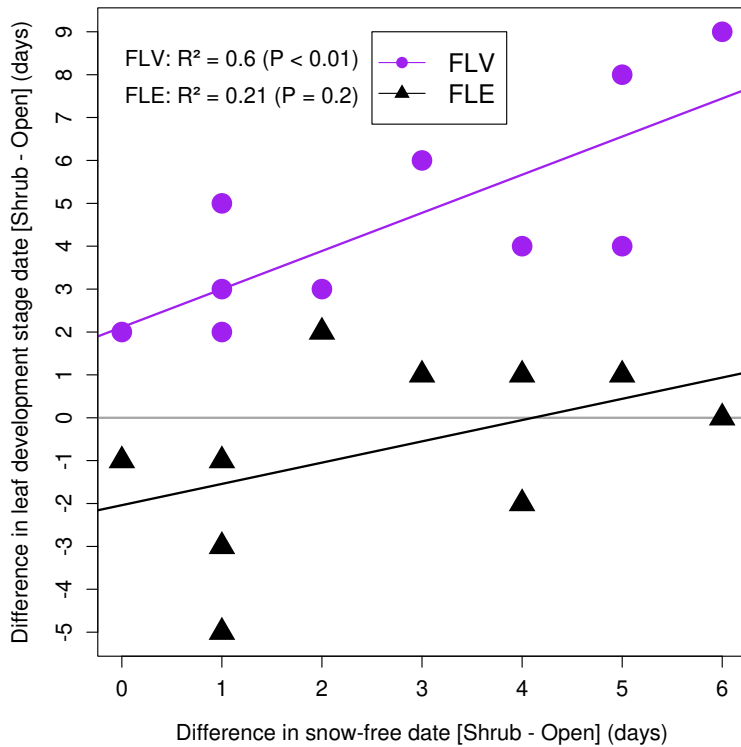
Figure 1.8. Across species, year, and site relationship between the difference in snow-free dates, and the difference in budburst (first leave visible: FLV; purple circles) or leaf expansion dates (FLE: first leaf expanded; black triangles). Values indicate the number of days later (positive values) or earlier (negative values) each stage was reached in Shrub areas compared to Open areas [Shrub - Open]. Values below the gray line drawn at zero indicate Shrub areas reached that stage earlier, and values above this line indicate Shrub areas reached that stage later. Each point represents the average for a species (*B. nana* or *S. pulchra*) in one year (2011 or 2012) for an entire site (TLFS, IMVT, or SDOT).

(measured at FLV and FLO) was generally higher in Shrub areas compared to Open areas (Figure 1.9b) (effect of cover: $F_{1,33} = 20.22$, $P < 0.0001$), but this significance varied across individual leaf development stage (Table 1.4). Because %N for *B. nana* was actually lower in Shrub areas at TLFS for the first two leaf development stages, and because the pattern across the three leaf development stages differed from site to site, there was a significant effect of site (effect of site: $F_{2,33} = 9.22$, $P < 0.001$). Both IMVT and SDOT had higher %N in *B. nana* buds (measured at FLB) in Shrub areas compared to Open areas (the opposite was true for TLFS), and the overall %N in both Open and Shrub areas and magnitude of difference between cover types was greatest at SDOT. Both IMVT and SDOT had higher %N in *B. nana* leaves at FLV in Shrub areas compared to Open areas (the opposite was true for TLFS), but again, the overall %N and magnitude of difference between cover types was greatest at SDOT. At FLO, the pattern of %N in *B. nana* leaves changed from that of the previous two leaf development stages, where all three sites (including TLFS) had higher %N in *B. nana* leaves in Shrub areas compared to Open areas. As opposed to FLB and FLV, the %N at FLO was highest at IMVT Open and Shrub areas, but the magnitude of difference between cover types was still greatest at SDOT (Figure 1.9b & Table 1.4).
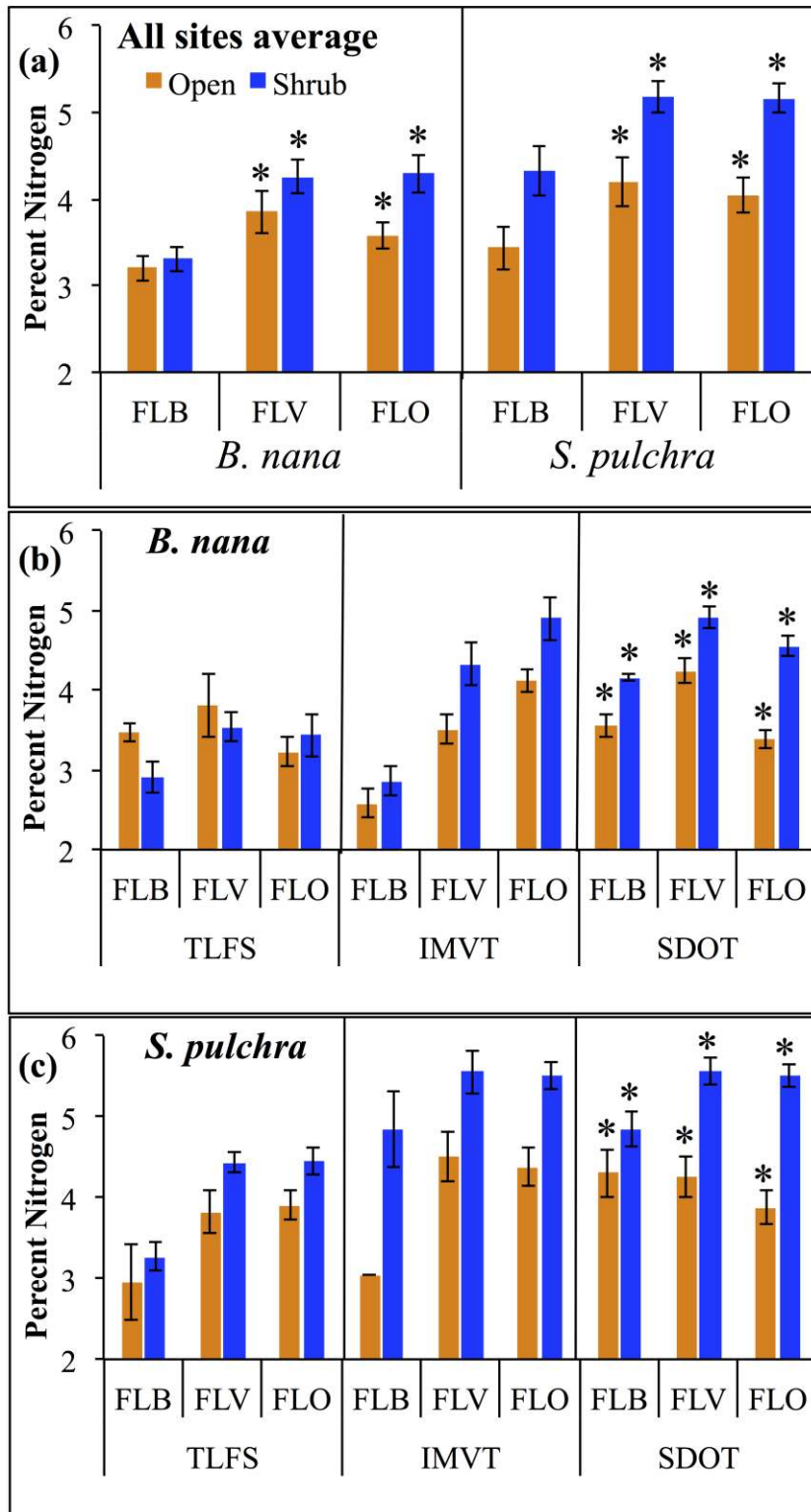
Figure 1.9. Average percent nitrogen in Open (orange bars) and Shrub (blue bars) areas at each of the three leaf development stages measured (FLB = first leaf bud; FLV = first leaf visible; and FLO = first leaf opening for (a) *B. nana* and *S. pulchra* averaged across all sites; (b) *B. nana* separated for all three sites; and (c) *S. pulchra* separated for all three sites. Bars represent areas averages (n = 10 per bar where data was available). Error bars represent 1 SEM. Asterisks (*) above bars indicate a significant difference (*P* < 0.05) in percent nitrogen at that site and leaf development stage (Note: at IMVT, there was not an adequate number of replicates at FLB stage at the Open area for statistical comparison (see Methods)).

Table 1.4. Repeated measures MANOVA *P*- and *F*-values for main effects (Site and Cover) as well as their interaction comparing percent nitrogen for *B. nana* and *S. pulchra* for each development stage measured (FLB, FLV, and FLO) for Open and Shrub areas from three sites (IMVT, TLFS, and SDOT) near the Toolik Lake field station in northern Alaska. Direction of significant effects (S = Shrub and O = Open) are noted for means comparisons significant at *P* < 0.05. Any effect with a *P*-value >s 0.05 is listed as NS. Degrees of freedom for *B. nana* = Cover: 1, 33; Site and Interaction: 2, 33. Degrees of freedom for *S. pulchra* = Cover: 1, 32; Site and Interaction: 2, 32.

Source			Cover		Site			Interaction	
			P : effect	*F*	*P* : effect		*F*	*P*	*F*
Species	**Variable**	**Leaf Stage**							
B. nana	%N	FLB	NS		< 0.0001 : SDOT > TLFS = IMVT		25.01	0.0228	4.27
B. nana	%N	FLV	0.0096 : S > O	7.6	0.0087 : SDOT = IMVT > TLFS		5.53	NS	
B. nana	%N	FLO	0.0002 : S > O	17.36	0.0076 : IMVT > SDOT = TLFS		5.7	NS	
S. pulchra	%N	FLB	NS		< 0.0001 : SDOT = IMVT > TLFS		15.41	NS	
S. pulchra	%N	FLV	0.0002 : S > O	17.59	0.0403 : SDOT = IMVT > TLFS		3.6	NS	
S. pulchra	%N	FLO	< 0.0001 : S > O	35.62	0.0177 : SDOT = IMVT > TLFS		4.65	0.0065	8.6

Although overall %N for *S. pulchra* was higher in Shrub areas compared to Open areas at all sites (effect of cover: $F_{1,32}$ = 16.99, *P* < 0.0002), the magnitude of difference between cover types differed from site to site at each leaf development (Figure 1.9c), driving a significant site effect (effect of site: $F_{2,32}$ = 34.42, *P* < 0.0001) (Table 1.4). The difference between %N for *S. pulchra* in Open versus Shrub areas was greatest at IMVT at FLB, but because this data was not actually included in the statistical analysis (see Methods), the main site effect was likely driven by the high %N at IMVT and SDOT Shrub areas and low %N at TLFS Shrub area. The magnitude of difference in %N for *S. pulchra* at FLV between cover types was greater at both IMVT and SDOT compared to TLFS, but was much greater at FLO at SDOT compared to either IMVT or TLFS (Figure 1.9c & Table 1.4).

The %N values in this study were higher than those reported for peak season biomass, likely because samples were collected prior to full leaf expansion (i.e. leaf bud and emerging leaf) (Chapin et al. 1980). Other studies in the Alaskan and Scandinavian Arctic have found that N concentrations in emerging leaves, shortly after snowmelt, tend to be high, and foliar N concentrations decrease as leaves continue to expand and arctic plants reach peak biomass (Chapin et al. 1975 & 1980, Torp et al. 2010).

1.4   Discussion

We found, similar to previous experimental and modeling studies (e.g. Sturm et al. 2001a, Liston et al. 2002), that spring snowmelt was delayed where snowpack was deeper in our tall stature deciduous shrub-dominated communities. Our results supported our hypothesis in that later snowmelt did delay the initial stages of leaf development (e.g. budburst and leaf opening) for tall stature *B. nana* and *S. pulchra* in deciduous shrub-dominated communities relative to short stature individuals of the same species in graminoid-dominated communities. However, in contrast with our predictions, taller individuals reached *subsequent* leaf development stages (e.g. when the leaf fully expanded) at similar times, or even *before* the shorter *B. nana* and *S. pulchra* found in graminoid-dominated tundra. In other words, the delay in leaf development in taller shrubs was short-lived, and the difference in timing between tall and short stature shrub leaf development decreased, or even disappeared in some cases, by the time full leaf expansion occurred.

It is important to note that though snow-free dates were 1 to 6 days later in Shrub areas compared to Open areas, budburst dates (i.e. FLV) were 2 to 12 days later. Although we are not certain as to why the delay in budburst was twice that of the delay in snowmelt, it is possible that taller, more densely packed deciduous shrubs in Shrub areas shaded the soil, which could reduce soil temperatures relative to shorter, less densely packed deciduous shrubs in Open areas (Blok et al. 2010, Myers-Smith & Hik 2013). This could lead to a slightly slower thawing of the active layer immediately following snowmelt in Shrub areas, which could delay water availability. Also, taller stature shrubs in deciduous shrub-dominated tundra likely have deeper roots due to deeper summer thaw depths (Shaver & Chapin 1991, Bonfils et al. 2012), which means the active layer would need to thaw deeper relative to shorter stature shrubs in graminoid-dominated tundra before roots had access to liquid water essential for leaf opening (Billings & Mooney 1968, Dale 1988).

Similar to our findings, other studies have found trends of accelerated plant development offsetting the effects of a later spring snowmelt in alpine and arctic regions (Dunne et al. 2003, Borner et al. 2008). For instance, in their combined natural snow depth and snow fence manipulation experiment at Toolik Lake, Alaska, Borner et al. (2008) found that increased snow depth decreased the effective growing season length for both *B. nana* and *S. pulchra*. Yet, leaf senescence of these species occurred at relatively similar times regardless of snow depth and

snowmelt date, suggesting that differences in the timing of early phenological stages diminished over the course of the growing season. However, because Borner et al. (2008) monitored only snow-free, budburst, and leaf senescence dates, the intermediate leaf stage at which the catch-up in development occurred was not known, nor was the mechanism driving the accelerated leaf development.

Although emergence and initial stages of leaf development of many species in the arctic tundra are cued by snowmelt and temperature (Pop et al. 2000, Hollister et al. 2005, Wipf et al. 2009), the rate of leaf expansion, shortly after leaves begin to open, is likely related to the amount of nitrogen in buds and emerging leaves (Radin & Boyer 1982, Vos & Biemond 1992). We surmise this relationship because it has been shown that enhanced nitrogen availability increases photosynthesis (Field & Mooney 1983, Evans 1989, Reich et al. 1998, Heskel et al. 2012), which increases metabolites important in leaf expansion (Dale 1988). Therefore, one possible explanation for the accelerated leaf development of taller shrubs in our Shrub areas could be related to the fact that our taller shrubs had higher nitrogen contents (approximately 16% to 25% more) in their leaf buds and emerging leaves compared to the shorter shrubs of our Open areas.

There are several ways in which taller shrubs may have access to more nitrogen during the period of leaf expansion and bud formation. First, higher nitrogen of taller shrubs may be related to the fact that tall deciduous shrubs tend to grow in areas where soil conditions facilitate their growth (Tape et al. 2012). For instance, increased subsurface water flow in naturally occurring deciduous shrub–dominated tundra compared to graminoid-dominated tundra increases nutrient flow (Giblin et al. 1991, Shaver & Chapin 1991) and access to nitrogen (Naito & Cairns 2011, Bonfils et al. 2012, Chapin et al. 1988). Second, their inherently thicker snowpack insulates soils from freezing air temperatures during the winter, thereby enabling higher rates of winter soil mineralization (Schimel et al. 2004, DeMarco et al. 2011), which would enable higher leaf nutrient contents. For example, in their snow fence experiment in the Alaskan Arctic, Walsh et al. (1997) found that deeper snow led to higher nitrogen concentrations in leaves of *B. nana* and *Salix planifolia*. Finally, a delay in snowmelt has been shown to limit dilution of leaf nitrogen throughout the growing season (Korner 1989, Welker et al. 2005). For these reasons, taller shrubs may have access to more nitrogen, which may allow for accelerated leaf development (Dale 1988, Radin & Boyer 1982, Vos & Biemond 1992).

Regardless of the exact driving mechanism, accelerated leaf expansion may be important from a canopy carbon gain perspective for several reasons. First, phenological events for arctic plants tend to be compressed in time (i.e. rapid development) relative to plants growing in more southern locations (Post et al. 2008, Steltzer & Post 2009). This rapid development of arctic plants (Billings & Mooney 1968, Bliss 1971) suggests that the expansion of the first leaf on an individual deciduous shrub likely corresponds with the expansion of most leaves on the entire canopy of that individual (Johnson & Tieszen 1976). Second, when leaves are fully expanded is when they are near their maximum photosynthetic capacity (Constable & Rawson 1980, Patankar et al. 2013). Therefore, accelerated leaf development could offset potential reductions in growing season carbon uptake by minimizing the effects of later snowmelt and delayed budburst. This is especially important in the Arctic, because the growing season is notoriously short and differences in canopy development of only a few days could significantly alter the tundra's annual carbon uptake potential (van Wijk et al. 2003). In fact, Euskirchen et al. (2006) suggested that for each day the growing season is extended in the arctic tundra, net carbon (C) uptake increases by 5.3 g C m^{-2} yr^{-1}. In addition, our findings have important implications for tundra fauna, since changes in tundra plant phenology associated with climate warming have been shown to create asynchrony in the timing of food resource availability for wildlife (Høye & Forchhammer 2008, Post et al. 2009).

Furthermore, deciduous shrub leaf expansion dates may be particularly important in the Arctic. At the beginning of the growing season, deciduous shrubs become photosynthetically active slightly later than other tundra plant functional groups (e.g. evergreens and sedges) (Starr & Oberbauer 2003, Euskirchen et al. 2013). However, deciduous shrubs have higher peak season leaf area (van Wijk et al. 2005) and greater maximum rates of photosynthesis (Johnson & Tieszen 1976, Oechel 1989, Aerts 1995) compared to other functional groups. Because of this, and because deciduous shrub dominance is expected to continue increasing in the arctic tundra (Walker et al. 2006, Pearson et al. 2013), changes in the timing of leaf expansion in deciduous shrubs may prove to be especially important for future carbon flux in the Arctic (Hobbie & Chapin 1998).

CHAPTER TWO:

Greater Deciduous Shrub Abundance Extends Tundra Peak Season and Increases Modeled Net CO$_2$ Uptake

Abstract. *Satellite studies of the terrestrial Arctic report increased summer greening and longer overall growing and peak seasons since the 1980s, which increases productivity and the period of carbon uptake. These trends are attributed to increasing air temperatures and reduced snow cover duration in spring and fall. Concurrently, deciduous shrubs are becoming increasingly abundant in tundra landscapes, which may also impact canopy phenology and productivity. Our aim was to determine the influence of greater deciduous shrub abundance on tundra canopy phenology and subsequent impacts on net ecosystem carbon exchange (NEE) during the growing and peak seasons in the arctic foothills region of Alaska. We compared deciduous shrub-dominated and evergreen/graminoid-dominated community-level canopy phenology throughout the growing season using the normalized difference vegetation index (NDVI). We used a tundra plant-community specific leaf area index (LAI) model to estimate LAI throughout the green season, and a tundra specific NEE model to estimate the impact of greater deciduous shrub abundance and associated shifts in both leaf area and canopy phenology on tundra carbon flux. We found that deciduous shrub canopies reached the onset of peak green 13 days earlier and the onset of senescence 3 days earlier compared to evergreen/graminoid canopies, resulting in a 10-day extension of the peak season. The combined effect of the longer peak season and greater leaf area of deciduous shrub canopies almost tripled the modeled net carbon uptake of deciduous shrub communities compared to evergreen/graminoid communities, while the longer peak season alone resulted in 84% greater carbon uptake in deciduous shrub communities. These results suggest that greater deciduous shrub abundance increases carbon uptake not only due to greater leaf area, but also due to an extension of the period of peak greenness, which extends the period of maximum carbon uptake.*

2.1 Introduction

Global air temperature has increased by about 0.72 °C since 1950 (IPCC 2013). Arctic air temperature has increased more than twice that amount (about 2 °C) over the same period (AMAP 2012, Overland et al. 2012), resulting in a particularly strong warming trend in the Arctic (Chapin et al. 2005, McBean et al. 2006, Serreze & Francis 2006). Ecological responses have already become apparent (Walther et al. 2002, ACIA 2004). Many regions, for instance, have experienced an earlier start and/or a later end to the growing season, resulting in longer growing seasons at the pan-arctic scale (Tucker et al. 2001, Jia et al. 2004). Some studies have found an increase in growing season length of 12 to 14 days per decade at high northern latitudes of North America (Myneni et al. 1997, Zeng et al. 2011) and 6 to 7 days per decade in northern Eurasia (Zhou et al. 2001, Jeong et al. 2011). Other studies suggest the lengthening of the growing season has been more significant in Eurasia than North America (Barichivich et al. 2013).

Some arctic regions are also experiencing shifts toward an earlier *peak* season (i.e. the period of maximum tundra greenness) (Goetz et al. 2005, Goetz et al. 2011, Jia et al. 2009, Tagesson et al. 2012). A longer peak season extends the period of maximum leaf out and photosynthetic activity (Kikuzawa 1995, Oberbauer et al. 1998), which extends the period of maximum carbon (C) uptake within a given year (Richardson et al. 2013, Mbufong et al. 2014). This is especially important in the Arctic, which has extremely short growing seasons (often < 100 days), and where an extension of just a few days can have significant effects on annual carbon uptake (van Wijk et al. 2003). Euskirchen et al. (2006), for instance, estimate that for each day the growing season is extended in the arctic tundra, net carbon uptake increases by 5.3 g C m^{-2} yr^{-1}. As the area of pan-arctic tundra that melts out annually covers approximately 6.5 million km^2, this suggests that a 1-day extension of the growing season could increase the tundra biome's annual carbon uptake by ~ 35 tons.

While changes in air temperature (Hollister et al. 2005, Delbart & Picard 2007, Xu et al. 2013) and snow cover duration (Stow et al. 2004, Wipf 2010, Pau et al. 2011) are key factors influencing recent shifts in arctic canopy phenology, other major changes may also be contributing. For example, over the same time period satellite sensors have observed changes in canopy phenology and growing season length, they have also detected an increase in the peak greenness of the arctic tundra (Bunn et al. 2007, Verbyla 2008, Jia et al. 2009), as measured by

increases in the normalized difference vegetation index (NDVI). This greening has been attributed to increased growth of extant deciduous shrubs (primarily birch, willow, and alder) as well as the expansion of deciduous shrubs into non-shrub tundra that is typically dominated by evergreens, graminoids, and cryptogams (Jia et al. 2003, Olthof et al. 2008, Forbes et al. 2010, Fraser et al. 2011). These findings are supported by comparative photo-interpretation (Sturm et al. 2001b, Tape et al. 2006) and field surveys (Sturm et al. 2001a, Hinzman et al. 2005, Elmendorf et al. 2012). Deciduous shrubs are predicted to continue to expand their range and grow larger (Sturm et al. 2005b, Wookey et al. 2009, Myers-Smith et al. 2011, Pearson et al. 2013), which is likely to result in the decline of shade-intolerant plant functional types, such as evergreens, graminoids, and cryptogams (Chapin et al. 1995, Cornelissen et al. 2001, Wahren et al. 2005, Walker et al. 2006). Since it has been shown that deciduous shrub-dominated tundra communities have accelerated green-up rates (Vierling et al. 1997), and reach peak NDVI earlier compared to graminoid and evergreen-dominated tundra (Jia et al. 2004), we hypothesized that the increased abundance of deciduous shrubs is likely contributing to satellite observations of earlier tundra peak seasons (Goetz et al. 2005, Goetz et al. 2011, Tagesson et al. 2012), and that this in turn is enhancing seasonal carbon uptake by tundra vegetation.

To test these hypotheses at a plot-level scale we tracked community-level phenology of deciduous shrub-dominated and evergreen/graminoid-dominated canopies in the arctic foothills region of Alaska throughout the duration of the 2013 growing season. We determined canopy phenology metrics (i.e. onset of greening, onset of peak green, and onset of senescence) by applying both threshold analysis and piecewise linear regression modeling to curves of growing season near-surface measurements of daily plot-level NDVI. We then estimated leaf area (LAI) using previously determined NDVI-LAI relationships for arctic vegetation (Street et al. 2007), and used the arctic-specific model of Shaver et al. (2007) to predict net ecosystem exchange (NEE) throughout the green season. A number of studies have shown differences in canopy phenology among different tundra types (e.g. Vierling et al. 1997, Jia et al. 2004, Narasimhan & Stow 2010), as well as differences between tundra vegetation communities in net carbon flux (e.g. Shaver et al. 2007, Street et al. 2007). However, to our knowledge this is the first field study to combine both, with a focus on peak season length, and to make comparisons between naturally occurring deciduous shrub and evergreen/graminoid tundra communities. This approach allows us to determine the influence of deciduous shrub abundance on canopy

phenology and to estimate the relative effect of deciduous shrub abundance on net ecosystem carbon exchange.

2.2 Methods

2.2.1 Study Sites

Datasets were collected from snowmelt until snowfall in 2013 (from 1 June to 5 September) at two field sites, near the Sagavanirktok River-Department of Transportation camp (SDOT) and Imnavait Creek (IMVT) (Figure 2.1). Average elevation at IMVT is ~ 900 m and at SDOT is ~ 500 m. The two field sites are located in the vicinity (within ~ 30 km) of Toolik Field Station in the northern foothills of the Brooks Range, Alaska (68º38' N, 149º34' W). Annual precipitation at Toolik is 200-400 mm, with 45% falling as snow (van Wijk et al. 2005). The average growing season at Toolik extends from approximately late May/early June until mid- to late August, during which time the average air temperature is 7 ºC (Johnson et al. 2000). Based on the canopy greenness metrics derived from our seasonal NDVI measurements, we define the growing season as the period from the onset of greening (shortly after snowmelt) until the end of senescence (after prolonged snowfall), and define the peak season as the period from the onset of peak green until the onset of senescence. Although our field sites experienced delayed snowmelt in 2013 relative to the three previous years, air temperature and photosynthetically active radiation (PAR) throughout the growing season (Figure 2.2) were within the average range of values for Toolik (Johnson et al. 2000, Heskel et al. 2013).

In May 2010, two 20,000 m^2 study areas were selected at each field site: one evergreen/graminoid study area (EG; the "Open" areas in Chapter one) and one deciduous shrub study area (DS; the "Shrub" areas in Chapter one). Two 100 m transects were established within each EG and DS study area at each field site (for a total of 8 transects), and ten 1 m^2 quadrats were established at 10 m intervals along each transect (for a total of 80 quadrats). Because only 18 instruments were available to measure canopy phenology for this study, two to three quadrats along each transect were chosen to best represent vegetation communities with naturally occurring maximum and minimum deciduous shrub dominance (see Percent Vegetation Cover). In total, we monitored 9 DS (n = 4 at IMVT & 5 at SDOT) and 9 EG (n = 5 at IMVT & 4 at SDOT) canopies.
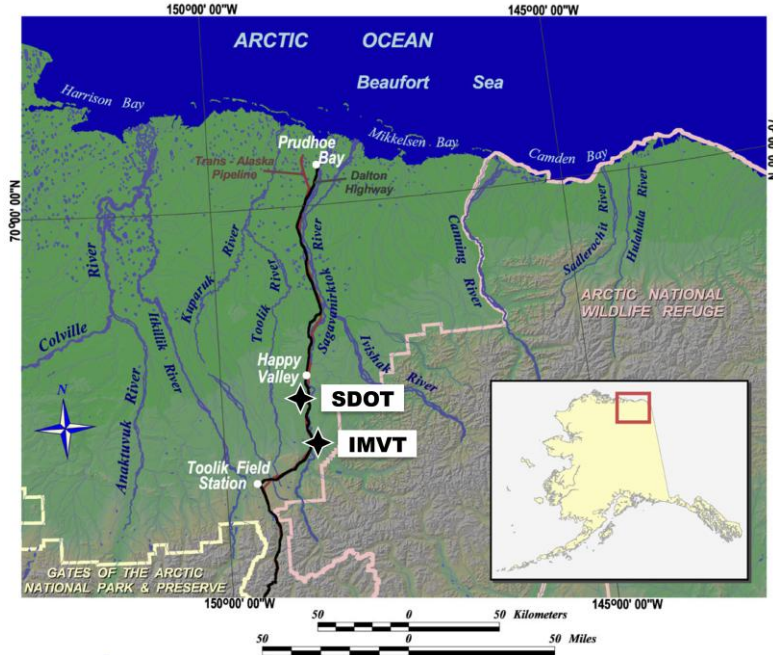
Figure 2.1. Map of Alaska and the North Slope of the Brooks Range (inset) showing the location of the two field sites near the Toolik Lake field station used in this study. IMVT = Imnavait Creek; and SDOT = Sagavanirktok River-Department of Transportation.
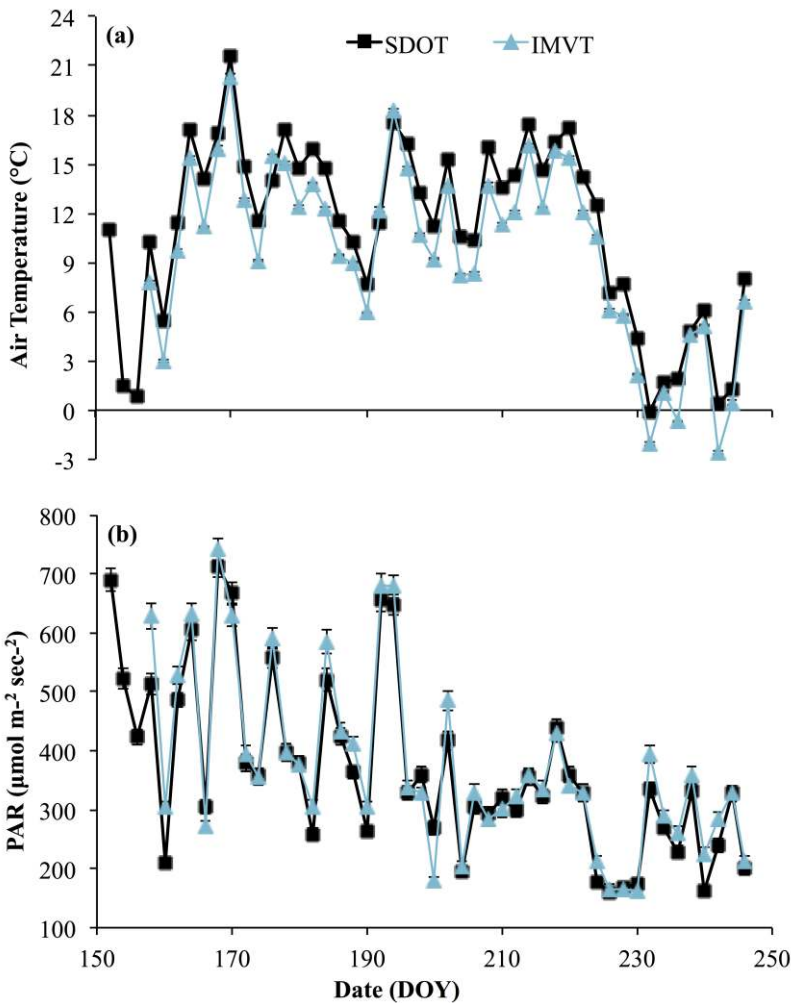
Figure 2.2. Two-day averages of seasonal (a) air temperature (Celsius) and (b) photosynthetic active radiation (PAR) at two field sites, used in this study, in the northern foothills of the Brooks Range, Alaska. Error bars represent +/- 1 SEM.

40

2.2.2 Percent Vegetation Cover

Plant cover was measured in each 1 m^2 quadrat in late July (period of maximum leaf area) of 2010 by placing a frame outlining 20 cm × 20 cm sub-quadrats over each 1 m^2 quadrat and visually estimating the plant canopy from directly above, with groups summing to 100%. The cover of leaves and plants hidden by over story vegetation was not included, which may have led to an underestimate for low-lying plants, such as mosses, in some quadrats. Based on this percent cover data (Figure 2.3), we selected nine DS quadrats that contained high percent cover (ranging from ~ 30-90%) of deciduous shrubs (mainly *Betula nana* and *Salix* spp.), and low percent cover of evergreens and graminoids (ranging from ~ 1-30%). We also selected nine EG quadrats that contained low percent cover of deciduous shrubs (ranging from ~ 7-30%) and high percent cover of evergreens and graminoids (ranging from ~ 20-70%). DS and EG canopies had similar amounts of moss cover and were interspersed with forbs and lichens.
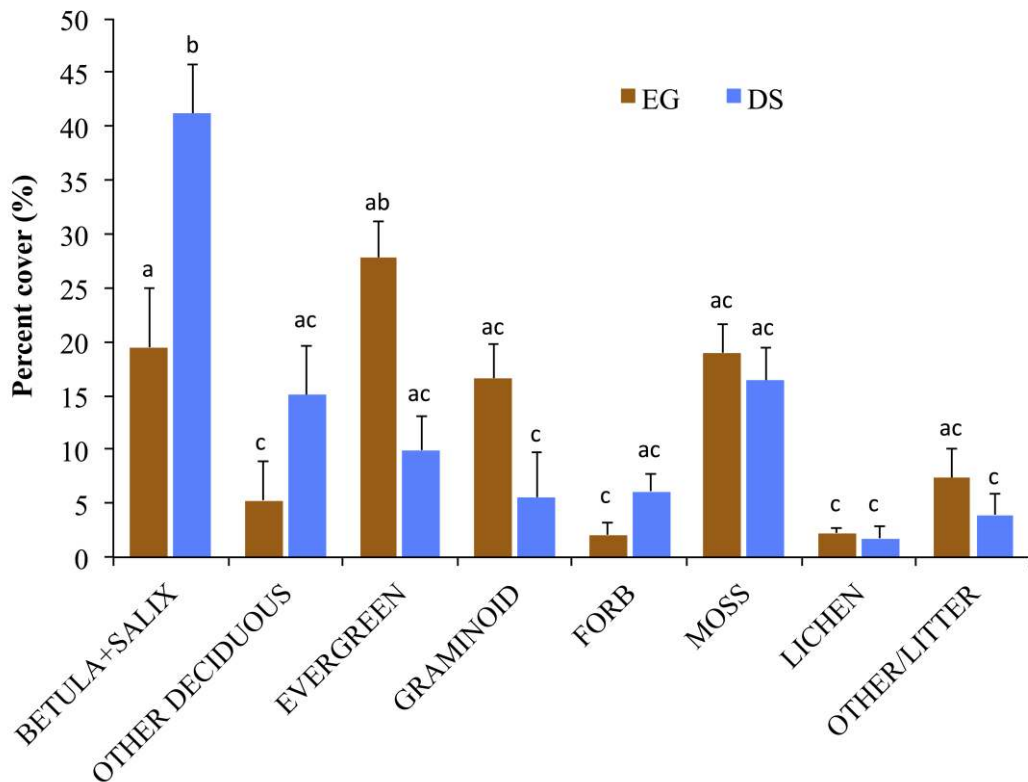
Figure 2.3. Percent cover of functional groups for deciduous shrub (DS) canopies (blue bars) and evergreen/graminoid (EG) canopies (brown bars). Bars represent averages for both sites (n = 9 per group, per cover type). ANOVA was used to compare means between DS and EG canopies. Bars marked with different letters are significantly different from one another ($P < 0.05$) based on Tukey's HSD comparisons. Error bars represent 1 SEM (standard error of the mean).

2.2.3 Canopy Phenology

2.2.3.1 Spectral Reflectance Measurements and Calculation of NDVI

The seasonal pattern in canopy greenness was determined from broadband NDVI calculated using two light sensors (Figure 2.4): (1) a PAR smart sensor, and (2) a Silicon Pyranometer smart sensor (Onset Computer Corporation, Bourne, MA, USA). Prior to snowmelt, downward-looking light sensors were fitted with cylindrical sheaths (Figure 2.4) to limit the full angle cone of acceptance field of view (FOV) to 45° and sensors were positioned 50 cm above the top of the canopy in each 1 m^2 quadrat, so that each measurement's circular footprint was approximately 0.75 m^2. Light sensors measured canopy reflectance every two minutes from 1 June to 5 September 2013, and data were stored on a HOBO Weather Station logger (Onset Computer Corporation). Only NDVI$_{broadband}$ values collected between 1200 and 1400 local time were used because solar noon occurs between 1300 and 1330 during the growing season in our study region.

Figure 2.4. Example of equipment assemblages in evergreen/graminoid (EG) canopy (left) and deciduous shrub (DS) canopy (right) used in this study to determine the normalized difference vegetation index (NDVI). Sensors collected photosynthetically active radiation (PAR), solar irradiance, and air temperature data every two-minutes from 1 June to 5 September 2013.

In one quadrat at each of the two sites, the same set of light sensors were placed looking upward to measure incoming light conditions and were used as calibration references and to filter data (Shory et al. in prep. 2014). Upward-looking sensors were not sheathed and thus

incorporated incoming solar light from the full upper hemisphere. Filters were developed to select clear sky data points. First, a clear day was selected by visual inspection of irradiance charts. A clear day has a characteristic smooth bell-shaped curve easily distinguished from the jagged curves of cloudy days. Based on this index day, thresholds were generated. For each sensor, the maximum irradiance value on the index day was internally extracted. This was the sensor's clear sky noon value (CSNV). Thresholds for each sensor were generated as 75–125% of the CSNV for that sensor. At each time point, if any of the sensor reading needed for NDVI$_{broadband}$ was outside the thresholds for that sensor, NDVI$_{broadband}$ was not calculated for that time point for that instrument. Clear sky conditions occurred frequently enough so that 80–120 values were obtained each day. Occasionally, an entire day's data were rendered invalid due to persistent inclement weather conditions (e.g. continuous precipitation or snow cover), and these data points were removed.

Equations 2.1 through 2.3, adapted from methods outlined in Huemmrich et al. (1999) and described in detail in Shory et al. (in prep. 2014), were used to calculate NDVI$_{broadband}$ from the two light sensors. PAR sensors recorded photosynthetically active radiation (µmol photons m^{-2} s^{-1}) over a broad visible band (PAR: 400 – 700 nm). Pyranometer sensors recorded irradiance (W m^{-2}) over a broad visible and infrared (shortwave) band (SW: 300 – 1100 nm). First, PAR measurements were converted to units of W m^{-2} by multiplying by 0.21 J µmol^{-1} (Huemmrich et al. 1999, Shory et al. in prep. 2014). PAR reflectance (ρPAR) was then calculated using Equation 2.1, where E$_{PARrefl}$ and E$_{PARin}$ (W m^{-2}) are the reflected and incoming PAR values, respectively. Optical infrared reflectance (ρOIR) was calculated using Equation 2.2, where E$_{SWin}$ and E$_{SWrefl}$ (W m^{-2}) are the shortwave (visible + infrared) irradiances for both incoming and reflected fluxes, respectively. These reflectance values were then used to calculate a broadband NDVI$_{broadband}$ using Equation 2.3.

$$\rho PAR = E_{PARrefl} / E_{PARin} \qquad \text{(Equation 2.1)}$$

$$\rho OIR = (E_{SWrefl} - E_{PARrefl}) / (E_{SWin} - E_{PARin}) \qquad \text{(Equation 2.2)}$$

$$NDVI_{broadband} = (\rho OIR - \rho PAR) / (\rho OIR + \rho PAR) \qquad \text{(Equation 2.3)}$$

In addition to high temporal resolution $NDVI_{broadband}$ data from PAR and pyranometer sensors, we also collected weekly spectral reflectance in all quadrats from 1 June to 16 July 2013 with a field portable spectroradiometer (FieldSpec3, Analytical Spectral Devices, Boulder, CO, USA) so that $NDVI_{broadband}$ values could be calibrated/converted and used to calculate leaf area (see Leaf Area Index Model). The FieldSpec3 has a 25° full angle cone of acceptance FOV with a spectral sampling interval of 1.4 nm. FieldSpec3 radiance measurements were preceded by a calibration scan of a 99% reflectance white standard (Spectralon, LabSphere, North Sutton, NH, USA) to normalize for changes in light conditions between measurements. The foreoptic was held 1 m above the top of the canopy, so that each measurement's circular footprint was approximately 0.15 m^2. Five measurements were made within each 1 m^2 quadrat to capture spatial heterogeneity of each quadrat. Spectral measurements were converted to reflectance values, and $NDVI_{spectroradiometer}$ was calculated using Equation 2.4 from visible red (R: 650 – 690 nm) and near-infrared (NIR: 750 – 850 nm) reflectance. The five $NDVI_{spectroradiometer}$ values associated with each quadrat were averaged to give a mean quadrat value.

$NDVI_{spectroradiometer}$ = (NIR - R) / (NIR + R) (Equation 2.4)

$NDVI_{spectroradiometer}$ and $NDVI_{broadband}$ values showed a strong linear correlation ($R^2 = 0.85$, $P < 0.001$, $F_{1,120} = 712.3$; Figure 2.5). We used this linear relationship (Equation 2.5) to convert the broadband $NDVI_{broadband}$ values to calculate leaf area with higher precision. Converted values are hereafter referred to as NDVI.

$y = 2.13085x - 0.91531$ (Equation 2.5)

2.2.3.2 Determination of Phenological Metrics

Prior to determining phenological metrics, a locally weighted regression (loess) was used to smooth data (Cleveland 1979, Cleveland & Loader 1996). To produce a relatively smooth curve while still capturing the important and intrinsic structure of the data, we set the smoothing parameter (α) = 0.2 (Jacoby 2000). Although α values > 0.5 are often used for highly variable and scattered data (Cleveland & Loader 1996, Jacoby 2000), we chose 0.2 because lower parameters ($\alpha < 0.2$) did not smooth the curve enough, yet our data were not so variable that we
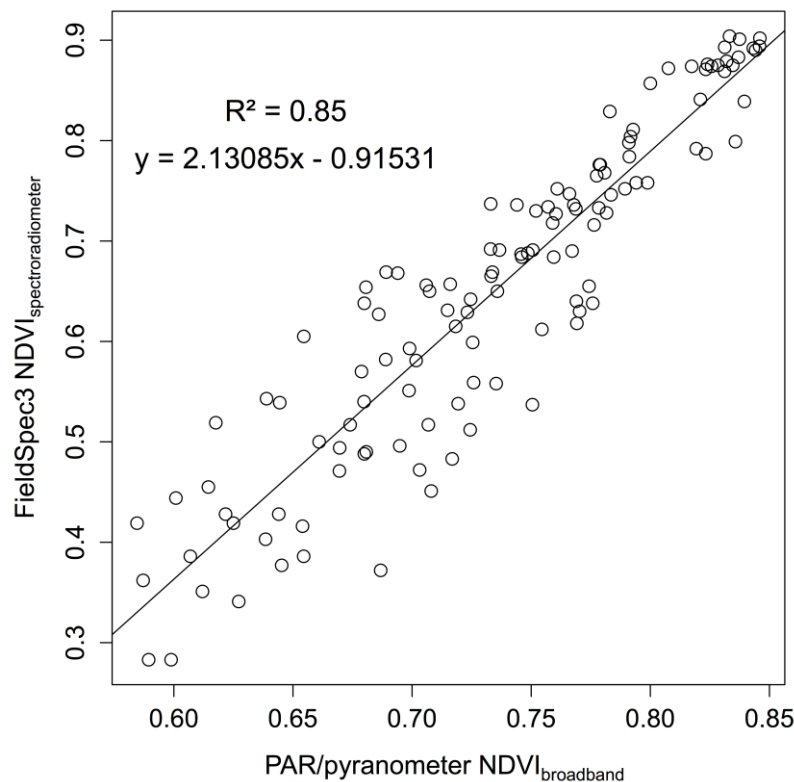
Figure 2.5. Relationship between $NDVI_{broadband}$ values derived from photosynthetically active radiation (PAR) and solar irradiance (pyranometer) light sensors, and $NDVI_{spectroradiometer}$ values derived from a FieldSpec3 (ASD) portable field spectroradiometer measurements. Data represents daily averages from all 18 quadrats at each site (IMVT and SDOT) from 1 June to 16 July 2013 (n = 140).

needed to use a high value ($\alpha > 0.2$), which would have removed valuable information in the seasonal NDVI curves used to determine precise phenological parameters. After smoothing, we used two methods (threshold analysis and piecewise regression modeling) to determine the date [day of the year (DOY)] of three canopy phenology metrics for each of the 18 seasonal NDVI curves: (1) onset of greening; (2) onset of peak green; and (3) onset of senescence. The fourth phenological metric, end of senescence (4), was determined as the date on which NDVI values dropped dramatically following multiple days of snowfall/snow cover, which occurred on 5 September (DOY 248) for all quadrats. Quadrat-specific dates on which each phenological metric was reached – as determined by both methods – can be found in Figure 2.6.

Although there are several methods to model land surface phenology from remotely sensed data (White et al. 2009, Klosterman et al. 2014), we chose thresholds and piecewise linear regression modeling for the following reasons. Thresholds are commonly used and considered to be the simplest method for phenological studies using NDVI (de Beurs & Henebry 2010, Zeng et al. 2011). However, threshold analysis can be problematic given the variability of NDVI among different sensors (van Leeuwen et al. 2006, Zeng et al. 2011), across different regions (White et

al., 2003), and over time. Although using the ratio method developed by Kogan (1995) alleviates some of the problems with using thresholds (White et al. 1997), threshold analysis may not be optimal when dealing with high temporal resolution NDVI data that exhibit daily variations and that have not been obtained throughout an entire 365-day year (de Beurs & Henebry 2010). In contrast, piecewise linear regression modeling has the potential to find precise inflection points (Vieth 1989) without relying on thresholds (Zhang et al. 2003, Chandola et al. 2010) and allows for the variable temporal nature of NDVI curves (de Beurs & Henebry 2010). Further, piecewise analysis best-matched our view of seasonal canopy development (e.g. that the onset of greening is when vegetation begins to quickly green, and that the peak season is when the canopy is constant in greenness), and has been successful in identifying ecological thresholds (Toms & Lesperance 2003, Wang et al. 2011) and modeling inflection points in NDVI data (Piao et al. 2011, Sun et al. 2011, Zhang et al. 2013).

For threshold analysis, a locally tuned NDVI threshold was used (White et al. 1997, de Beurs & Henebry 2010), where the state of the ecosystem is indexed by transforming the NDVI to a 0 to 1 $NDVI_{ratio}$, using Equation 2.6, where NDVI is the daily NDVI, and $NDVI_{max}$ and $NDVI_{min}$ are the seasonal maximum and minimum of the NDVI curve, respectively. Onset of greening was defined as the date when the $NDVI_{ratio}$ value of 0.5 was exceeded. Onset of peak green was defined as the date when a $NDVI_{ratio}$ value of 0.9 was reached and consistently exceeded. Onset of senescence was defined as the date when $NDVI_{ratio}$ values dropped below 0.9.

$$NDVI_{ratio} = (NDVI - NDVI_{min}) / (NDVI_{max} - NDVI_{min}) \qquad \text{(Equation 2.6)}$$

Piecewise linear regression modeling was applied to seasonal NDVI curves using the 'segmented' package in R (R Core Team 2014). The conceptual framework and mathematical calculations used to find inflection points in nonlinear models are detailed in Muggeo (2003 & 2008). Onset of greening was defined as the point in the curve (i.e. the date) when NDVI began to increase rapidly following snowmelt. Onset of peak green was defined as the point in the curve when NDVI began to level out. Onset of senescence was defined as the point in the curve when NDVI began to decrease. Prior to modeling, phenology metrics were visually estimated in Excel (Microsoft Excel 2008 for Mac, v. 12.0, Redmond, WA, USA) and inflection points determined from piecewise modeling closest to visual estimates and with the lowest standard

46

errors were chosen as representative dates.

Using the above four canopy phenology metrics determined via both the threshold and piecewise regression techniques, we calculated growing season length (from the onset of greening to the end of senescence) and peak season length (from the onset of peak green to the onset of senescence) for each quadrat. To determine the daily rate of change in NDVI during green-up (i.e. rate of green-up), linear slopes of the segments of NDVI curves from the onset of greening to the onset of peak green were calculated. These canopy metrics were determined for each of the 18 quadrats, and means were then calculated for DS (n = 9) and EG (n = 9) canopies. Although we present phenology metrics determined from both threshold and piecewise regression methods, we used dates determined from piecewise regressions to model NEE (see Net Ecosystem Exchange Model) for several reasons. First, both methods yielded similar results for the onset of peak green and the onset of senescence (Figure 2.6). Also, because piecewise regression analysis is more robust, it better matched our view of seasonal canopy development in terms of the onset of greening (e.g. that the onset of greening is when NDVI increases rapidly after a flat period following snowmelt).

2.2.4 Leaf Area Index Model

Calibrated daily values of canopy NDVI were used to model daily changes in leaf area index (LAI) (Equation 2.7) in m^2 leaf m^{-2} ground using the model developed by Street et al. (2007).

$$LAI = a * e^{b*NDVI}$$
<div align="right">(Equation 2.7)</div>

Model parameters in Equation 2.7 were varied for each quadrat depending on species composition (see table 1 in Street et al. 2007), which was determined from our percent cover data described above. Parameters from Street et al. (2007) for *Betula* and *Salix* vegetation communities were used to derive DS canopy LAI, and parameters for Tussock and Sedge vegetation communities were used to derive EG canopy LAI (Table 2.1). Although this NDVI-LAI model does not explicitly include biophysical variables (e.g. leaf layering and orientation) (Baret & Guyot 1991), the model parameters from Street et al. (2007) were chosen because these
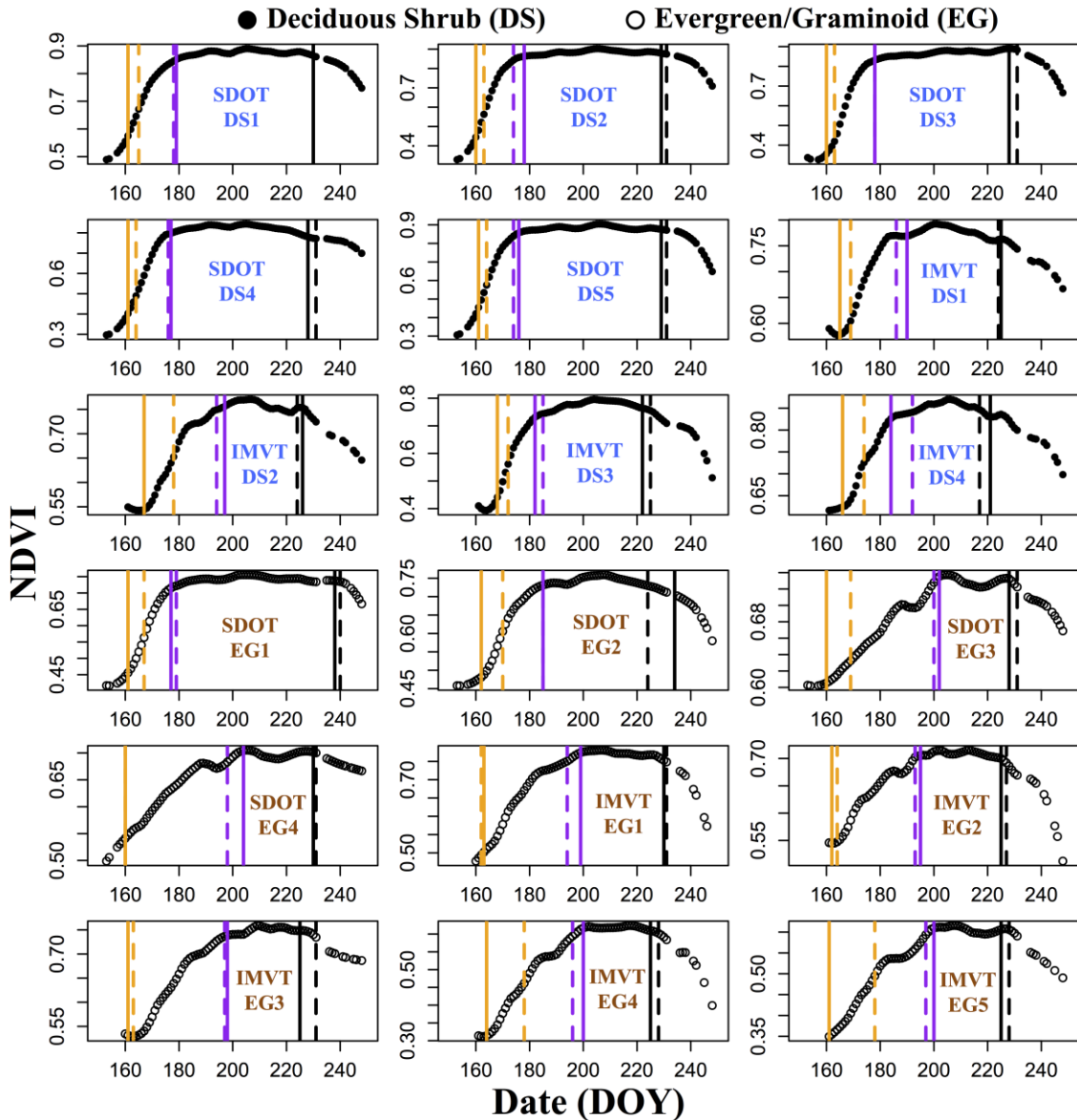
Figure 2.6. Quadrat-level phenology modeling of seasonal loess smoothed NDVI curves of deciduous shrub canopies (DS – solid circles; blue font) and evergreen/graminoid canopies (EG – open circles; brown font). Horizontal lines extending to dates on the *x-axis* depict dates of onset of greening (orange lines), (2) onset of peak green (purple lines), and (3) onset of senescence (black lines). Dashed lines represent dates determined using threshold analysis, and solid lines represent dates determined using piecewise regression analysis. For phenology dates where both methods yielded the same results only a solid line is visible.

vegetation specific parameters were derived from nearby low arctic sites (including from our IMVT site) with similar vegetation characteristics as those used in this study, and take into account changes in leaf area across different vegetation communities. Also, although other

studies have developed models to estimate LAI using NDVI through space (van Wijk & Williams 2005, Steltzer & Welker 2006), the relationships derived by Street et al. (2007) were developed from mid-June through August, and include changing canopy phenology dynamics over time. It is important to note that this LAI model was not developed during senescence and assumes changes in NDVI are due to changes in leaf area. However, after the onset of senescence, reductions in NDVI are due to changes in both leaf color and leaf area. To capture trends during the period of rapid greening that occurs shortly after snowmelt, we therefore defined a new period termed the 'green season', which extends from the onset of greening to the onset of senescence, and modeled LAI data during this green season period only.

Study area (this study)	Vegetation Type (Street et al. 2007)	a	b
Deciduous shrub	*Betula*	0.0132	6.271
	Salix	0.0323	5.625
Evergreen/graminoid	Tussock	0.0064	7.210
	Sedge	0.1516	2.663

Table 2.1. Model parameters used to predict leaf area indices (LAI) using NDVI (Equation 2.7: LAI = a * e^{b*NDVI}) based on best-fit exponential regression parameters for the LAI-NDVI relationship from table 2 in Street et al. (2007). Vegetation types selected for use in this study were based on a comparison of aerial percent cover of our research areas compared to information in table 1 in Street et al. (2007).

2.2.5 Net Ecosystem Exchange Model

Net ecosystem exchange of CO_2 (NEE) was calculated using the model of Shaver et al. (2007) (Equations 2.8 through 2.10), using measurements of PAR and air temperature (air T) made every two minutes throughout the season, and daily estimates of LAI based on the midday measurements of NDVI described above. Because it has been shown that photosynthesis per unit leaf area is relatively constant throughout the growing season in the Alaskan arctic tundra (Heskel et al. 2013), knowing only the amount of leaf area of the canopy (as estimated by LAI), as well as PAR and air T, allows for reasonable estimation of NEE throughout the season even though the NEE model was developed mid-season.

NEE (μmol CO_2 m^{-2} s^{-1}), calculated using Equation 2.8, is the difference between overall ecosystem respiration (R_E) and gross primary production (GPP), where negative values of NEE

represent net CO_2 uptake. We used parameter values for P_{maxL}, k, E_0, β, R_0, and R_X as determined by Shaver et al. (2013) for the low Arctic.

$$\text{NEE} = R_E - \text{GPP} \hspace{4cm} \text{(Equation 2.8)}$$

R_E was calculated using Equation 2.9, where R_0 (1.177 µmol CO_2 m^{-2} leaf s^{-1}) is the basal respiration rate, which accounts for a majority of both autotrophic and heterotrophic respiration (Shaver et al. 2013), and varies with changes in LAI, the parameter β (0.046 °C^{-1}), and air T (°C). Air T used in Equation 2.9 was recorded ~ 50 cm above ground level in all 18 quadrats with a HOBO TMC20-HD Sensor (Onset Computer Corporation). The additional source of respiration in Equation 2.9, R_x (0.803 µmol CO_2 m^{-2} ground s^{-1}), comes from deeper soil horizons and is independent of LAI and short-term fluctuations in air T (Shaver et al. 2007). R_x was added to the model because it improves accuracy of predictions and the fit of the model, and prevents R_E from going to zero when there is no leaf area (Shaver et al. 2007).

$$R_E = (R_0 * e^{\beta * \text{airT}} * \text{LAI}) + R_x \hspace{3cm} \text{(Equation 2.9)}$$

GPP was calculated using Equation 2.10, where P_{maxL} (14.747 µmol m^{-2} leaf s^{-1}) is the light saturated photosynthetic rate per unit leaf area, k (0.5 m^{-2} ground m^{-2} leaf) is a Beer's law extinction coefficient, and E_0 (0.041 µmol CO_2 fixed µmol^{-1} photons absorbed) is the initial slope of the light response curve. Incoming solar irradiance (I), which is the top-of-the-canopy photosynthetic photon flux density (µmol PAR m^{-2} ground s^{-1}) (Rastetter et al. 1992), was recorded ~ 50 cm above the canopy in one quadrat at each site using upward-looking PAR sensors described above. All air T and I data (Figure 2.2) were recorded every two-minutes from 1 June to 5 September 2013 and stored on a HOBO Weather Station logger (Onset Computer Corporation, USA).

$$\text{GPP} = (P_{maxL} / k) * \ln (P_{maxL} + E_0 * I) / (P_{maxL} + E_0 * I * e^{(-k*\text{LAI})}) \hspace{1cm} \text{(Equation 2.10)}$$

We calculated R_E, GPP, and NEE (µmol CO_2 m^{-2} s^{-1}) at two-minute intervals through each day (24 hours) for each of the 18 quadrats, and estimated seasonal NEE based on each

quadrat's respective phenology dates derived from piecewise linear regression analysis. Total peak season NEE (g C m^{-2} season^{-1}) was estimated by integrating daily average NEE values from the onset of peak green to the onset of senescence. As with LAI, the NEE model was not developed after the period of senescence, and because modeled LAI was used for NEE calculations, we modeled NEE data during the green season only. Because we did not estimate total growing season NEE, to capture the period of green-up/leaf expansion (prior to peak green), we estimated total green season NEE (g C m^{-2} season^{-1}) by integrating daily average NEE values from the onset of greening to the onset of senescence. To tease out the effect of differences in leaf area between communities and further examine the effect of changing season length on NEE, total integrated NEE was also estimated for all nine DS quadrats using average EG peak and green season dates, as well as for all nine EG quadrats using average DS peak and growing season dates (see Statistical Analysis).

The NEE model used in this study has been tested across a wide array of arctic ecosystems. For instance, in comparing 1,410 modeled versus *in-situ* measured CO_2 flux measurements from Alaskan and Swedish arctic sites, Shaver et al. (2007) found the NEE model confidently predicted CO_2 fluxes ($R^2 = 0.8$) with no *a priori* knowledge of species composition and using model inputs of only PAR, air T, and LAI derived from NDVI. Further testing of the model using eddy covariance data was performed by Rastetter et al. (2010), where they were able to reliably predict NEE for all major vegetation types in the low Arctic ($R^2 > 0.77$). Still further testing performed by Shaver et al. (2013) across the pan-Arctic showed good agreement between 4,834 measured versus predicted NEE ($R^2 = 0.76$). The model has also proven effective at predicting fluctuations in NEE over large regions using satellite-derived NDVI. Loranty et al. (2010), for instance, used MODIS satellite-based estimates of NDVI to calculate LAI and predict NEE over approximately 1 km^2 at low arctic sites in Alaska and Canada. Across a wide range of sites and years, Loranty et al. (2010) found good agreement between NEE measured at eddy covariance towers and modeled NEE ($R^2 = 0.76$).

2.2.6 Model Sensitivity Analysis

We assessed the sensitivity of modeled NEE to changes in air T, PAR, LAI, and the onset date of the peak season by varying the original/baseline values of these four parameters by ± 10%, 20%, and 30% for each quadrat. We then recalculated NEE for every two-minute interval

(applying the same methods described above). The percent changes in model parameters were applied equally across both DS and EG canopies. A peak season beginning on DOY 189 and 40 days long was assumed as the baseline value because this was the average date of onset and length of the peak season across all DS and EG canopies using piecewise regression analysis.

2.2.7 Statistical Analysis

Data were checked for normality in distribution and homogeneity of variances using the Shapiro-Wilk and Bartlett's tests. Data that did not meet assumptions of normality (Shapiro-Wilk: $P < 0.05$) and/or homogeneity (Bartlett's: $P < 0.05$) was log- or square-root-transformed prior to statistical analysis. For all between subject tests, we report Wilks' Lambda results. Differences were considered significant at $P < 0.05$. All statistical analysis was done in R (R Core Team 2014).

A multivariate analysis of variance (MANOVA) was conducted to test for differences in the three canopy-level phenology stages between canopy types (n = 9 DS canopy, n = 9 EG canopy), with site (IMVT & SDOT) as a blocking factor. Main effects determined from both phenology analysis methods are reported in tables, and main and interaction effects from results of piecewise regression analysis are reported in the text.

One-way analysis of variance (ANOVA), with site as a blocking factor, was used to test for differences between canopy types in the rate of green-up, growing and peak season lengths, and total green season and peak season NEE.

One-way ANOVA, with site as a blocking factor, was also used to test the effects of changing season length on total green and peak season NEE (determined using piecewise regression phenology dates) within each canopy type. To do this, NEE was estimated for all quadrats using average DS and EG green and peak season lengths. And changes in total green season NEE with changing season length were compared within vegetation communities (i.e. DS NEE at 63 days was compared to DS NEE at 68 days; and EG NEE at 63 days was compared to EG NEE at 68 days). The same comparison was made for peak seasons within each vegetation community (DS NEE at 44 days compared to at 34 days; EG NEE at 44 days compared to at 34 days).

A repeated measures ANOVA, with date and canopy type as the main effects and site as a blocking factor, was used to test for differences between canopy types for variables measured

(NDVI) or estimated (LAI, R_E, GPP, and NEE) repeatedly throughout the season. Linear regression models were used to evaluate relationships between percent cover of deciduous shrubs and 1) onset of greening, 2) rate of green-up, 3) onset of peak green, 4) onset of senescence, 5) peak season length, 6) growing season length, 7) green season NEE, and 8) peak season NEE.

2.3   Results

2.3.1 Canopy phenology

Following snowmelt, DS canopies had lower NDVI values than EG canopies (Figure 2.7), but faster greening rates quickly led to greater NDVI values in DS canopies (effect of date*canopy type: NDVI - $F_{1,248}$ = 14.54, P < 0.01). Although the pattern of NDVI changed throughout the season (effect of date: NDVI - $F_{1,88}$ = 51.04, P < 0.001) and differed between sites (effect of site: NDVI - $F_{1,248}$ = 332.16, P < 0.001), DS canopies maintained higher NDVI values than EG canopies throughout the majority of the season (effect of canopy type: NDVI - $F_{1,248}$ = 702.15, P < 0.001).

The pattern of canopy phenology (Figure 2.7 & Table 2.2a) differed between canopy types (effect of canopy type: phenology - $F_{3,13}$ = 12.85, P < 0.001) and sites (effect of site: phenology - $F_{3,13}$ = 18.78, P < 0.001) largely due to earlier onset of the peak season and onset of senescence for DS canopies in general, and at SDOT in particular. Because DS canopies reached the onset of greening 2 days later (P < 0.05) than EG canopies (Table 2.2a), but ended senescence at the same time, the growing season length was 2 days shorter for all DS compared to EG canopies (Table 2.2b). However, because DS canopies had an accelerated rate of green-up (P < 0.001), they reached the onset of peak green 13 days earlier than EG canopies (P < 0.001). In addition, DS canopies reached the onset of senescence only 3 days earlier than EG canopies. Thus, though SDOT had faster green-up rates (effect of site: green-up rate - P < 0.05, $F_{1,15}$ = 5.54) and longer peak seasons compared to IMVT (effect of site peak season length: $F_{1,15}$ = 13.31, P < 0.05), the average peak season for all DS canopies (SDOT and IMVT combined) was 10 days longer (P < 0.05) compared to EG canopies (Table 2.2b).
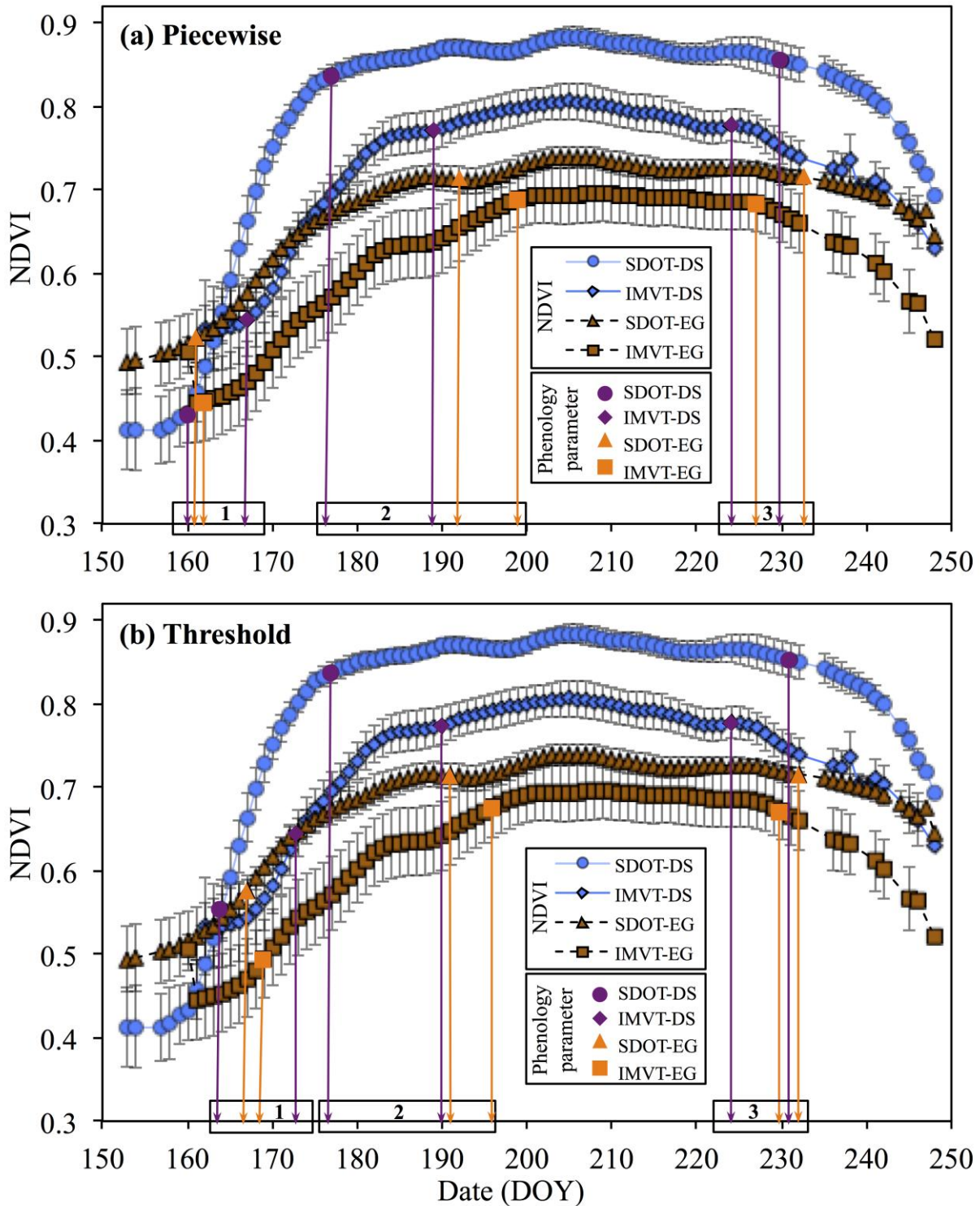
Figure 2.7. Seasonal canopy greenness (loess smoothed NDVI) for deciduous shrub (DS – blue symbols) and evergreen/graminoid (EG – brown symbols) canopies at the two study sites. Error bars represent 1 SEM. On the respective NDVI curves, dates when canopy phenology metrics were reached are marked with purple (DS) and orange (EG) points, with arrows of matching colors extended to the *x-axis*. Canopy phenology parameters are indicated by numbered boxes on the *x-axis*: [1] onset of greening, [2] onset of peak green, and [3] onset of senescence. Phenology dates were determined (a) using piecewise linear regression analysis and (b) using threshold analysis.

Table 2.2. Canopy phenology metrics ± 1 SEM determined from piecewise linear regression modeling and threshold analysis. (a) Dates of canopy-level phenological parameters [day of year (DOY)]. Differences indicate number of days earlier (minus sign) or later (no sign) deciduous shrub (DS) canopies reached each stage compared to evergreen/graminoid (EG) canopies. (b) Lengths (number of days) of growing and peak seasons, and rates of green-up (slopes). Differences indicate shorter (minus sign) or longer (no sign) seasons, and faster rates of green up for DS compared to EG canopies. Asterisks (*) indicate dates or values in a row were significantly different from one another, and "ns" indicates no significant difference. Significant main effects of mean comparisons of DS and EG canopy values in each row are shown.

Phenological parameter	DS	EG	Difference	P	F	df
(a)	Average canopy phenology stage date					
Onset of greening						
Piecewise	163 ± 1	161 ± 1	2*	< 0.05	4.97	1,15
Threshold	168 ± 2	168 ± 2	0	ns		
Onset of peak green						
Piecewise	182 ± 2	195 ± 3	−13*	< 0.001	16.93	1,15
Threshold	182 ± 3	193 ± 2	−11*	< 0.001	18.47	1,15
Onset of senescence						
Piecewise	226 ± 1	229 ± 2	−3	ns		
Threshold	227 ± 2	230 ± 2	−3	ns		
(b)	Average canopy phenology parameter					
Growing season length						
Piecewise	85 ± 1	87 ± 1	−2	ns		
Threshold	80 ± 2	80 ± 2	0	ns		
Peak season length						
Piecewise	44 ± 3	34 ± 4	10*	< 0.05	7.39	1,15
Threshold	45 ± 4	37 ± 3	8*	< 0.05	4.91	1,15
Rate of green-up						
Piecewise	0.018 ± 0.003	0.007 ± 0.002	0.011*	< 0.001	16.94	1,15
Threshold	0.016 ± 0.003	0.005 ± 0.001	0.010*	< 0.01	15.46	1,15

To further examine the effect of increasing deciduous shrub cover, we evaluated the relationship between percent deciduous shrub cover and canopy phenology variables across all quadrats (Figure 2.8). We found that, although the onset of greening did not occur earlier as deciduous shrub cover increased, the rate of green-up became significantly faster ($R^2 = 0.7$, $F_{1,16} = 37.59$, $P < 0.001$; Figure 2.8b) and the onset of peak green occurred significantly earlier ($R^2 = 0.8$, $F_{1,16} = 58.64$, $P < 0.001$; Figure 2.8c). Although increasing deciduous shrub cover did not

affect the date of the onset of senescence, nor the overall growing season length, the peak season lengthened significantly ($R^2 = 0.71$, $F_{1,16} = 39.38$, $P < 0.001$; Figure 2.8e).
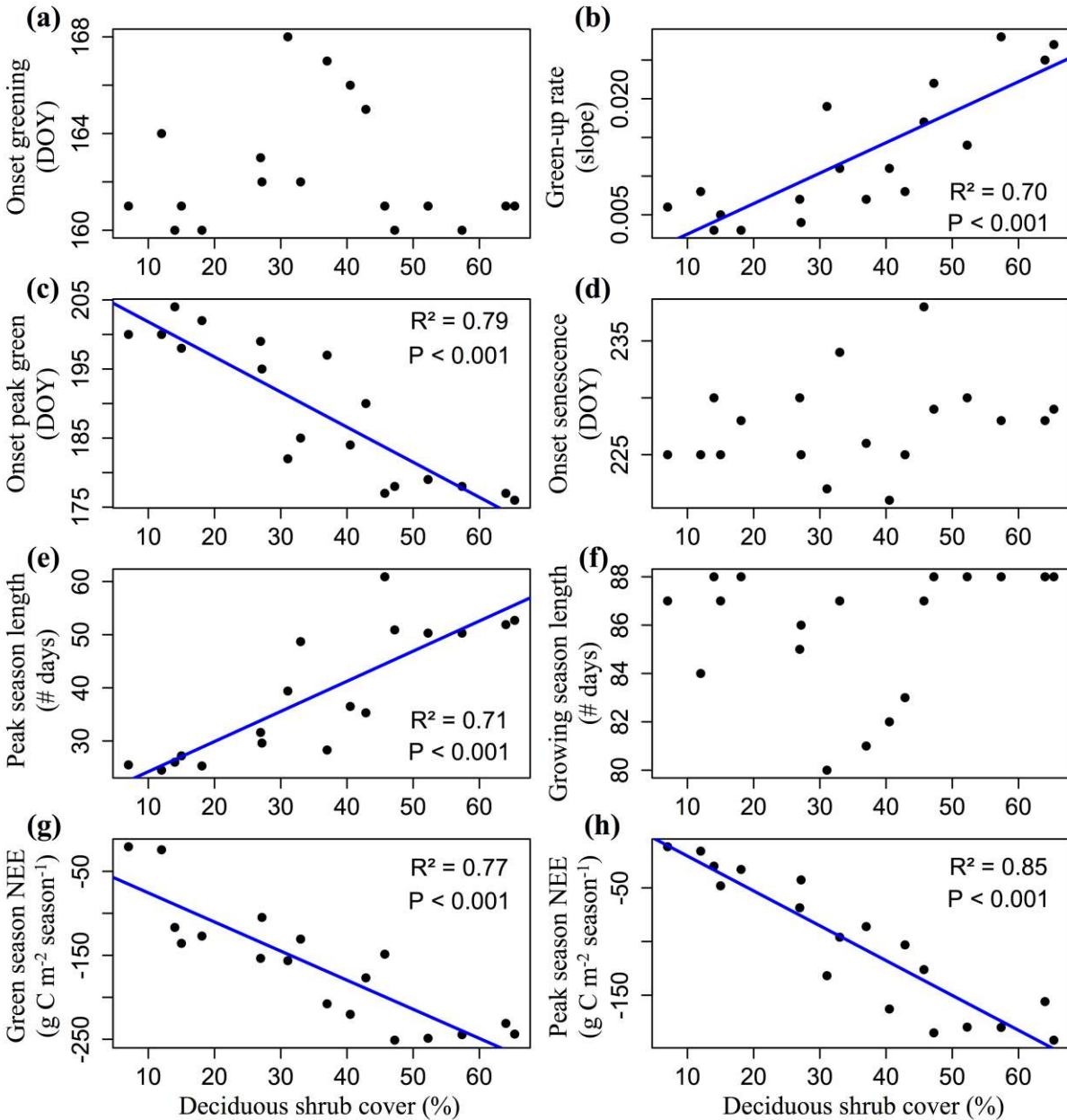
Figure 2.8. Relationships between percent deciduous shrub cover of canopies along all transects (n = 18) and canopy (a) onset of greening, (b) rate of green-up, (c) onset of peak green, (d) onset of senescence, (e) length of the peak green season, (f) length of the growing season; and modeled estimates of total net ecosystem exchange (NEE) in grams of carbon (C) m^{-2} season^{-1} for (g) the green season and (h) the peak season. Canopy metrics were determined using piecewise linear regression modeling. Only trend lines (blue) of significant relationships are shown.

2.3.2 Leaf Area Index Model

Similar to the pattern of NDVI, the increase in the leaf area index (LAI) during green-up was more pronounced for DS canopies compared to EG canopies (effect of date*canopy type: LAI - $F_{1,203}$ = 25.44, P < 0.001; Figure 2.9a). Although the pattern of LAI changed throughout the season (effect of date: LAI - $F_{1,71}$ = 93.6, P < 0.001), DS canopies maintained higher LAI throughout most of the green season compared to EG canopies (effect of canopy type: LAI - $F_{1,203}$ = 1070.86, P < 0.001). As with NDVI, SDOT maintained higher LAI values compared to IMVT throughout most of the green season (effect of site: LAI - $F_{1,203}$ = 318.6, P < 0.001).

2.3.3 Net Ecosystem Exchange Model

The change in respiration (R_E) during green-up and senescence was more pronounced for DS canopies compared to EG canopies (effect of date*canopy type: R_E - $F_{1,203}$ = 33.59, P < 0.001; Figure 2.9b). Throughout most of the green season, although the pattern of R_E changed (effect of date: R_E - $F_{1,71}$ = 43.8, P < 0.05), DS canopies had greater CO_2 release from R_E compared to EG canopies (effect of canopy type: R_E - $F_{1,203}$ = 1030.81, P < 0.001). There was also a difference between sites because SDOT maintained higher R_E values compared to IMVT throughout most of the green season (effect of site: R_E - $F_{1,203}$ = 414.36, P < 0.001).

Similar to R_E, there was a significant interaction effect for the overall gross primary production (GPP) data (effect of date*canopy type: GPP - $F_{1,203}$ = 11.61, P < 0.001; Figure 2.9c) and the pattern of GPP changed throughout the season (effect of date: GPP - $F_{1,71}$ = 13.26, P < 0.001). Also similar to R_E, throughout most of the green season, DS canopies had greater CO_2 uptake from GPP compared to EG canopies (effect of canopy type: GPP - $F_{1,203}$ = 969.14, P < 0.001) and SDOT maintained higher GPP values compared to IMVT (effect of site: GPP - $F_{1,203}$ = 305.59, P < 0.001).

The pattern of change throughout the season in net ecosystem exchange (NEE) was similar for both DS and EG canopies (Figure 2.9d). However, DS canopies had greater net CO_2 uptake throughout most of the green season compared to EG canopies (effect of canopy type: NEE - $F_{1,203}$ = 342.69, P < 0.001). Also, SDOT tended to have greater net CO_2 uptake compared to IMVT throughout most of the green season (effect of site: NEE - $F_{1,203}$ = 52.19, P < 0.001).

Because DS canopies had higher LAI values during both green and peak seasons, and longer peak seasons, DS canopies took up about twice as much C (P < 0.001) during their green

season (an estimated additional 113 g C m^{-2} season^{-1}), and nearly three times the amount of C (P < 0.001) during their peak season (an estimated additional 101 g C m^{-2} season^{-1}) compared to EG canopies (Table 2.3). SDOT took up more total carbon compared to IMVT during both the green and peak seasons (effect of site: green season NEE - $F_{1,15}$ = 8.22, P < 0.05; peak season NEE - $F_{1,15}$ = 10.07, P < 0.01).
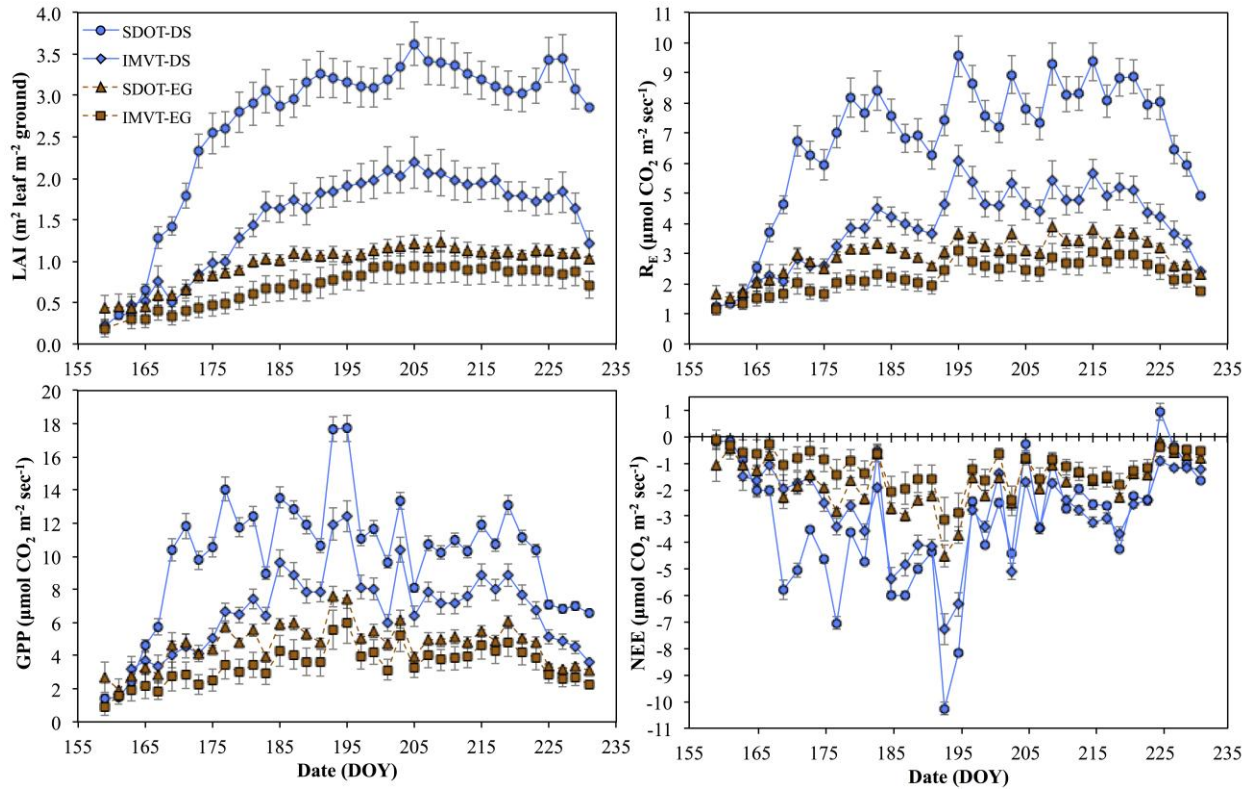
Figure 2.9. Modeled estimates of two-day averages of seasonal (a) leaf area index (LAI), (b) respiration (R$_E$), (c) gross primary production (GPP), and (d) net ecosystem exchange (NEE) for deciduous shrub (DS, blue symbols) and evergreen/graminoid (EG, brown symbols) canopies at each of the two study sites. Error bars represent 1 SEM.

Table 2.3. Modeled estimates of integrated total net ecosystem exchange (NEE) in grams of carbon (C) m^{-2} season^{-1} ± 1 SEM for green and peak seasons, as determined by piecewise linear regression modeling. Differences indicate amount of additional grams C uptake for deciduous shrub (DS) compared to evergreen/graminoid (EG) canopies; and percentages indicate the percent additional carbon gain for DS relative to EG canopies. Asterisks (*) indicate values in a row were significantly different from one another. Significant main effects of mean comparisons of DS and EG canopy NEE values in each row are shown.

	DS	EG	Difference (% additional)	P	F	df
Green season NEE (g C m^{-2} season^{-1})	− 220 ± 11	− 107 ± 17	113 (106%)*	< 0.001	45.47	1,15
Peak season NEE (g C m^{-2} season^{-1})	− 153 ± 13	− 52 ± 13	101 (192%)*	< 0.001	49.36	1,15

To tease out the effect of different LAI across vegetation communities, and further examine the effect of changing season length, we estimated green and peak season NEE for each community type under changing season lengths (Table 2.4). Increasing the green season length by 5 days increased carbon uptake for both DS and EG canopies by 3% and 4%, respectively (Table 2.4a). Extending the peak season by 10 days increased C uptake by 84% ($P < 0.001$) for DS canopies (an estimated additional 71 g C m^{-2} season^{-1}) and by 64% ($P < 0.05$) for EG canopies (an estimated additional 30 g C m^{-2} season^{-1}) (Table 2.4b).

To further examine the effect of increasing deciduous shrub cover on NEE, we evaluated the relationship between percent deciduous shrub cover and seasonal NEE across all quadrats (Figures 2.8g & 2.8h). We found that both green and peak season NEE were significantly greater when percent deciduous shrub cover was greater (green season NEE - $R^2 = 0.76$, $F_{1,16} = 51.28$, $P < 0.001$; peak season NEE - $R^2 = 0.85$, $F_{1,16} = 87.31$, $P < 0.001$).

Table 2.4. Modeled estimates of integrated total net ecosystem exchange (NEE) in grams of carbon (C) m^{-2} season^{-1} ± 1 SEM for deciduous shrub (DS) or evergreen/graminoid (EG) canopies, as determined by piecewise linear regression modeling. (a) Comparing total NEE under two green season length scenarios: 1) DS green season (DOY 163 to 226, 63 days) and 2) EG green season (DOY 161 to 229, 68 days). Differences indicate amount of additional grams C uptake during the longer green season (i.e. 5 days longer). Percentages indicate the percent additional carbon uptake during the longer green season. (b) Comparing total NEE under two peak season length scenarios: 1) DS peak season (DOY 182 to 226, 44 days) and 2) EG peak season (DOY 195to 229, 34 days). Differences indicate amount of additional grams C uptake during the longer peak season (i.e. 10 days longer). Percentages indicate the percent additional carbon uptake during the longer peak season scenario. Asterisks (*) indicate values in a row were significantly different from one another, and "ns" indicates no significant difference. Significant main effects of mean comparisons of NEE values across one canopy type in each row are shown.

(a)	DS green season (63 days)	EG green season (68 days)	Difference (% additional)	P	F	df
DS NEE (g C m^{-2} season^{-1})	− 221 ± 10	− 228 ± 10	7 (3%)	ns		
EG NEE (g C m^{-2} season^{-1})	− 103 ± 16	− 107 ± 16	4 (4%)	ns		
(b)	DS peak season (44 days)	EG peak season (34 days)				
DS NEE (g C m^{-2} season^{-1})	− 156 ± 5	− 85 ± 4	71 (84%)*	< 0.001	114.84	1,15
EG NEE (g C m^{-2} season^{-1})	− 77 ± 12	− 47 ± 7	30 (64%)*	< 0.05	5.58	1,15

2.3.4 Model Sensitivity Analysis

To assess the sensitivity of total peak season net ecosystem exchange (peak NEE) to changes in air T, PAR, LAI, and the onset date of the peak season, we varied individual model

parameters by stepwise percentages (Figure 2.10). On average, peak NEE was most sensitive to changes in PAR and the timing of the onset of the peak season, and least sensitive to changes in LAI. For instance, if considering average percent change (i.e. across both canopy types), a 20% increase in LAI increased peak NEE by 12%, whereas a 20% earlier onset of the peak season or 20% increase in PAR increased peak NEE by 33% and 21%, respectively. The effect changing air T had on peak NEE was relatively similar in magnitude of effect, but opposite in directional effect compared to other model parameters, where an increase in air T of 20% *decreased* peak NEE by 19%.
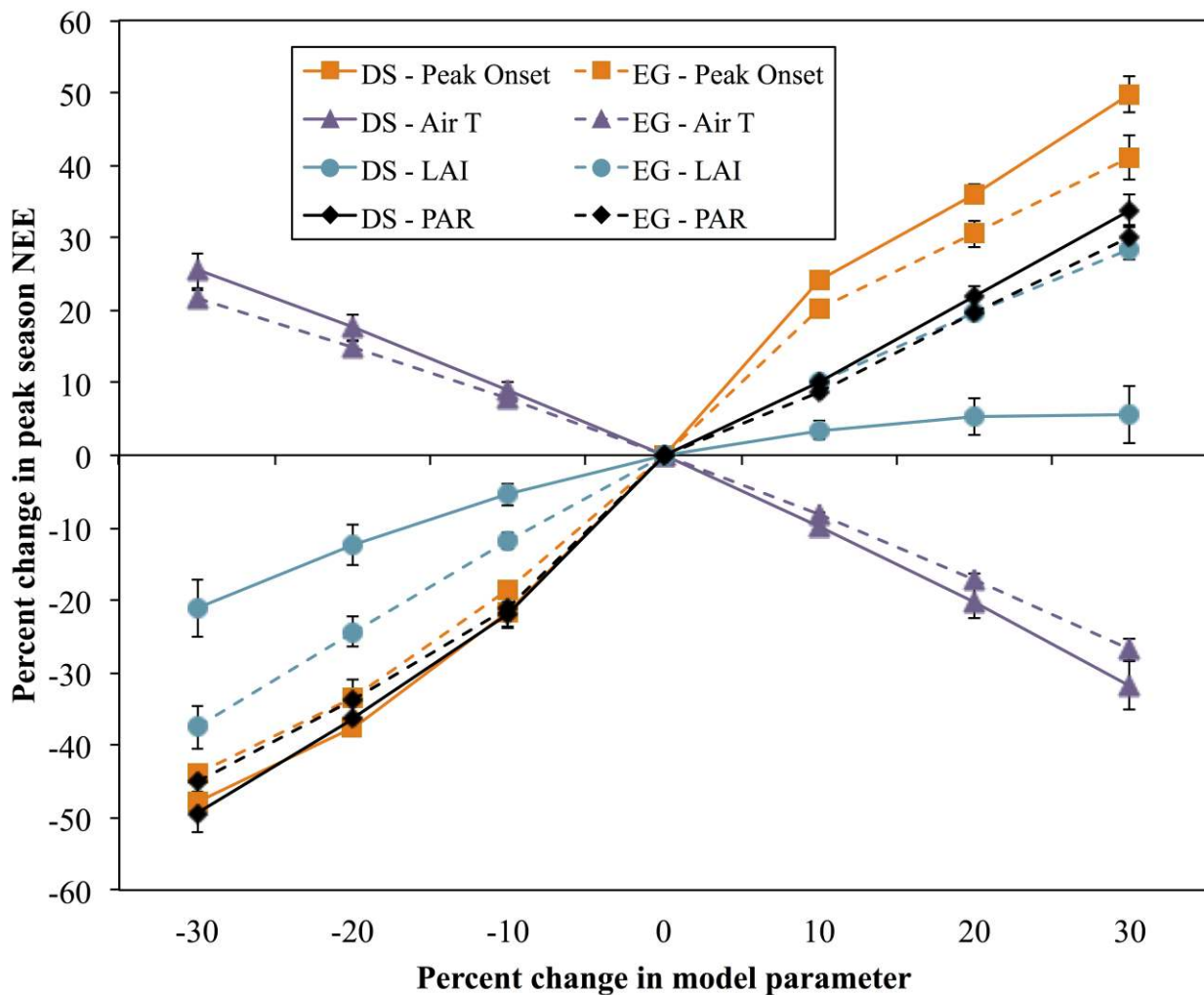
Figure 2.10. Sensitivity of modeled estimates of total peak season net ecosystem exchange (NEE) for deciduous shrub (DS) and evergreen/graminoid (EG) canopies to changes in four NEE model parameters: irradiance (PAR), air temperature (Air T), leaf area (LAI), and onset date of the peak season (Peak Onset). Percent differences from original values of PAR, Air T, and LAI and a baseline peak onset date of DOY (day of year) 189 are shown on the *x-axis*. Percent change in total peak green season NEE with changes in model parameters are on the *y-axis*. The percent changes in model parameters were applied equally across DS and EG canopies. Error bars represent 1 SEM.

60

Decreases in PAR led to larger magnitude changes compared to the same percentage increases in PAR. As this was not the case for the onset of the peak season, peak NEE was, on average, most sensitive to the earlier onset of the peak season. For instance, if considering average percent change across both canopy types, a 30% increase in PAR increased peak NEE by 32%, while a 30% decrease in PAR decreased peak NEE by 47%. On the other hand, a 30% earlier (or later) onset of the peak season led to an increase (or decrease) in peak NEE of 46%.

Although DS and EG canopies' peak NEE was similarly sensitive to changes in PAR, air **T**, and onset of the peak season, DS canopies were much less sensitive to changes in LAI compared to EG canopies (Figure 2.10). For instance, increasing LAI by 30% increased peak NEE for DS canopies by 6% and for EG canopies by 28%. And decreasing LAI by 30% decreased peak NEE for DS canopies by 21% and for EG canopies by 38%.

2.4 Discussion

2.4.1 Deciduous Shrubs Lengthen the Period of Peak Canopy Greenness

We found that deciduous shrub canopies had an accelerated rate of green-up, and reached the period of peak greenness 13 days earlier compared to evergreen/graminoid canopies. Because deciduous shrub canopies reached the onset of senescence only 3 days earlier, the period of peak tundra greenness (from the onset of peak green to the onset of senescence) was 10 days longer for deciduous shrub canopies compared to evergreen/graminoid canopies. However, because deciduous shrub and evergreen/graminoid canopies began greening at similar times and ended senescence at the same time, greater deciduous shrub dominance did not lengthen the overall growing season. These results suggest that the ongoing increase in deciduous shrub dominance in the arctic tundra (Forbes et al. 2010, Myers-Smith et al. 2011) may be contributing to the concurrent satellite-detected trend toward an earlier onset of the peak green season (Goetz et al. 2005, Jia et al. 2009, Tagesson et al. 2012),), but not necessarily to observed lengthening of the entire growing season (Zhou et al. 2001, Jeong et al. 2011, Zeng et al. 2011). Longer overall growing seasons are more likely related to increases in air temperature (Hollister et al. 2005, Delbart & Picard 2007, Xu et al. 2013) and reductions in snow cover duration (Stow et al. 2004, Wipf 2010, Pau et al. 2011), which cause an earlier onset of greening and/or a later end of senescence (Tucker et al. 2001, Jia et al. 2004).

2.4.2 Deciduous Shrubs Lengthen the Period of Maximum Carbon Uptake

We found that due to the combined effects of higher leaf area and a longer peak season, deciduous shrub canopies took up nearly three times the amount (an estimated additional 101 g C m^{-2} season^{-1}) of carbon compared to evergreen/graminoid canopies. However, we also found that a 10-day extension of the peak season alone nearly doubled the net carbon uptake in deciduous shrub canopies, increasing uptake by an estimated 71 g C m^{-2} season^{-1}. Thus, while a portion ($\sim$ 29%) of the additional carbon uptake by deciduous shrub communities during the period of peak greenness was due to greater leaf area, a significant portion ($\sim$ 71%) was due to the extended duration of the peak season exhibited by deciduous shrub communities compared to evergreen/graminoid communities. Our results are supported by previous work showing that the carbon gain potential of the tundra is enhanced when the arctic peak season is extended (Tagesson et al. 2012). Our findings on the effect deciduous shrub abundance has on the length of the peak season are important since carbon uptake at its maximum for all tundra communities during the peak season (Richardson et al. 2013, Ueyama et al. 2013, Mbufong et al. 2014). Our results suggest that greater deciduous shrub abundance increases carbon uptake not only due to greater leaf area, but also due to an extension of the period of peak greenness, which extends the period of maximum carbon uptake, and may increase tundra carbon gain as deciduous shrubs become increasingly abundant.

It is important to note that by focusing on the growing season only, this study examined the influence of greater deciduous shrub cover on net carbon exchange during only the snow-free season, but respiratory carbon flux during the winter may also be altered by increasing deciduous shrub cover. Some studies suggest that increasing deciduous shrub cover may enhance carbon loss in winter through changes in snow cover dynamics and winter soil temperature regimes (Walker et al. 1999, Schimel et al. 2004) that in turn influence heterotrophic respiration. Further, it has been suggested that evergreens may be photosynthetically active under the snow in spring (Starr & Oberbauer 2003), which may enhance annual carbon uptake where evergreen species are abundant. Also, although the model has shown great accuracy in estimating entire ecosystem carbon flux across a variety of tundra landscapes (Shaver et al. 2007, Loranty et al. 2010, Rastetter et al. 2010), a portion of the unexplained variance may be due in part to respiration from shallow soil depths, or differences in plant species composition not incorporated into the NEE model (Shaver et al. 2013). While it is not possible to predict with 100% certainty what the

62

future of net carbon flux will be for arctic tundra, our results suggest that increasing deciduous shrub cover significantly increases the carbon uptake potential of the tundra by both increasing leaf area and extending the length of the peak season.

2.4.3 Modeling Tundra Carbon Uptake

Our sensitivity analysis suggests that the magnitude of change in total peak season net ecosystem exchange (peak NEE) is most sensitive to changes in photosynthetically active radiation (PAR) and the timing of the onset of the peak season, and least sensitive to changes in leaf area (LAI). Peak NEE was most sensitive to the earlier onset of the peak season. The sensitivity of peak NEE to changes in the onset of the peak season supports the main finding of our study, where we found that the earlier onset of the peak season significantly increased carbon gain in both deciduous shrub and evergreen/graminoid tundra. The sensitivity analysis suggests that the effect deciduous shrub cover has on the length of the peak season may be just as, if not more, important than the effect deciduous shrub cover has on leaf area when considering tundra carbon gain potential.

The sensitivity of peak NEE to changes in PAR suggests that changes in insolation, such as might be the result of increased cloudiness, may have large effects on peak season NEE. Light-attenuation studies in the Alaskan arctic tundra have shown that reduced light (representative of increased cloud cover) may decrease photosynthesis (Chapin & Shaver 1996), nutrient uptake and plant biomass (Chapin et al. 1995). This may prove important given that satellite records suggest summer cloud cover has increased in Alaska (Chapin et al. 2005) and the pan-Arctic (Wang & Key 2003) over the last several decades.

Increases in PAR and LAI, and an earlier peak season onset increased carbon uptake, while increases in air temperature (air T) had the opposite effect, since carbon loss from respiration increased with increasing air T, while GPP was unaffected. This sensitivity of respiration to changes in air T could prove important given that air T is predicted to continue rising in the arctic tundra (IPCC 2013). Increasing air T could increase respiration (Cahoon et al. 2012, Heskel et al. 2013), and potentially offset any increases in carbon uptake due to longer peak green seasons and greater leaf area associated with increasing deciduous shrub cover (Belshe et al. 2013).

We found that deciduous shrub canopy NEE was less sensitive to changes in LAI than evergreen/graminoid canopies. Although higher LAI during peak season increased the *daily rate* of carbon gain in both canopy types, earlier seasons had a critical impact on NEE by increasing the *number of days* early in the peak season when carbon gain was greater than carbon loss. Thus, in deciduous shrub tundra, which already has a much higher LAI compared to evergreen/graminoid tundra, an earlier onset of the peak season increased carbon uptake much more substantially than proportional increases in LAI.

CHAPTER THREE:

NDVI as a Predictor of Canopy Arthropod Biomass in the Alaskan Arctic Tundra

Abstract. The physical and biological responses to rapid arctic warming are proving acute, and as such, there is a need to monitor, understand, and predict ecological responses over large spatial and temporal scales. The use of the normalized difference vegetation index (NDVI) acquired from airborne and satellite sensors addresses this need as it is widely used as a tool for detecting and quantifying spatial and temporal dynamics of tundra vegetation cover, productivity, and phenology. Such extensive use of the NDVI to quantify vegetation characteristics suggests that it may be similarly applied to characterizing primary and secondary consumer communities. Here we develop empirical models to predict canopy arthropod biomass with canopy-level measurements of the NDVI both across and within distinct tundra vegetation communities over four growing seasons in the arctic foothills region of the Brooks Range, Alaska. When canopy arthropod biomass is predicted with the NDVI across all four growing seasons, our overall model that includes all four vegetation communities explains 63% of the variance in canopy arthropod biomass. Whereas each of our four vegetation community-specific models explain 74% (moist tussock tundra), 82% (erect shrub tundra), 84% (riparian shrub tundra), and 87% (dwarf shrub tundra) of the observed variation in canopy arthropod biomass. Our field-based study suggests that measurements of the NDVI made from air and spaceborne sensors may be able to quantify spatial and temporal variation in canopy arthropod biomass at landscape to regional scales.

3.1 Introduction

Arctic regions have been warming at a rate two to three times higher than the global average since the 1950s (AMAP 2012, Overland et al. 2012, IPCC 2013), and the physical and biological responses are proving acute (ACIA 2004, Callaghan et al. 2004, McBean et al. 2006). These trends have amplified the need to better monitor, understand, and predict the arctic tundra's ecological responses to climate change over large spatial and temporal scales (Gauthier et al. 2013, Nielsen & Wall 2013, Post & Høye 2013). However, arctic landscapes are generally vast and largely inaccessible, are characterized by short growing seasons, and can exhibit considerable heterogeneity in dominant vegetation cover over small spatial scales (Walker et al. 1994). Within an area of less than 1 km^2 on the north slope of Alaska, for example, vegetation cover often includes dry heath tundra on windblown ridge tops, tussock tundra on mesic slopes, dwarf-shrub communities in riparian areas, and wet sedge tundra in low-lying, waterlogged areas (Shaver et al. 1996, Walker & Walker 1996). Ecosystem phenology and production in the Arctic also exhibit a high degree of temporal interannual variability (Markon et al. 1995, Artf et al. 1999, Hope et al. 2004). Although these factors pose challenges, previous modeling efforts have achieved a high degree of predictive ability across diverse tundra communities with widely different dominant plant species (Williams & Rastetter 1999, Epstein et al. 2001, Shaver et al. 2013). Small-scale, localized modeling successes can then be scaled up to address the problems of vastness and inaccessibility of the Arctic. The problem then becomes collecting large-scale data.

One solution to the limitations of collecting large-scale data in the Arctic is the use of airborne and satellite remote sensing to characterize and monitor ecological change (Pettorelli et al. 2005). Several arctic studies have found strong correlations between plot level measurements of the normalized difference vegetation index (NDVI) and aboveground biomass (Boelman et al. 2003, Raynolds et al. 2006), plant community dominance and biophysical structure (Gould et al. 2002, Boelman et al. 2011), leaf area (van Wijk & Williams 2005, Steltzer & Welker 2006), primary productivity (Nemani et al. 2003, Street et al. 2007), carbon flux (Vourlitis et al. 2000), and net ecosystem exchange (Boelman et al. 2005, Shaver et al. 2007). Satellite NDVI datasets have already been used to quantify regional and pan-arctic trends in the spatial and temporal dynamics of various tundra vegetation characteristics, such as vegetation cover type (Stow et al.

2004, Jia et al. 2009), productivity (Myneni et al. 1997, Beck & Goetz 2011, Shaver et al. 2013), and phenology (Zhou et al. 2001, Zeng et al. 2011).

A number of arctic studies have also documented predictive relationships between tundra vegetation and arthropod abundance (Masters et al. 1998, Haddad et al. 2001, Richardson et al. 2002), biomass (Schaffers et al. 2008), and density (Coulson et al. 2003). In addition, predictive models for arctic arthropod abundance and biomass as a function of climatic factors such as temperature, thawing degree days, wind speed, and solar radiation have been successfully employed (Høye & Forchammer 2008, Bolduc et al. 2013). Because the NDVI is representative of primary productivity and integrates the climatic conditions that affect plant phenology and biomass (Jia et al. 2003, Raynolds et al. 2006, Tagesson et al. 2012), and given the strong empirical relationships between the NDVI and tundra vegetation characteristics mentioned above, the NDVI may also be a good predictor of tundra canopy arthropod biomass. Yet, to our knowledge, no studies have explored the use of NDVI as a predictor of consumer biomass in the arctic tundra. However, the NDVI has been used in a variety of temperate and tropical ecosystems to identify insect infestations (Ji et al. 2004, Zha et al. 2005, Board et al. 2007, Jepsen et al. 2009), and quantify the impact of insect herbivory on vegetation biomass (Vogelmann 1990, de Beurs & Townsend 2008, Eklundh et al. 2009).

The goal of this study was to determine empirical relationships between the NDVI and canopy arthropod biomass, and subsequently develop an empirical model to predict canopy arthropod biomass in arctic tundra landscapes from the NDVI. We established empirical relationships between measurements of near-surface, canopy-level NDVI and plant canopy-dwelling arthropod biomass within and across four distinct vegetation types, over four consecutive growing seasons in the arctic foothills region of the Brooks Range, Alaska. As such, this is a first step towards assessing the potential for datasets acquired by air and spaceborne sensors to quantify spatial and temporal dynamics in canopy arthropod biomass at landscape and regional scales. Developing predictive relationships between remotely sensed NDVI and arthropod biomass will contribute to our ability to quantify how changes in tundra vegetation cover and phenology will affect higher trophic levels as arctic warming continues.

3.2 Methods

3.2.1 Study Sites and Observational Setup

Datasets were collected at four field sites located in the vicinity (within ~ 30 km) of the Arctic Long Term Ecological Research (ARC LTER) site at Toolik Field Station in the northern foothills of the Brooks Range, Alaska (68º38' N, 149º34' W, elevation 760 m): Roche Mountonnee (ROMO), Toolik Lake Field Station (TLFS), Imnavait Creek (IMVT), and the Sagavanirktok River-Department of Transportation camp (SDOT) (Figure 3.1). Annual precipitation at Toolik is 200 – 400 mm, with 45% falling as snow; annual average temperature is -10 ºC, and average July temperature is 14 ºC (van Wijk et al. 2005).
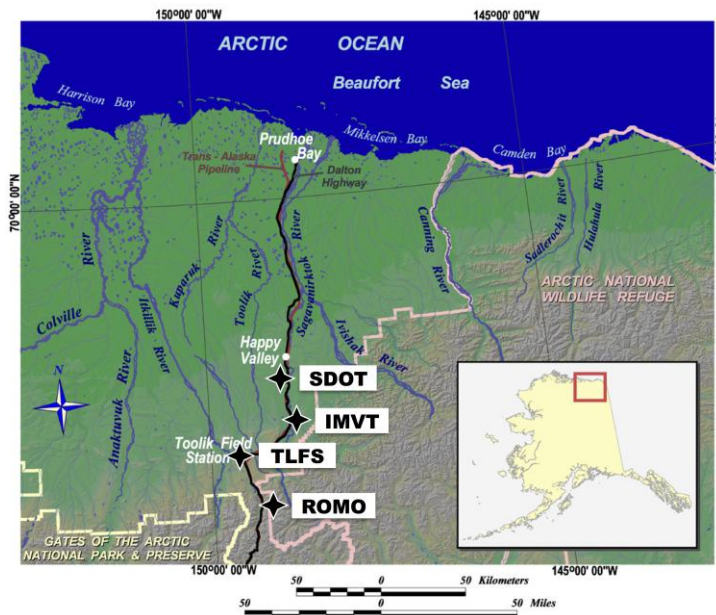
Figure 3.1. Map of Alaska and the North Slope of the Brooks Range (inset) showing the location of the four field sites near the Toolik Lake field station used in this study: Roche Mountonee (ROMO), Toolik Lake Field Station (TLFS), Imnavait Creek (IMVT), and the Saga-vanirktok River Depart-ment of Transportation camp (SDOT).

Each of the four sites included two 20,000 m^2 study areas, for a total of eight study areas. Within each of the eight 20,000 m^2 study areas, two 100 m transects were established and ten quadrats (1 m^2) were established at 10 m intervals along each transect (for a total of 16 transects and 160 quadrats). The eight study areas were categorized into four vegetation communities, based on differences in vegetation height and dominant vegetation and surface cover (Table 3.1), and using existing vegetation classifications for the Alaskan arctic tundra (e.g. Walker et al. 2005, Walker & Maier 2008). Methodology used to determine aerial percent vegetation cover and shrub height in this study are described in Chapter one and in Rich et al. (2013).

The four vegetation communities used in this study overlap somewhat in species composition but are distinct in the relative abundance of dominant species and other characteristics (Table 3.1). The riparian shrub tundra community (RST) was located at ROMO and was less than 100 m from the Roche Mountonnee Creek. The RST was dominated by *Salix* spp., interspersed with forbs. The RST was also characterized by well-drained, rocky soils with the tallest shrubs of all the communities. Because the large stature shrubs at the RST were widely spaced, there was considerable surface exposure of bare soil and rock, litter, and woody stem material. The two erect shrub tundra communities (EST) were located at TLFS (approximately 200 m from the Toolik Lake outlet) and at SDOT (approximately 200 m from the Oksrukuyik Creek), where proximity to a large body of water (TLFS) or flowing water (SDOT) may increase thaw depths and promote root lengthening and shrub growth (Naito & Cairns 2011). The TLFS EST represents vegetation typical of shrub tundra described in Shaver and Chapin (1991). The SDOT EST represents vegetation typical of riverside shrub tundra as described in Giblin et al. (1991). The EST communities were dominated primarily by tall stature *Betula nana*, and secondarily by *Salix* spp. and other deciduous shrubs, interspersed with moss, evergreens, and forbs. Unlike the RST, EST had little to no litter and bare soil and rock surface cover. The prostrate/dwarf deciduous shrub tundra community (DST) was located in an area of water tracks (McNamara et al. 1999) at IMVT, and represents vegetation typical of water track tundra as described in Chapin et al. (1988). The DST was characterized by medium stature *Betula nana* and *Salix* spp. as well as moss, interspersed with graminoids, evergreens, and forbs. The four moist tussock tundra communities (MTT) were located at all four sites in tundra with tussock-forming and other sedges (*Eriophorum* and *Carex*) and substantial evergreen and moss cover, interspersed with forbs and short stature deciduous shrubs.

These four vegetation communities together consist of approximately 77% of the total vegetation cover in this studies region (subzone E of the Circumpolar Arctic Vegetation Map (CAVM) – Walker et al. 2005). The current study does not include observations in two other less common vegetation communities (i.e. wet sedge and barren/cryptogam tundras), primarily because together, these two communities consist of only approximately 10% of the total vegetation cover of our study region (subzone E of the CAVM – Walker et al. 2005). Not only do the vegetation communities used here represent a large portion of the cover in the northern foothills region of the Brooks Range, but they also make up approximately 70% of the North

69

Slope of Alaska's vegetation cover (subzones D and E of the CAVM – Walker et al. 2005), and 57% of the entire arctic tundra biome (subzones B, C, D, and E of the CAVM – Walker et al. 2005).

Table 3.1. Vegetation communities and codes (number of quadrats per community), descriptions (with average maximum shrub height), and percent cover of plant species, lichen, moss, and other surface cover materials in 1-m^2 quadrats in each vegetation type used in this study. *Notes:* Data were collected in late July 2010. Total percent cover does not always add to 100**%** because (1) standing water is not included and (2) percentages were rounded to the nearest whole number, and any value ≤ 0.4**%** is listed as 0**%**.

Community (no. quadrats)	Description (shrub height range)	Species and functional group cover (%)	Coarse cover categories (%)
Riparian shrub tundra; RST (20)	dominated by tall willows, leaf litter and woody material (45 – 165 cm)	*Betula nana* (0), *Salix* spp. (25), other deciduous shrubs (1), *Eriophorum* and *Carex* spp. (0), other graminoids (0), *Vaccinium vitis-idaea* and *Ledum palustre* (0), other evergreens (1), forbs (9), moss (8), lichen (4)	woody stem material (23), litter (21), bare soil surface and rock (7)
Erect shrub tundra; EST (40)	dominated by medium-to-tall birch and other deciduous shrubs (20 – 90 cm)	*B. nana* (22), *Salix* spp. (10), other deciduous shrubs (12), *Eriophorum* and *Carex* spp. (3), other graminoids (1), *V. vitis-idaea* and *L. palustre* (5), other evergreens (2), forbs (8), moss (13), lichen (4)	woody stem material (14), litter (4), bare soil surface and rock (0)
Dwarf/prostrate deciduous shrub tundra; DST (20)	mixture of dwarf birch and willow, with scattered moss (10 – 45 cm)	*B. nana* (11), *Salix* spp. (16), other deciduous shrubs (0) *Eriophorum* and *Carex* spp. (9), other graminoids (1), *V. vitis-idaea* and *L. palustre* (9), other evergreens (1), forbs (11), moss (19), lichen (1)	woody stem material (8), litter (10), bare soil surface and rock (0)
Moist tussock tundra; MTT (80)	dominated by moss, graminoids and evergreens (5 – 30 cm)	*B. nana* (8), *Salix* spp. (7) other deciduous shrubs (3), *Eriophorum* and *Carex* spp. (18), other graminoids (0), *V. vitis-idaea* and *L. palustre* (14), other evergreens (10), forbs (6), moss (17), lichen (3)	woody stem material (5), litter (10), bare soil surface and rock (1)

3.2.2 Spectral Reflectance and NDVI

Quadrat-level spectral radiance measurements were made weekly with a field portable spectroradiometer (FieldSpec3, Analytical Spectral Devices, Boulder, CO, USA) from late May through late July over four years (2010 through 2013). The spectroradiometer has a 25° full angle cone of acceptance field-of-view (FOV) fiber optic with a spectral range from 350 to 1050

nm. The spectral sampling interval of the spectroradiometer is 1.4 nm. Radiance measurements were preceded by a calibration scan of a 99% reflectance white standard (Spectralon, LabSphere, North Sutton, NH, USA) to normalize for changes in light conditions between measurements. The foreoptic was held approximately 1 m above the top of the canopy, so that each measurement's circular footprint was approximately 0.15 m^2. Spectral measurements were made in the 1 m^2 quadrats along each of the 16 transects described above. Five measurements were collected within each 1 m^2 quadrat in order to ensure that the spatial heterogeneity of each quadrat was captured, which resulted in 50 spectral measurements for each transect. All spectral measurements were converted to reflectance values.

We employ the normalized difference vegetation index (NDVI), which is indicative of the quantity of photosynthetically active, green vegetation (Rouse et al. 1974), and has proven to be sensitive to variations in aboveground biomass (Boelman et al. 2003) and leaf area (van Wijk & Williams 2005, Street et al. 2007) in tundra landscapes. The five NDVI values associated with each quadrat were averaged to give a mean quadrat NDVI value, and these were averaged to obtain mean transect values for each week. The NDVI was calculated from visible red (R: 650 to 690 nm) and near-infrared (NIR: 750 to 850 nm) reflectance using Equation 3.1.

NDVI = (NIR – R) / (NIR + R)   (Equation 3.1)

3.2.3 Sweep Net Sampling and Canopy Arthropod Biomass

Canopy-dwelling arthropod biomass was measured via sweep netting using a standard insect net (Robel et al. 1995). Although it is possible that sweep netting captures arthropods differently within and across vegetation communities (Southwood 1978), we chose this method to collect canopy-dwelling arthropods for several reasons including: 1) all canopy arthropod sampling methods introduce some bias (Doxon et al. 2011), but sweep netting may introduce less sampling bias compared to other techniques (Sørensen et al. 2002); and 2) samples associated with sweep netting tend to overlap in abundance and composition with other collection methods (Noyes 1989, Spafford & Lortie 2013). Samples were collected weekly from late May to mid- to late July over four years (2010 through 2013). One 100 m sweep net transect was established in each of the eight 20,000 m^2 study areas. Using an iron bar as the center point, the direction of the transect was randomly determined at each sample time using a compass bearing generated from a

random numbers table to avoid repeated sampling of the same area. Each sweep set involved ten horizontal passes of the net (at 10 m intervals out to approximately 5 m on each side of the transect) along the ground vegetation and up into the shrubs to about 2 m where necessary. The ten sweep set was duplicated on each side of the transect line, for a total of 100 sweeps and so that each sampling area covered approximately 100 m^2. No effort was made to avoid or contact particular vegetation, and all contents of the samples from each sweep set (including any vegetation material) were transferred to plastic bags with 1 cm^2 pieces of Shell pest strips to kill arthropods, for a total of 10 plastic bags (each containing the contents from 10 sweeps) per study area per date. In the laboratory, samples were sorted (e.g. vegetation was removed/separated from arthropods), and arthropods were transferred to scintillation vials to be counted and dried in the laboratory. The samples were dried for a minimum of 48 hours at 40°C, after which arthropods were weighed for dry biomass. The ten samples associated with each transect were summed, and divided by 100 (the area covered for each sample set) and reported as the mean mass of arthropods per m^2 of ground area (mg m^{-2}). Captured arthropods included a diverse array of functional and taxonomic groups. Abundance and biomass were overwhelmingly dominated by Diptera, which included many midges, mosquitoes and Muscoid flies. Web-building spiders, Homopteran herbivores, and parasitic wasps were also abundant (Gough unpublished data).

3.2.4 Data Analysis

In all four years, mean values of the NDVI and measured arthropod biomass were calculated to give average weekly values for each vegetation community (RST, EST, DST, and MTT) through the plant-growing season. The average date of each measurement week is used to account for irregularity of spacing between dates across vegetation communities. We analyzed seasonal changes in the NDVI and canopy arthropod biomass using a repeated measures ANOVA with vegetation community as the between-subject factor, and week and year of measurement as the within-subject factors. Univariate results are presented. Tukey's honestly significant differences (Tukey's HSD) post-hoc analysis was used to compare means of each vegetation community in more detail.

We determined model parameters from best-fit exponential regression models of the NDVI-measured canopy arthropod biomass relationships for each vegetation community separately (Table 3.1), as well as across all vegetation communities (all data n = 130). Canopy

72

arthropod biomass (mg m^{-2}) was predicted from the NDVI using Equation 3.2, where α and β are parameters specific to each vegetation community (Table 3.2):

Biomass = α * $e^{(β * NDVI)}$ (Equation 3.2)

We quantified linear relationships between measured canopy arthropod biomass and predicted canopy arthropod biomass (using Equation 3.2) between vegetation communities, as well as across all vegetation communities, and report the accuracy of prediction and amount of variance in Table 3.2 (*RMSE* and R^2). Statistical analysis was done in R (R Core Team 2014).

Vegetation community	n	Model parameters		Predicted vs. observed	
		α	β	*RMSE*	R^2
RST	20	0.009	10.160	0.75	0.84
EST	38	0.004	9.129	1.39	0.82
DST	19	0.001	11.950	0.93	0.87
MTT	53	0.004	10.370	1.05	0.74
All data	130	0.008	8.835	1.51	0.63

Table 3.2. Number of quadrats (*n*), best-fit exponential regression parameters (α and β), root mean squared errors of prediction (RMSE), and R^2 values for the NDVI-canopy arthropod biomass relationships used to predict canopy arthropod biomass (mg/m^2) (Equation 3.2) in different communities. *Note:* Regressions were calculated using data from weekly NDVI and sweep net samples collected late May through mid- to late July (2010 to 2013) in vegetation communities classified according to species composition and shrub height (see Table 3.1 for vegetation community descriptions).

3.3 Results

3.3.1 Seasonal Patterns of NDVI and Arthropod Biomass

There was significant variation in the NDVI throughout the growing seasons (effect of week: $F_{1,30}$ = 287.67, P < 0.001), and among vegetation communities (effect of vegetation community type: $F_{3,90}$ = 36.02, P < 0.001), but there was no significant variation across years. Post-hoc analysis showed that NDVI values of the vegetation communities, with the exception of DST and EST, were each significantly different from one another (P < 0.05) (Figure 3.2).

Similar to the NDVI, canopy arthropod biomass varied significantly throughout the growing seasons (effect of week: $F_{1,30}$ = 40.04, P < 0.001) and among vegetation communities (effect of vegetation community type: $F_{3,90}$ = 4.85, P < 0.01). Unlike the NDVI however, arthropod biomass also varied significantly across years (effect of year: $F_{1,2}$ = 4.88, P < 0.05). Post-hoc analysis showed significant differences in arthropod biomass between EST and all other

73
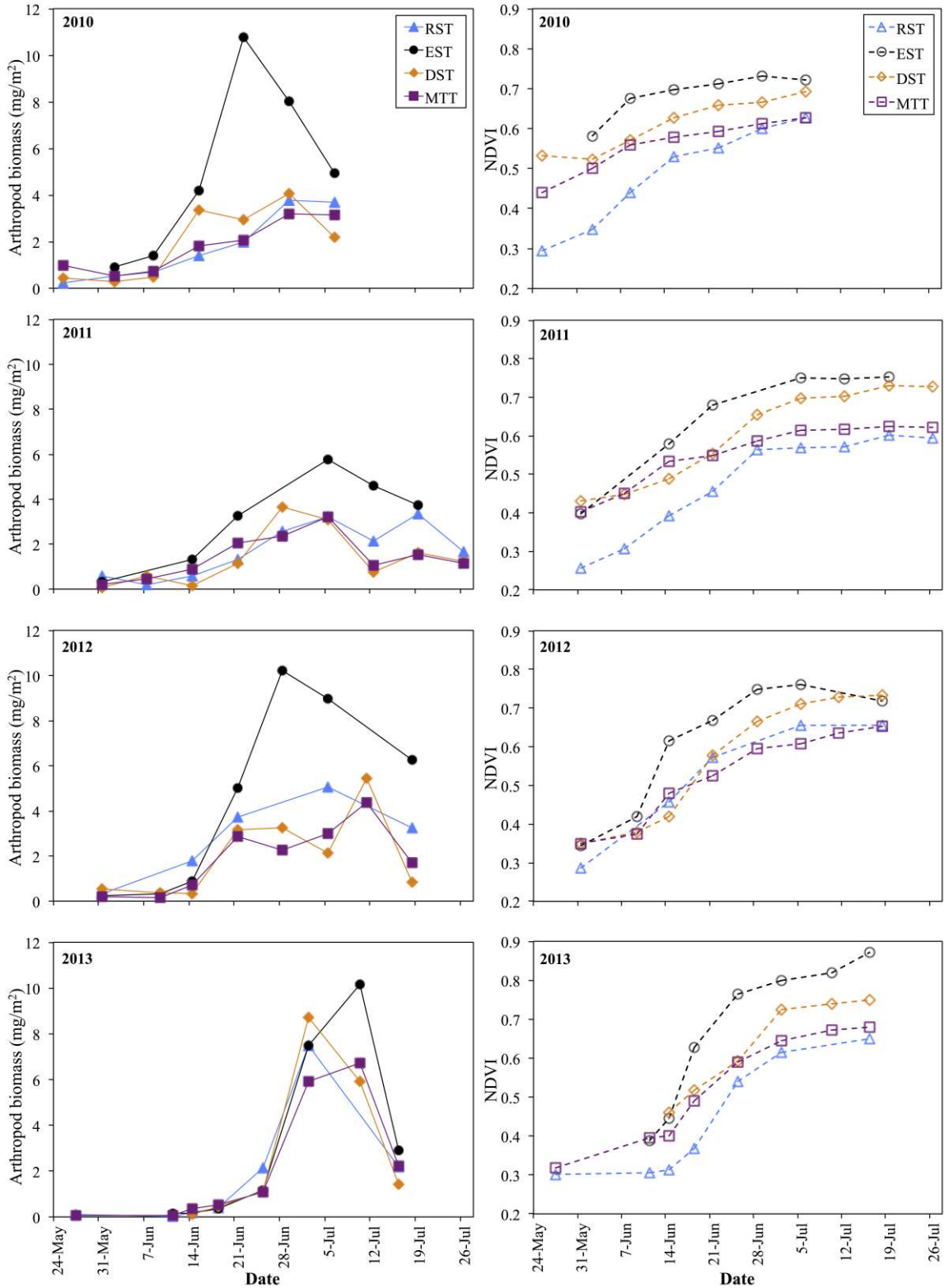
Figure 3.2. Weekly canopy arthropod biomass (let-hand panels) and NDVI (right-hand panels) from late May to mid- to late July for field seasons in 2010 through 2013. Different lines represent different vegetation communities (Table 3.1): riparian shrub tundra (RST), erect shrub tundra (EST), dwarf/prostrate deciduous shrub tundra (DST), and moist tussock tundra (MTT).

74

vegetation communities ($P < 0.05$), but no significant differences among RST, DST, and MTT communities (Figure 3.2).

Across all four years and vegetation types, the NDVI and arthropod biomass generally increased concurrently from late May through late June or mid-July, although there was interannual and vegetation community specific variability in the timing of maximum arthropod biomass (Figure 3.2). Also, while the NDVI values remained high through late July, arthropod biomass reached maximum values and began to decline in late June through early-July (depending on the year and vegetation community). Despite some variation, the NDVI and arthropod biomass followed similar overall patterns throughout the seasons, where vegetation communities with higher deciduous shrub cover (i.e. EST and DST) typically had both higher NDVI values and canopy arthropod biomass relative to communities with more bare soil surface, woody stem material, and litter (i.e. RST) or graminoids and evergreens (i.e. MTT) (Figure 3.2).

3.3.2 NDVI-Arthropod Biomass Relationships

Across all vegetation communities and time periods, 76% of the variance in measured arthropod biomass was explained by the NDVI. A majority of the variation in the overall regression relationship occurred at NDVI values > 0.6 (Figure 3.3a), at which point arthropod biomass was more variable across vegetation communities (Figure 3.2). For instance, when NDVI values were > 0.6 in EST in late June to early July, EST communities often supported dramatic increases in arthropod biomass. Other vegetation communities did not have such large increases in arthropod biomass at this time. In fact, DST tended to support slight declines in arthropod biomass when NDVI values were > 0.6.

When examining vegetation communities separately, relationships between the NDVI and measured arthropod biomass improved (Figures 3.3b & 3.3c). Correlations between the NDVI and measured canopy arthropod biomass were: RST ($R^2 = 0.95$); EST ($R^2 = 0.89$); DST ($R^2 = 0.84$); and MTT ($R^2 = 0.79$). (Figures 3.3b & 3.3c). Similar to the overall relationship, the NDVI-arthropod biomass relationships tended to saturate at NDVI > 0.6 for EST and MTT communities.

3.3.3 Arthropod Biomass Models

The overall model was a fairly good predictor of arthropod biomass (Table 3.2 & Figure 3.4a). In general, the largest variance in the overall predictive model occurred at higher arthropod biomasses, which generally corresponded with NDVI > 0.6 (Figure 3.3a).

Compared to the overall model, vegetation community-specific models were better predictors of arthropod biomass (Table 3.2 & Figures 3.4b & 3.4c). The best individual models were from the DST and RST communities, although EST and MTT community models also showed a high degree of accuracy at estimating arthropod biomass. Similar to the overall model, the largest variance in the vegetation-specific predictive models was at higher arthropod biomasses.

3.4 Discussion

We found that the NDVI is significantly correlated with spatial and temporal variation in canopy arthropod biomass both among and within the four distinct vegetation communities used in this study, thus the NDVI is able to effectively estimate canopy arthropod biomass regardless of vegetation community type. Our study complements previous studies showing strong empirical relationships between the NDVI and various characteristics of vegetation form and function, and which work across diverse arctic tundra plant communities (van Wijk et al. 2005, van Wijk & Williams 2005, Street et al. 2007, Shaver et. al. 2013).

The correlation between the NDVI and canopy arthropod biomass was strongest prior to the period of maximum tundra leaf out (when NDVI < 0.6), suggesting that canopy arthropods and canopy leaf expansion share similar early-season phenological cues, such as spring snowmelt timing (Wipf et al. 2009, Tulp & Schekkerman 2008) and air temperature (Pop et al. 2000, Danks 1999). Later in the season, once maximum tundra leaf out is reached, NDVI values remain relatively stable through mid to late July while canopy arthropod biomass is comparatively plastic. This may be due to a greater sensitivity of arthropods to temperature (Hodkinson et al. 1998, Tulp & Schekkerman 2008) compared to plant biomass (Johnson & Tieszen 1976, Shaver et al. 1986) at this later time in the season. Favorable weather conditions, for example, may allow mosquitoes and midges – the most dominant members of the canopy
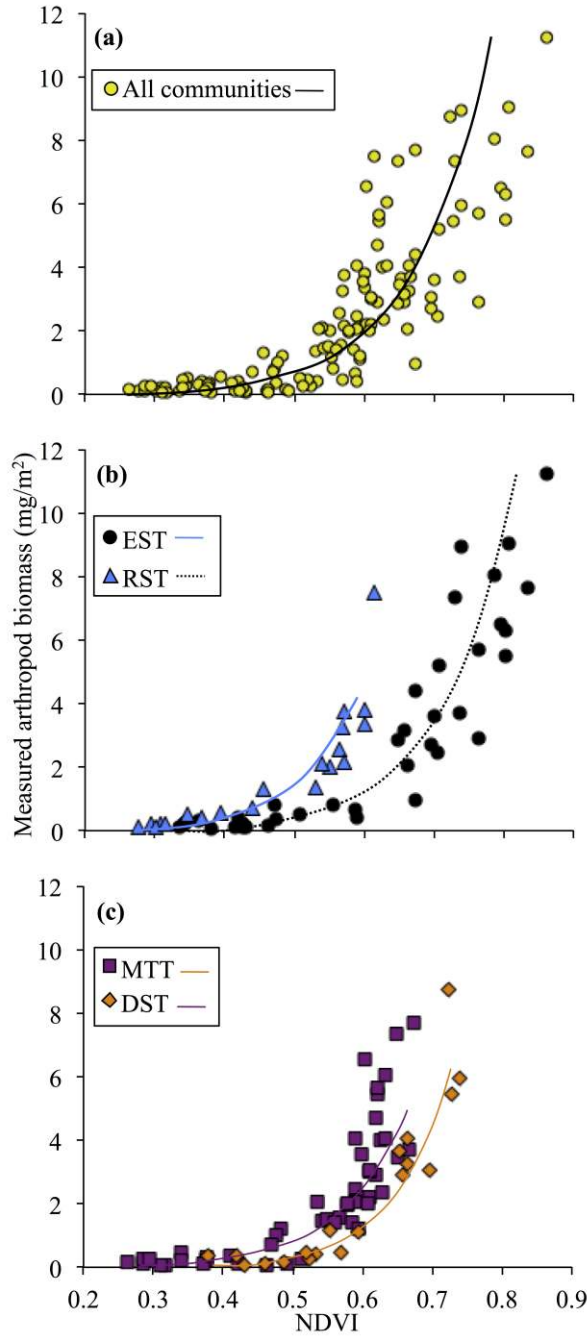
Figure 3.3. Exponential relationships between NDVI and measured arthropod biomass. **(a)** Relationship for all vegetation communities (n = 130 quadrats; y = $0.008e^{8.835x}$; R^2 = 0.76). **(b)** Relationships for erect shrub tundra (n = 38 quadrats; y = $0.004e^{9.129x}$; R^2 = 0.89) and riparian shrub tundra (n = 20 quadrats; y = $0.009e^{10.16}$; R^2 = 0.95). **(c)** Relationships for moist tussock tundra (n = 53 quadrats; y = $0.004e^{10.37x}$; R^2 = 0.79) and dwarf deciduous shrub tundra (n = 19 quadrats: y = $0.001e^{11.95x}$; R^2 = 0.84). Abbreviations are as in Figure 3.2.
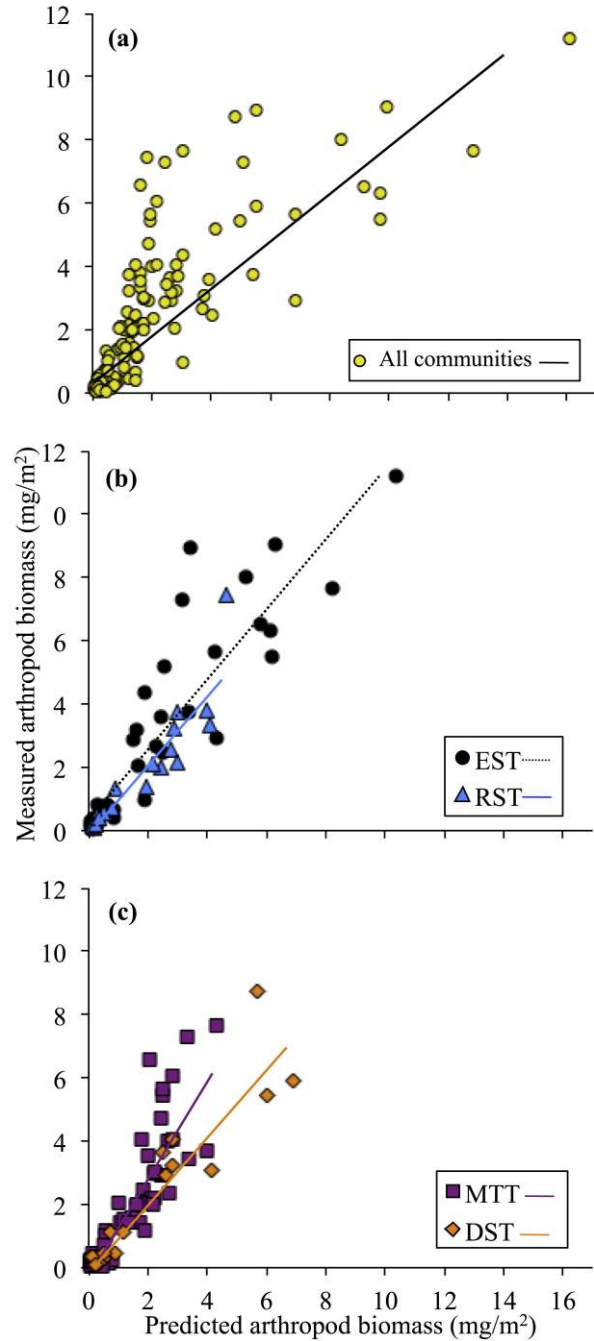
Figure 3.4. Linear relationships between predicted and measured arthropod biomass. Predicted biomass was determined using Equation 3.2 and parameters in Table 3.2. **(a)** Relationship for all vegetation communities (y = 0.75x + 0.87; R^2 = 0.63). **(b)** Relationships for erect shrub (y = 1.11x + 0.41; R^2 = 0.82) and riparian shrub tundra (y = 1.11x − 0.12; R^2 = 0.84). **(c)** Relationships for moist tussock (y = 1.54x − 0.16; R^2 = 0.74) and dwarf deciduous shrub tundra (y = 1.05x + 0.06; R^2 = 0.87). Abbreviations are as in Figure 3.2. Number of quadrats are as in Figure 3.3.

77

arthropod community (Danks 1992) – to emerge simultaneously, creating a larger and earlier peak in biomass (Hodkinson et al. 1996). Peak canopy arthropod biomass may also fluctuate depending on previous years' growing conditions: midges and mosquitoes may respectively lay one to two (Oliver & Roussel 1983), or up to five (Wood et al. 1979), batches of eggs in a single summer.

Similar to previous vegetation studies (Shaver et al. 2007, Street et al. 2007), our individual vegetation community specific models – developed from NDVI and canopy arthropod biomass measurements made within specific vegetation communities - increased model precision relative to our overall model. This is likely due to differences in species composition (Schaffers et al. 2008), plant biomass (Haddad et al. 2001), canopy structure (Price et al. 1980), leaf nutrient status (Bryant et al. 1983), and secondary metabolite content (Dudt & Shure 1994, Unsicker et al. 2009) among the tundra community types sampled – all of which are known to affect arthropod abundance and biomass.

For instance, we found that canopy arthropod biomass was greatest in our erect shrub tundra communities, where taller deciduous shrubs were dominant and the NDVI was high relative to our other vegetation communities. This is in line with other studies that suggest the abundance of erect shrubs has a direct and positive impact on arthropod abundance (Den Herder et al. 2004). This may be due to the higher leaf area (Johnson & Tieszen 1976, Shaver & Chapin 1991), fewer secondary metabolites (Richardson et al. 2002), higher nutritive value (Chapin et al. 1986), and greater digestibility (Chapin et al. 1986) of many deciduous shrubs relative to other plant functional groups. The effect of plant functional group on abundance and palatability of forage available to canopy-dwelling arthropods likely also explains why we found that canopy arthropod biomass was lowest at our moist tussock tundra communities. In our moist tussock tundra communities there is a high percent cover of evergreen species relative to our other vegetation communities, which, as opposed to the erect shrub tundra, likely resulted in lower leaf area (Shaver & Chapin 1991), lower nutritive value (Chapin et al. 1986), greater secondary metabolite content (Price et al. 1980, Aerts 1995), and lower digestibility (Chapin et al. 1986) of the canopy.

Non-consumptive resources may also explain the trend towards higher biomass in taller stature shrub-dominated canopies. For instance, the tundra canopy-dwelling arthropod community is, at times, dominated by midges and mosquitoes (Danks 1992) that likely find

78

refuge from unfavorable abiotic conditions in the increased structural complexity of tall erect shrubs (Boelman et al. 2011), which enables greater flight activity (Service 1980). These same structurally complex habitats may also provide arthropods with protection from vertebrate predators (Price et al. 1980), cannibalism (Langellotto 2002), and intra-guild predation (Finke & Denno 2002). Additionally, orb-weaving spiders and coccinellid beetles - also significant components of the canopy-dwelling arthropod biomass - depend on complex-structured canopies for increased web attachment sites (McNett & Rypstra 2000) and increased mobility during foraging (Langelletto & Denno 2004).

CONCLUSIONS

Catch-up in Leaf Development Minimizes Effect of Later Snowmelt

Since the majority of studies examining the effect of shrub-induced delays in snowmelt on the timing of leaf development use experimental manipulations of snow depth, our results presented in Chapter one are important as they provide valuable supporting evidence through observations made along a naturally occurring gradient of increasing deciduous shrub (*B. nana* and *S. pulchra*) stature. We found that, relative to low stature shrubs of the same species in graminoid-dominated tundra, taller stature shrubs in shrub-dominated tundra were surrounded by deeper snowpack and experienced later snowmelt and delayed budburst. However, contrary to our hypothesis, the delay in leaf development was short-lived, and as a result both short and tall stature deciduous shrubs reached full leaf expansion on approximately the same date. Further, despite delayed budburst, tall shrubs occasionally reached full leaf expansion *before* short shrubs, suggesting an accelerated rate of leaf development. We also found that taller shrubs had higher bud and emerging leaf nitrogen compared to shorter shrubs, suggesting that environmental conditions conducive to taller shrubs are correlated with higher soil nitrogen availability, which may have further accelerated leaf development.

Although the intermediate leaf development stages monitored in this study may provide detailed temporal insight into the timing of canopy development as it controls timing in canopy carbon uptake (Johnson & Tieszen 1976, Constable & Rawson 1980, Patankar et al. 2013), we acknowledge that the short-term nature, small spatial scale, and novelty of this study should be taken into consideration in interpreting our results. Because this study was conducted over two years and in a single location, caution should be taken in extrapolating our findings to determine the potential impacts of observed pan-arctic increases in deciduous shrub stature (Myers-Smith et al. 2011) on leaf and canopy development and canopy carbon gain. Further, the precise mechanisms involved in the accelerated leaf expansion of tall shrubs relative to short shrubs remains uncertain, and while our results are suggestive, we cannot conclusively state that increased nitrogen availability is the only mechanism driving accelerated leaf development. For these reasons, we believe high temporal resolution monitoring of leaf development, in both observational and experimental studies at more sites across the pan-Arctic, as well as a better

mechanistic understanding of early season leaf expansion and canopy development across different types of tundra will be important to understanding the future consequences of the greening Arctic.

Deciduous Shrubs Lengthen Peak Season and Increase Carbon Uptake

A number of studies have shown differences in canopy phenology among different tundra types (e.g. Jia et al. 2004, Narasimhan & Stow 2010), as well as differences between tundra vegetation communities in net carbon flux (e.g. Shaver et al. 2007, Street et al. 2007). However, to our knowledge the study presented in Chapter two is the first study to combine both in unmanipulated, naturally occurring deciduous shrub and evergreen/graminoid tundra, thereby contributing new insight into the effect of deciduous shrub cover on the length of the peak season (i.e. the period of maximum tundra greenness). The main findings in Chapter two suggest that in the Alaskan arctic tundra, greater deciduous shrub abundance causes a net lengthening of the period of peak tundra greenness by advancing the onset of peak leaf out. Although the peak season was longer, we did not find that greater deciduous shrub abundance extended the entire growing season (from the onset of greening to the end of senescence). This suggests that the observed lengthening of the entire growing season in the Arctic (Jeong et al. 2011, Zeng et al. 2011) may be due less to changes in vegetation cover and more to changes in air temperature (Hollister et al. 2005, Xu et al. 2013) and snow cover duration (Stow et al. 2004, Wipf 2010) associated with climate change. As a combined effect of higher leaf area and an extended period of peak greenness, we estimate that deciduous shrub tundra may take up nearly three times as much carbon during the peak season compared to evergreen/graminoid tundra. Our results suggests that, while additional carbon uptake of deciduous shrub tundra is due in part to greater leaf area (~ 29%), a significant portion is also due to the longer peak season (~ 71%) exhibited by deciduous shrub compared to evergreen/graminoid tundra. These findings provide valuable insight into how changes in vegetation community composition may be driving large-scale (regional and biome-level) satellite detected trends in arctic tundra phenology that will be useful for reducing uncertainties in modeling future changes in vegetation phenology (Steltzer & Post 2009) and associated carbon budgeting (Nemani et al. 2002, Jeong et al. 2012).

Potential to Estimate Arthropod Biomass From Air and Spaceborne Sensors

The normalized difference vegetation index (NDVI) has become a widely adopted tool for detecting and quantifying large scale spatial and temporal dynamics in tundra vegetation cover (Stow et al. 2004, Jia et al. 2009), productivity (Myneni et al. 1997, Beck & Goetz 2011), and phenology (Zhou et al. 2001, Zeng et al. 2011). To our knowledge, the study presented in Chapter three is the first to show that the NDVI has the potential to be similarly applied to consumer biomass in the arctic tundra. Because the study in Chapter three included a variety of vegetation communities that cover a large percentage of the arctic foothills region of Alaska, as well as the entire arctic tundra biome (Walker et al. 2005), the overall model developed therein, which incorporates data from four vegetation communities, may be applicable across vast expanses of arctic tundra. To employ the community specific models presented in Chapter three, researchers should either: (1) make field-based, near-surface measurements of the NDVI so that seasonal changes within vegetation communities are known, or; (2) couple high spatial resolution air- or space-borne NDVI datasets with spatially explicit *a priori* information on vegetation community cover when working at landscape or regional scales. Our findings suggest that, with this *a priori* information, high spatial resolution NDVI datasets acquired by satellite sensors (e.g. from Worldview, IKONOS, and Quickbird) may be able to quantify spatial and temporal dynamics in tundra canopy arthropod biomass at landscape and regional scales. This step was beyond the scope of the study presented in Chapter three because: (1) high temporal resolution NDVI products currently available have low spatial resolutions (e.g. such as acquired by MODIS with a minimum pixel size of 250 m), while; (2) high spatial resolution imagery (e.g. acquired by Worldview, IKONOS, and Quickbird) tends to be low in temporal resolution due to a combination of several limitations (e.g. high costs, cloud cover, and the need to task these sensors). In other words, spaceborne imagery does not currently provide both the high spatial and temporal resolution imagery that is needed for us to easily test our field-based relationships at larger scales.

Since our initial assessment was successful, we suggest that it is worth future investments to task airborne and spaceborne sensors with high spatial and temporal resolutions to acquire NDVI data in arctic regions so that the ecological community can work towards applying our current relationships at larger spatial scales. Given the strong relationship between the NDVI and canopy-dwelling arthropod biomass found in this study, future research examining relationships

between the NDVI and ground-dwelling arthropod biomass would be of great value. In addition, validation of our model at larger spatial scales is a critical next step. This is particularly valuable for vast and remote arctic tundra regions where shifts in seasonality and vegetation characteristics are likely to impact arthropod communities (Rich et al. 2013, Boelman et al. 2014). This, in turn, could have cascading effects throughout the food web (Seastedt & MacLean 1979, Post et al. 2009, Tulp & Schekkerman 2008, Ims & Henden 2012), and alter rates of nutrient cycling (Hodkinson et al. 2001, Hunter 2001).

REFERENCES

ACIA (Arctic Climate Impact Assessment) (2004) Impacts of a warming Arctic. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Adamczewski JZ, Gates CC, Soutar BM, Hudson RJ (1988) Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. *Canadian Journal of Zoology*, 66, 1986-1996.

Aerts R (1995) The advantages of being evergreen. *Trends in Ecology and Evolution*, 10, 402-407.

Aerts R, Cornelissen JHC, Dorrepaal E (2006) Plant performance in a warmer world: general response of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology*, 182, 65-77.

AMAP (Arctic Monitoring and Assessment Programme) (2012) SWIPA Overview Report. In: *Arctic climate issues 2011: Changes in Arctic snow, water, ice and permafrost*. pp 30-40. Oslo, Norway.

Angerbjörn A, Tannerfeld M, Erlinge S (1999) Predator-prey relationships: arctic foxes and lemmings. *Journal of Animal Ecology*, 68, 34-49.

Arft AM, Walker MD, Gurevitch J, Alatalo ZM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jonsdottir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenström A, Stenström M, Totland Ø, Turner O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69, 491-511.

Badhwar GD, Carnes JG, Austin WW (1982) Use of Landsat-derived temporal profiles for corn-soybean feature extraction and classification. *Remote Sensing of Environment*, 12, 57-79.

Baret F, Guyot G (1991) Potentials and limits of vegetation indices for LAI and APAR assessment. *Remote Sensing of Environment*, 35, 161–173.

Barichivich J, Briffa KR, Myneni RB, Osborn TJ, Melvin TM, Ciais P, Piao S, Tucker C (2013) Large-scale variations in the vegetation growing season and annual cycles of atmospheric CO_2 at high northern latitudes from 1950 to 2011. *Global Change Biology*, 19, 3167-3183.

Batzli GO (1993) Food selection by lemmings. In: *Biology of Lemmings*. Stenseth NC, Ims RA (eds). pp 281-301. Academic Press Ltd, London.

Batzli GO, Lesieutre C (1991) The influence of high quality food on habitat use by arctic microtine rodents. *Oikos*, 60, 299-306.

Batzli GO, Sobaski ST (1980) Distribution, abundance, and foraging pattern of ground squirrels near Atkasook, Alaska. *Arctic and Alpine Research*, 12, 501-510.

Beck PS, Goetz SJ (2011) Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters*, 6, 045501.

Belshe EF, Schuur EAG, Bolker BM (2013) Tundra ecosystems observed to be CO_2 sources due to differential amplification of the carbon cycle. *Ecology Letters*, 16, 1316-1324.

Billings WD, Mooney HA (1968) The ecology of arctic and alpine plants. *Biological Reviews*, 43, 481-529.

Bliss LC (1971) Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics*, 2, 405-438.

Blok D, Heijmans MMPD, Schaepman-Strub G, Kononov AV, Maximov TC, Berendse F (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology*, 16, 1296-1305.

Board JE, Maka V, Price R, Knight D, Baur ME (2007) Development of vegetation indices for identifying insect infestations in soybeans. *Agronomy Journal*, 99, 650-656.

Boelman NT, Gough L, McLaren JR, Greaves H (2011) Does NDVI reflect variation in the structural attributes associated with increasing shrub dominance in arctic tundra? *Environmental Research Letters*, 6, 035501.

Boelman NB, Gough L, Wingfield J, Goetz S, Asmus A, Chmura H, Krause J, Perez J, Sweet S, Guay K (2014) Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology*, doi: 10.1111/gcb.12761.

Boelman NT, Stieglitz M, Griffin KL, Shaver GR, Gamon JA (2005) Inter-annual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. *Oecologia*, 143, 588-597.

Boelman NT, Stieglitz M, Rueth HM, Sommerkorn M, Griffin KL, Shaver GR, Gamon JA (2003) Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia*, 135, 414-421.

Bolduc E, Casajus N, Legagneaux P, Mcinnon L, Gilchrist HG, Leung M, Morrison RIG, Reid D, Smith PA, Buddle CM, Bety J (2013) Terrestrial arthropod abundance and phenology in the Canadian Arctic: modeling resource availability for Arctic-nesting insectivorous birds. *The Canadian Entomologist*, 145, 155-170.

Bonfils CJW, Phillips TJ, Lawrence DM, Cameron-Smith P, Riley WJ, Subin ZM (2012) On the influence of shrub height and expansion on northern high latitude climate. *Environmental Research Letters*, 7, 015503.

Borner AP, Kielland K, Walker MD (2008) Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan arctic tundra. *Arctic, Antarctic, and Alpine Research*, 40, 27-38.

Bowden JJ, Buddle CM (2010) Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. *Arctic*, 63, 261–272.

Boxall PC, Lein MR (1982) Feeding ecology of snowy owls (*Nyctea scandiaca*) wintering in southern Alberta. *Arctic*, 35, 282-290.

Bret-Harte M, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman RF IV, Lippert SC, Laundre JA (2001) Developmental plasticity allows Betula nana to dominate tundra subjected to an altered environment. *Ecology*, 82, 18-32.

Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance or boreal plants in relation to vertebrate herbivory. *Oikos*, 40, 357-368.

Bunn AG, Goetz SJ, Kimball JS, Zhang K (2007) Northern high-latitude ecosystems respond to climate change. *Eos*, 88, 333-335.

Cahoon SM P, Sullivan PF, Shaver GR, Welker JM, Post E (2012) Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters*, 15, 1415-1422.

Callaghan TV, Björn LO, Chernov Y, Chapin T, Christensen TR, Huntley B, Ims RA, Johansson M, Jolly D, Jonasson S, Matveyeva N, Panikov N, Oechel W, Shaver G, Elster J, Jónsdóttir IS, Laine K, Taulavuori KT, Taulavuori E, Zöckler C (2004) Responses to projected changes in climate and UV-B at the species level. *AMBIO: A Journal of the Human Environment*, 33, 418-435.

Chandola V, Hui D, Gu L, Bhaduri B, Vatsavai RR (2010) Using time series segmentation for deriving vegetation phenology indices from MODIS NDVI data. In: *Proceedings of the 2010 IEEE International Conference on Data Mining Workshops*. pp 202-208.

Chapin FS III, Fetcher N, Kielland K, Everett KR, Linkins AE (1988) Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, 69, 693-702.

Chapin FS III, Johnson DA, McKendrik JD (1980) Seasonal movement of nutrients in plants of differing growth form in an Alaskan arctic tundra ecosystems: implications for herbivory. *Journal of Ecology*, 68, 189-209.

Chapin FS III, McKendrick JD, Johnson DA (1986) Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth forms: implications for herbivory. *Journal of Ecology*, 74, 707-731.

Chapin FS III, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climate change. *Ecology*, 77, 822-840.

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre, JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, 76, 694-711.

Chapin FS III, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in arctic summer warming. *Science*, 310, 657-660.

Chapin FS III, Van Cleve K, Tieszen LL (1975) Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. Arctic and Alpine Research, 7, 209-226.

Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*, 74, 829-836.

Cleveland WS, Loader CR (1996) Smoothing by local regression models. In: *Statistical theory and computational aspects of smoothing*. Hardle W, Schimek MG (eds). pp 10-49. Heidelberg, Physica-Verlag.

Collins WB, Smith TS *(*1991) Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*). *Arctic*, 44, 217–222.

Constable GA, Rawson HM (1980) Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. *Australian Journal of Plant Physiology*, 7, 89-100.

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graclia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Gwynn Jones D, Jonasson S, Chapin FS, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjörnsson B, Aert R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, 89, 984-994.

Coulson S, Hodkinson ID, Strathdee A, Bale JS, Block W, Worland MR, Webb NR (1992) Simulated climate change: the interaction between vegetation type and microhabitat temperatures at Ny Alesund, Svalbard. *Polar Biology*, 13, 67-70.

Coulson S, Hodkinson ID, Webb NR (2003) Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography* 26, 801-809.

Dale BW, Adams LG, Bowyer RT (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology*, 63, 644-652.

Dale JE (1988) The control of leaf expansion. *Annual Review of Plant Physiology*, 39, 267-295.

Danks HV (1992) Arctic insects as indicators of environmental change. *Arctic* 45:159-166.

Danks HV (1999) Life cycles in polar arthropods – flexible or programmed? *Journal of Entomology*, 96, 83-102.

Danks HV (2004) Seasonal adaptations in arctic insects. *Integrative and Comparative Biology*, 44, 85-94.

de Beurs KM, Henebry GM (2010) Spatio-temporal statistical methods for modeling land surface phenology. In: *Phenological research,* Hudson IL, Keatley MR (eds). pp 177-208. Springer, Dordrecht, Netherlands.

de Beurs KM, Townsend PA (2008) Estimating the effect of gyspsy moth defoliation using MODIS. *Remote Sensing of Environment*, 112, 3983-3990.

Delbart N, Picard G (2007) Modeling the date of leaf appearance in low-arctic tundra. *Global Change Biology*, 13, 2551-2562.

DeMarco J, Mack MC, Bret-Harte MS (2011) The effects of snow, soil microenvironment, and soil organic matter quality on N availability in three Alaskan arctic plant communities. *Ecosystems*, 14, 804-817.

Den Herder M, Virtanen R, Roininen H (2004) Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology*, 41, 870-879.

Doxon ED, Davis CA, Fuhlendorf SD (2011) Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling. *Journal of Field Ornithology*, 82, 60-67.

Dudt FJ, Shure DJ (1994) The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology*, 75, 86-98.

Dunne JA, Harte J, Taylor KJ, (2003) Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs*, 73, 69-86.

Dunne JA, Saleska SR, Fischer WL, Harte J, (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85, 904-916.

Eklundh L, Johansson T, Solberg S (2009) Mapping insect defoliation in Scots pine with MODIS time-series data. *Remote Sensing of Environment*, 113, 1566-1573.

Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Collier L S, Cooper EJ., Cornelissen JHC, Day TA, Fosaa AM, Gould WA, Grétarsdóttir J, Harte J, Hermanutz L, Hik DS, Hofgaard A, Jarrad F, Jónsdóttir IS, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Loewen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenström A, Tolvanen A, Totland O, Troxler T, Wahren CH, Webber PJ, Welker JM, Wookey PA (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, 15, 164-175.

Epstein HE, Chapin FS III, Walker MD, Starfield AM (2001) Analyzing the functional type concept in arctic plants using a dynamic vegetation model. *Oikos*, 95, 239-252.

Euskirchen ES, Carman TB, McGuire AD (2013) Changes in the structure and function of northern Alaskan ecosystems when considering variable leaf-out times across groupings of species in a dynamic vegetation model. *Global Change Biology*, 20, 963-98.

Euskirchen ES, McGuire AD, Kicklighter DW, Zhuang Q, Cleain JS, Dargaville RJ, Dye DG, Kimball JS, McDonald KC, Melillo JM, Romanovsky VE (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology*, 12, 731–750.

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, 78, 9-19.

Ferguson MAD, Gauthier L, Messier F (2001) Range shift and winter foraging ecology of a population of arctic tundra caribou. *Canadian Journal of Zoology*, 79, 746-758.

Field C, Mooney HA (1983) Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. *Oecologia*, 56, 348-355.

Finke DL, Denno RF (2002) Intraguild predation diminished in complex-structured vegetation: implication for prey suppression. *Ecology*, 83, 643-652.

Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia*, 149, 265–275.

Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, 16, 1542-1554.

Foster JL, Robinson DA, Hall DK, Estilow TW (2008) Spring snow melt timing and changes over Arctic lands. *Polar Geography*, 31, 145-157.

Fraser RH, Olthof I, Carrière M, Deschamps A, Pouliot D (2011) Detecting long-term changes to vegetation in northern Canada using the Landsat satellite image archive. *Environmental Research Letters*, 6, 045502.

Galindo C, Krebs CJ (1985) Habitat use by singing voles and tundra voles in the southern Yukon. *Oecologia*, 66, 430-436.

Gauthier G, Bêty J, Cadieux M-C, Legagneaux P, Doiron M, Chevallier C, Lai S, Tarroux A, Berteaux D (2013) Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian arctic tundra. *Philosophical Transactions of The Royal Society B: Biological Science*, 368, 20120482.

Giblin AE, Nadelhoffer GR, Shaver GR, Laundre JA, McKerrow AJ (1991) Biogeochemical diversity along riverside toposequence in arctic Alaska. *Ecological Monographs*, 61, 415-435.

Gilg O, Sittler B, Hanski I (2009) Climate change and cyclic predator-prey population dynamics in the high arctic. *Global Change Biology*, 15, 2634-2652.

Goetz SJ, Bunn AG, Fiske GJ, Houghton RA, Woodwell GM (2005) Satellite-observed trends across Boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Science U.S.A.*, 102, 13521-13525.

Goetz SJ, Epstein HE, Bhatt US, Jia GJ, Kaplan JO, Lischke H, Yu Q, Bunn A, Lloyd AH, Alcaraz-Segura D, Beck PSA, Comiso JC, Raynolds MK, Walker DA (2011) Recent changes in Arctic vegetation: satellite observations and simulation model predictions. In: *Eurasian Arctic land cover and land use in a changing climate.* Gutman G (eds). Ch. 2, pp 9-36. Springer, Netherlands.

Gould WA, Edlund S, Zoltai S, Raynolds M, Walker DA, Maier (2002) Canadian Arctic vegetation mapping. *International Journal of Remote Sensing*, 23, 4597-4609.

Graven HD, Keeling RF, Piper SC , Patra PK, Stephens BB, Wofsy SC, Welp LR, Sweeney C, Tans PP, Kelley JJ, Daube, BC, Kort EA, Santoni GW, Bent JD (2013) Enhanced seasonal exchange of CO_2 by northern ecosystems wince 1960. *Science*, 341, 1085-1089.

Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist*, 158, 17-35.

Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist*, 186, 890-899.

Hanson HC (1953) Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. *Ecology*, 34, 111-140.

Hartley AE, Neill C, Melillo JM, Crabtree R, Bowles F (1999) Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. *Oikos*, 86, 331-343.

Heskel M, Anderson OR, Atkin OK, Turnbull MH, Griffin K (2012) Leaf and cell-level carbon cycling responses to a nitrogen and phosphorous gradient in two arctic tundra species. *American Journal of Botany*, 99, 1702-1714.

Heskel MA, Betterman D, Atkin OK, Turnbull MH, Griffin KL (2013) Seasonality of foliar respiration in two dominant plant species from the arctic tundra: response to long-term warming and short-term temperature variability. *Functional Plant Biology*, 41, 287-300.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyurgerov MB, Fasti CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, Yoshikawa K (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climate Change*, 72, 251-298.

Hobbie SE, Chapin FS III (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. *Ecology*, 79, 1526-1544.

Hodkinson ID, Coulson SJ, Harrison J, Webb NR (2001) What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic-some counter-intuitive ideas on community assembly. *Oikos,* 95, 349-352.

Hodkinson ID, Coulson SJ, Webb NR, Block W, Strathdee AT, Bale JS, Worland MR (1996) Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos* 75, 241-248.

Hodkinson ID, Webb NR, Bale JS, Block W, Coulson SJ, Strathdee AT (1998) Global change and arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. *Arctic and Alpine Research*, 30, 306-313.

Hollister RD, Webber PJ, Bay C (2005) Plant response to temperature in northern Alaska: implications for predicting vegetation change. *Ecology*, 86, 1562-1570.

Hope AS, Pence KR, Stow DA (2004) NDVI from low altitude aircraft and composited NOAA AVHRR data for scaling Arctic ecosystem fluxes. *International Journal of Remote Sensing*, 25, 4237-4250.

Høye TT, Forchhammer MC (2008) Phenology of high-arctic arthropods: effects of climate on spatial, seasonal, and inter-annual variation. *Advances in Ecological Research*, 40, 299-324.

Høye TT, Forchhammer MC (2008) The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations. *BMC Ecology*, 8, 8.

Huemmrich KF, Black TA, Jarvis PG, McCaughty JH, Hall FG (1999) High temporal resolution NDVI phenology from micrometeorological radiation sensors. *Journal of Geophysical Research*, 104, 27,935-27,944.

Hunter MD (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology*, 3, 77-84.

Hurlbert AH, Haskell JP (2003) The effect of energy and seasonality on avian species richness and community composition. *The American Naturalist*, 161, 83–97.

Ims RA, Henden JA (2012) Collapse of an arctic bird community resulting from ungulate-induced loss of erect shrubs. *Biological Conservation*, 149, 2-5.

IPCC - Intergovernmental Panel on Climate Change (2007) In: *Fourth Assessment Report Climate Change 2007: Working Group I: The Physical Science Basis*. Solomon SD, Qin M, Manning Z, Chen M, Marquis KB, Averyt M, Tignor, Miller HL (eds). Cambridge University Press, Cambridge, New York, NY, USA.

IPCC - Intergovernmental Panel on Climate Change (2013) In: *Fifth Assessment Report Climate Change 2013: Working Group I: The Physical Science Basis.* Stocker TF, Qin D, Plattner G-K, Tignor MMB, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds). Cambridge University Press, New York, NY, USA.

Jacoby MG (2000) Loess: a nonparametric, graphical tool for depicting relationships between variables. *Electoral Studies*, 19, 577-613.

Jeong S J, Medvigy D, Shevliakova E, and Malyshev S (2012) Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research*, 117, G01030.

Jeong SJ, Ho CH, Gim HJ, Brown ME (2011) Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. *Global Change Biology*, 17, 2385-2399.

Jepsen JU, Hagen SB, Høgda KA, Ims RA, Karlsen SR, Tømmervik H, Yoccoz NG (2009) Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Remote Sensing of Environment*, 113, 1939-1947.

Ji R, Xie BY, Li DM, Li Z, Zhang X (2004) Use of MODIS data to monitor the oriental migratory locust plague. *Agriculture, Ecosystems and Environment*, 104, 615-620.

Jia GJ, Epstein HE, Walker DA (2003) Greening of arctic Alaska, 1981-2001. *Geophysical Research Letters*, 30, 2067.

Jia GJ, Epstein HE, and Walker DA (2009) Vegetation greening in the Canadian arctic related to decadal warming. *Journal of Environmental Monitoring*, 11, 2231-2238.

Jia GJ, Epstein HE, Walker DA (2004) Controls over intra-seasonal dynamics of AVHRR NDVI for the arctic tundra in northern Alaska. *International Journal of Remote Sensing*, 25,1547-1564.

Jia G. J., Epstein H. E., and Walker D. A. 2006. Spatial heterogeneity of tundra vegetation response to recent temperature changes. *Global Change Biology,* 12, 42-55.

Johnson DA, Tieszen LL (1976) Aboveground biomass, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. *Oecologia*, 24, 159-173.

Johnson LC, Shaver GR, Cades DH, Rastetter E, Nadelhoffer K, Giblin A, Laundre J, Stanley A (2000) Plant carbon-nutrient interactions control CO_2 exchange in Alaskan wet-sedge tundra ecosystems. *Ecology*, 81, 453-469.

Joly K, Jandt RR, Klein DR (2009) Decrease of lichens in arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Research, 28, 433-442.

Joly K, Jandt RR, Meyers CR, Cole MJ (2007) Changes in vegetative cover on Western Arctic Herd winter ranges from 1981 to 2005: potential effects of grazing and climate change. *Rangifer Special Issue,* 17, 199.

Karels TJ, Byrom AE, Boonstra R, Krebs CJ (2000) The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. *Journal of Animal Ecology*, 69, 235-247.

Kikuzawa K (1995) Leaf phenology as an optimal strategy for carbon gain in plants. Canadian *Journal of Botany*, 73, 158-163.

Klosterman ST, Hufkens K, Gray JM, Melaas E, Sonnentag O, Lavine I, Mitchell L, Norman R, Friedl MA, Richardson AD (2014) Evaluating remote sensing of deciduous forest phenology at multiple spatial scales using PhenoCam imagery. *Biogeosciences Discussions*, 11, 2305-2342.

Kogan FN (1995) Droughts of the late 1980's in the United States as derived from NOAA polar-orbiting satellite data. *Bulletin of the American Meteorological Society*, 76, 655-668.

Körner C (1989) The nutritional status of plants from high altitudes. A world-wide comparison. *Oecologia,* 81, 379-391.

Langellotto GA (2002) Aggregation of invertebrate predators in complex structured habitats: role of altered cannibalism, intraguild predation, prey availability, and microclimate. PhD, *University of Maryland* (Entomology), College Park, MD.

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, 139, 1-10.

Liston GE, McFadden JP, Sturm M, Pielke RA Sr. (2002) Modeled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change Biology*, 8, 17-32.

Loranty MM, Goetz SJ, Rastetter EB, Rocha AV, Shaver GR, Humphreys ER, Lafleur PM (2010) Scaling an instantaneous model of tundra NEE to the Arctic landscape. *Ecosystems*, 14, 76-93.

Markon CJ, Fleming MJ, Binnian EF (1995) Characteristics of vegetation phenology over the Alaskan landscape using AVHRR time-series data. *Polar Record*, 31, 179–190.

Masters GJ, Brown VK, Clarke IP, Whittaker JB, Hollier JA (1998) Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology*, 23, 45-52.

Mbufong HN, Lund M, Aurela M *et al.* (2014) Assessing the spatial variability in peak season CO_2 exchange characteristics across the Arctic tundra using a light response curve parameterization. *Biogeosciences Discussions*, 11, 6419-6460.

McBean G, Alekseev G, Chen D, Førland E, Fyfe J, Groisma PY, King R, Melling H, Vose R, Whitefield PH (2006) Arctic Climate Impact Assessment – *Scientific Report: Arctic Climate: Past and Present*. Symon C, Arris L, Heal B (eds). pp 22-55. Cambridge University Press: Cambridge, UK.

McDonald KC, Kimball JS, Njoku E, Zimmerman R, Zhao M (2004) Variability in springtime thaw in the terrestrial high latitudes: monitoring a major control on the biospheric assimilation of atmospheric CO_2 with spaceborne microwave remote sensing. *Earth Interactions*, 8, 1-23.

McNamara JP, Kane DL, Hinzman LD (1999) An analysis of an arctic channel network using a digital elevation model. *Geomorphology*, 29, 339-353.

McNett BJ, Rypstra AL (2000) Habitat selection in a large orb-weaving spider: vegetation complexity determines site selection and distribution. *Ecological Entomology*, 25, 423-432.

Molau U, Mølgaard P (eds) (1996) *International tundra experiment (ITEX) manual: second edition*. Danish Polar Center, Denmark.

Muff P, Kropf C, Frick H, Nentwig W, Schmidt-Entling MH (2009) Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline. *Insect Conservation and Diversity*, 2, 36–44.

Muggeo VMR (2003) Estimating regression models with unknown break-points. *Statistics in Medicine*, 22, 3055-3071.

Muggeo VMR (2008) segmented: an R Package to Fit Regression Models with Broken-Line Relationships. R News, 8/1, 20-25. URL http://cran.r-project.org/doc/Rnews/. Accessed on 6 August 2014.

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier L S, Weijers S, Rozema J, Rayback S A, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard C B, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik D S (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6, 045509.

Myers-Smith IH, Hik DS (2013) Shrub canopies influence soil temperature but not nutrient dynamics: an experimental test of tundra snow-shrub interactions. *Ecology and Evolution*, 3, 3683-3700.

Myneni RB, Keeling D, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981-1991. *Nature*, 386, 698-702.

Naito AT, Cairns DM (2011) Relationships between arctic shrub dynamics and topographically derived hydrologic characteristics. *Environmental Research Letters*, 6, 045506.

Narasimhan R and Stow D (2010) Daily MODIS products for analyzing early season vegetation dynamics across the North Slope of Alaska. *Remote Sensing of Environment*, 114, 1251-1262.

Nemani R, White M, Thornton P, Nishida K, Reddy S, Jenkins J, Running S (2002) Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. *Geophysical Research Letters*, 29, 1468-1471.

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560-1563.

Nielsen UN, Wall DH (2013) The future of soil invertebrate communities in polar regions: different climate change responses in the Arctic and Antarctic. *Ecology Letters*, 16, 409-419.

Noyes JS (1989) A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, 23, 285-298.

Oberbauer SF, Starr G, Pop EW (1998) Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska. *Journal of Geophysical Research*, 103, 29,075-29,082.

Oechel WC (1989) Nutrient and water flux in a small arctic watershed: an overview. *Holarctic Ecology*, 12, 229-237.

Oksanen T, Oksanen L, Dahlgren J, Olofsson J (2008) Arctic lemmings, *Lemmus* spp. And *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. *Evolutionary Ecology Research*, 10, 415-434.

Oliver DR, Roussel ME (1983) *The insects and arachnids of Canada. Part 11. The genera of larval midges of Canada. Diptera: Chironomidae*. Canadian Government Publishing Centre.

Olthof I, Pouliot D, Latifovic R, Chen W (2008) Recent (1986-2006) vegetation-specific NDVI trends in northern Canada from satellite data. *Arctic*, 61, 381-394.

Overland J, Key J, Kim BM, Kim SJ, Liu Y, Walsh J, Wang M, Bhatt U (2012) Air temperature, atmospheric circulation and clouds. In: *Arctic Report Card: Update for 2012*. URL http://www.arctic.noaa.gov/report12/temperature_clouds.html. Accessed on 12 January 2014.

Patankar R, Mortazavi B, Oberbauer SF, Starr G (2013) Diurnal patterns of gas-exchange and metabolic pools in tundra plants during three phases of the arctic growing season. *Ecology and Evolution*, 3, 375-388.

Pau S, Wolkovich EM, Cook BI, Davies TJ, Kraft NJB, Bolmgren K, Betancourt JL, Cleland EE (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, 17, 3633-3643.

Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, Goetz SJ (2013) Shifts in arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3, 673-677.

Person SJ (1975) Digestibility of indigenous plants utilized by *Rangifer tarandus*. (Ph.D. thesis), University of Alaska, Fairbanks.

Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, 20, 503-510.

Piao SL, Friedlingstein P, Ciais P, Viovy N, Demarty J (2007) Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles*, 21, GB3018.

Pop EW, Oberbauer SF, Starr G (2000) Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana*. *Oceologia*, 124, 176-184.

Post E, Forchhammer MC, Bret-Harte S, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT, Ims RA, Jeppesen E, Klein D, Madesn J, McGuire AD, Rysgaard S, Schindler DE, Stirling I, Tamstorf MP, Tyler NJC, van der Wal R, Welker J, Wookey PA, Schmidt NM, Aastrup P (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325, 1355-1358.

Post E, Høye TT (2013) Advancing the long view of ecological change in tundra systems. *Philosophical Transactions of The Royal Society B: Biological Science*, 368, 20120477.

Post E, Pedersen C, Wilmers CC, Forchhammer MC (2008) Warming, plant phenology and the spatial dimensions of trophic mismatch for large herbivores. *Proceedings of the Royal Society: Biological Sciences*, 275, 2005-213.

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology, Evolution, and Systematics*, 11, 41-65.

R Core Team (2011-2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Versions 2.12.2 through 3.1.1. URL http://www.R-project.org/.

Radin, JW, Boyer JS (1982) Control of leaf expansion by nitrogen nutrition in sunflower plants. *Plant Physiology*, 69, 771-775.

Rastetter EB, King AW, Cosby BJ, Hornberger GM, O'Neill RV, Hobbie JE (1992) Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications*, 2, 55-70.

Rastetter EB, Williams M, Griffin KL, Kwiatkowski BL, Tomasky G, Potosnak MJ, Stoy PC, Shaver GR, Stieglitz M, Hobbie JE, Kling GW (2010) Processing arctic eddy-flux data using simple carbon-exchange model embedded in the ensemble Kalman filter. *Ecological Applications*, 20, 1285-1301.

Raynolds MK, Walker DA, Maier HA (2006) NDVI patterns and phytomass distribution in the circumpolar Arctic. *Remote Sensing of Environment*, 102, 271-281.

Reich PB, Ellsworth DS, Walters MB (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology*, 12, 948-958.

Rich ME, Gough L, Boelman NT (2013) Arctic arthropod assemblages in habitat of differing shrub dominance. *Ecography*, 36, 1-10.

Richardson AD, Hollinger DY, Dail DB, Lee JT, Munger JW, O'Keefe J (2009) Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiology*, 29, 321-331.

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156-173.

Richardson SJ, Press MC, Parsons AN, Hartley SE (2002) How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year sturdy from a sub-Arctic heath. *Journal of Ecology*, 90, 544-556.

Robel RJ, Press BM, Henning BL, Johnson KW, Blocker HD, Kemp KE (1995) Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology*, 66, 44-53.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57-60.

Rouse JW, Haas RH, Schell JA, Deering DW (1974) Monitoring vegetation systems in the Great Plains with ERTS. In: *Proceedings of the Third Earth Resources Technology Satellite-1 Symposium*. Greenbelt, MD: NASA, pp 301–317.

Schaffers AP, Raemakers IP, Sýkora KV, ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. *Ecology*, 89, 782-794.

Schimel JP, Bilbrough C, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two arctic tundra communities. *Soil Biology and Biochemistry*, 36, 217-227.

Seastedt TR, MacLean SF (1979) Territory size and composition in relation to resource abundance in Lapland longspurs breeding in Arctic Alaska. *The Auk*, 96, 131-142.

Serreze MC, Francis JA (2006) The arctic on the fast track of change. *Weather*, 61, 65-69.

Serreze MC, Walsh JE, Chapin FS, Osterkamp T, Dyurgero M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Climate Change*, 46, 159-207.

Service MW (1980) Effects of wind on the behaviour and distribution of mosquitoes and blackflies. *International Journal of Biometeorology*, 24, 347-353.

Shaver GR, Bret-Harte MS, Jones MH, Johnstone J, Gough L, Laundre J, Chapin FS III (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, 82, 3163–3181.

Shaver GR, Chapin FS III (1991) Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, 61, 1-31.

Shaver GR, Chapin FS III, Gartner BL (1986) Factors limiting growth and biomass accumulation of Eriophrum vaginatum L. in Alaskan tussock tundra. *Journal of Ecology*, 74, 257-278.

Shaver GR, Laundre JA, Giblin AE, Nadelhoffer KJ (1996) Changes in vegetation biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska. *Arctic and Alpine Research*, 28, 363–379.

Shaver GR, Rastetter EB, Salmon V, Street LE, van de Weg MJ, Rocha A, van Wijk MT, Williams M (2013) Pan-Arctic modeling of net ecosystem exchange of CO_2. *Philosophical Transactions of the Royal Society B: Biological Science*, 368, 20120485.

Shaver GR, Street LE, Rastetter EB, van Wijk MT, Williams M (2007) Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, 95, 802-817.

Shindell D, Faluvegi G (2009) Climate response to regional radiative forcing during the twentieth century. *Nature Geoscience*, 2, 294-300.

Shory R (2014) rickshory/NDVI-modules: for processing logged spectral data into NDVI; x-platform using wxPython. On: GitHub, Inc. URL http://github.com/rickshory/NDVI-modules. Accessed on 28 October 2014.

Shory R, Steltzer H, Chong G, (in prep - 2014) Mantis manual: instrumentation, data management, and normalized difference vegetation index (NDVI) calibration. In preparation for submission to *Prometheus*. Contacts: Heidi Steltzer - Steltzer_H@fortlewis.edu, Rick Shory - rick.shory@colostate.edu.

Southwood TR (1978) Ecological methods: with particular reference to the study of insect populations. Second Edition. Chapman and Hall, New York.

Sørensen LL, Coddington JA, Scharff N (2002) Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afromontane forest. *Environmental Entomology*, 31, 319-330.

Spafford RD, Lortie CJ (2013) Sweeping beauty: is grassland arthropod community composistion effectively estimated by sweep netting? *Ecology and Evolution*, 3, 3347-3358.

Starr G, Oberbauer SF (2003) Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology*, 84, 1415-1420.

Starr G, Oberbauer SF, Pop EW (2000) Effects of lengthened growing season and soil warming on the phenology and physiology of Polygonum bistorta. *Global Change Biology*, 6, 357-369.

Steltzer H, Post E (2009) Seasons and life cycles. *Science*, 324, 886- 887.

Steltzer H, Welker JM (2006) Modeling the effects of photosynthetic vegetation properties on the NDVI-LAI relationship. *Ecology*, 87, 2765-2772.

Storeheier PV, Mathiesen SD, Tyler NJC, Olsen MA (2002) Nutritive value of terricolous lichens for reindeer in winter. *Lichenologist*, 34, 247-257.

Stow DA, Hope A, McGuire D, Verbyla D, Gamon J, Huemmrich F, Houston S, Racince C, Sturm M, Tape K, Hinzman L, Yoshikawa K, Tweedie C, Noyle B, Silapaswan C, Douglas D, Griffith B, Jia G, Epstein H, Walker D, Daeschner S, Petersen A, Zhou L, Myneni R (2004) Remote sensing of vegetation and land-cover change in arctic tundra ecosystems. *Remote Sensing of Environmen*t, 89, 281-308.

Street LE, Shaver GR, Williams M, van Wilk MT (2007) What is the relationship between changes in leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems? *Journal of Ecology*, 95, 139-50.

Sturm M, Douglas T, Racine C, Liston GE (2005a) Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research*, 110, G01004.

Sturm M, McFadden JP, Liston GE, Chapin FS, Racine CH, Holmgren J (2001a) Snow-shrub interactions in arctic tundra: a hypothesis with climate implications. *Journal of Climate*, 14, 336-344.

Sturm M, Racine CR, Tape K (2001b) Increasing shrub abundance in the Arctic. *Nature*, 411, 546–547.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005b) Winter biological processes could help convert arctic tundra to shrubland. *BioScience*, 55, 17-26.

Sun J, Wang X, Chen A, Ma Y, Cui M, Piao S (2011) NDVI indicated characteristics of vegetation cover change in China's metropolises over the last three decades. *Environmental monitoring and assessment*, 179, 1-14.

Tagesson T, Mastepanov M, Tamstorf MP, Eklundh L, Schubert P, Ekberg A, Sigsgaard C, Christensen T R, Ström L (2012) High-resolution satellite data reveal an increase in peak growing season gross primary production in a high-arctic we tundra ecosystem. 1992-2008. *International Journal of Applied Earth Observation and Geoinformation*, 18, 407-416.

Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in arctic Alaska. *Ecosystems*, 15, 711-724.

Tape KD, Sturm M, Racine C (2006) The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12, 686-702.

TFS (Toolik Field Station) (2012) and the Institute of Arctic Biology (IAB), GIS and Remote Sensing, the University of Alaska, Fairbanks. URL http://toolik.alaska.edu/gis/index.php. Accessed in December 2013.

Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, 84, 2034-2041.

Torp M, Olofsson J, Witzell J, Baxter R (2010) Snow-induced changes in dwarf birch chemistry increases moth larval growth rate and level of herbivory. *Polar Biology,* 33, 693-702.

Tucker CJ, Slayback DA, Pinzon JE, Los SO, Myneni RB, Taylor MG (2001) Higher northern latitude NDVI and growing season trends from 1982 to 1999. *International Journal of Biometeorology,* 45, 184-190.

Tulp I, Schekkerman H (2008) Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic*, 61, 48-60.

Ueyama M, Iwata H, Harazono Y, Euskirchen ES, Oechel WC, Zona D (2013) Growing season and spatial variations of carbon fluxes of Arctic and boreal ecosystems in Alaska (USA). *Ecological Applications*, 23, 1798-1816.

Unsicker SB, Kunert G, Gershenzon J (2009) Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. *Current Opinion in Plant Biology*, 12, 479-485.

Usher MB, Callaghan TV, Gilchrist G, Heal B, Juday GP, Loeng H, Muir MAK, Prestrud P (International Arctic Science Committee) (2010) Arctic environments north of the treeline. In: *Arctic Climate Impact Assessment*, Sec. 10.2.3.

van Leeuwen WJ, Orr BJ, Marsh SE, Herrmann SM (2006) Multi-sensor NDVI data continuity: uncertainties and implications for vegetation monitoring applications. *Remote Sensing of Environment*, 100, 67-81.

van Wijk MT, Williams M (2005) Optical instruments for measuring leaf area index in low vegetation: application in Arctic ecosystems. *Ecological Applications*, 15, 1462-1470.

van Wijk MT, Williams M, Laundre JA, Shaver GR (2003) Interannual variability of plant phenology in tussock tundra: modeling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biology*, 9, 743-758.

van Wijk MT, Williams M, Shaver GR (2005) Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, 142, 421-427.

Verbyla D (2008) The greening and browning of Alaska based on 1982-2003 satellite data. *Global Ecology and Biogeography*, 17, 547-555.

Vierling LA, Deering DW, Eck TF (1997) Differences in arctic tundra vegetation type and phenology as seen using bidirectional radiometry in the early growing season. *Remote Sensing of Environment*, 60, 71-82.

Vieth E (1989) Fitting piecewise linear regression functions to biological responses. *Journal of Applied Physiology*, 67, 390-396.

Vogelmann JE (1990) Comparison between two vegetation indices for measuring different types of forest damage in the north-eastern United States. *Remote Sensing*, 11, 2281-2297.

Vos J, Biemond H (1992) Effects of nitrogen on the development and growth of the potato plant. 1. Leaf appearance, expansion growth, life spans of leaves and stem branching. *Annals of Botany*, 70, 27-35.

Vourlitis GL, Oechel WC, Hope A, Stow D, Boynton B, Verfaillie J Jr., Zulueta R, Hastings SJ (2000) Physiological models for scaling plot measurements of CO_2 flux across an arctic tundra landscape. *Ecological Applications*, 10, 60-72.

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, 6, 19-34.

Walker DA, Maier HA (2008) Vegetation in the vicinity of the Toolik Field Station, Alaska. Biological Papers of the University of Alaska, No. 28, Institute of Arctic Biology, University of Alaska, Fairbanks.

Walker DA, Raynolds MK, Daniels FJ, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumpolar Arctic vegetation map (CAVM). *Journal of Vegetation Science*, 16, 267-282.

Walker DA, Walker MD (1996) Terrain and vegetation of the Imnavait Creek Watershed. In: *Landscape function and disturbance in arctic tundra, Ecological Studies.* Reynolds JF, Tenhunen JD (eds.), vol 120, pp 73–108. Springer, Berlin Heidelberg, New York.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnússon B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland Ø, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community response to experimental warming across the tundra biome. *Proceedings of the National Academy of Science U.S.A.*, 103, 1342-1346.

Walker MD, Walker DA, Auerbach NA (1994) Plant communities of a tussock landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science*, 5, 843– 866.

Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, Fahnestock JT, Jones MH, Losleben M, Parsons AN, Seastedt TR, Turner PL (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, 13, 2315-2330.

Walsh NE, McCabe TR, Welker JM, Parsons AN (1997) Experimental manipulations of snow-depth: effects on nutrient content of caribou forage. *Global Change Biology*, 3, 158-164.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature,* 416, 389-395.

Wang X, Key JR (2003) Recent trends in Arctic surface, cloud, and radiation properties from space. *Science*, 299, 1725-1728.

Wang X, Piao S, Ciais P, Li J, Friedlingstein P, Koven C, Chen A (2011) Spring temperature change and its implication in the change of vegetation growth in North America from 1982 to 2006. *Proceedings of the National Academy of Sciences*, 108, 1240-1245.

Welker JM, Fahenstock JT, Sullivan PF, Chimner RA (2005) Leaf mineral nutrition of arctic plants in response to warming and deeper snow in northern Alaska. *Oikos*, 109, 167-177.

White MA, Brunsell N, Schwartz MD (2003) Vegetation phenology in global change studies. In: *Phenology: An integrative environmental science*. Schwartz MD (ed.), pp 453-466. Kluwer Academic Publishers, New York, NY.

White MA, de Beurs KM, Didan K, Inouye DW, Richardson AD, Jensen OP, O'Keefe J, Zhange G, Nemani RR, van Leeuwen WJD, Brown JF, de Wit A, Schaepman M, Lin X, Dettinger M, Bailey AS, Kimball J, Schwartz MD, Baldocchi DD, Lee JT, Lauenroth WK (2009) Intercomaprison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982-2006. *Global Change Biology*, 15, 2335-2359.

White MA, Thornton PE, Running SW (1997) A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles*, 11, 217-234.

White RG, Trudell J (1980) Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. *Arctic and Alpine Research*, 12, 511-529.

Williams M, Rastetter EB (1999) Vegetation characteristics and primary productivity along an arctic transect: implications for scaling up. *Journal of Ecology*, 87, 885–898.

Williamson FSL (1957) Ecological distribution of birds in the Napaskiak area of the Kuskokwim River delta, Alaska. *The Condor*, 59, 317-338.

Wingfield JC, Owen-Ashley N, Benowitz-Fredericks ZM, Lynn SE, Hahn TP, Wada H, Breuner C, Meddle SL, Romero M (2004) Arctic spring: the arrival biology of migrant birds. *Acta Zoologica Sinica*, 50, 948-960.

Wipf S (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, 207, 53-66.

Wipf S, Rixen C (2010) A review of snow manipulation experiments in arctic and alpine tundra ecosystems. *Polar Research*, 29, 95-109.

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climate Change*, 94, 105-121.

Wood DM, Dang PT, Ellis RA (1979) *The insects and arachnids of Canada. Part 6. The mosquitoes of Canada. Diptera: Culicidae.* Canadian Publishing Centre.

Wookey PA, Aerts R, Bardgett RD, Baptist F, Bråthen KA, Cornelissen JHC, Gough L, Hartley IP, Hopkins DW, Lavorel S, Shaver GR (2009) Ecosystem feedbacks and cascade processes: understanding their role in the response of arctic and alpine ecosystems to environmental change. *Global Change Biology*, 15, 1153-1172.

Wookey PA, Parsons AN, Welker JM, Potter JA, Callghan TV, Lee JA, Press MC (1993) Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos*, 67, 490-502.

Xu L, Myneni RB, Chapin FS III, Callaghan TV, Pinzon JE, Tucker CJ, Zhu Z, Bi J, Ciais P, Tømmervik H, Euschirchen ES, Forbes BC, Piao SL, Anderson BT, Ganguly S, Nemani RR, Goetz SJ, Beck PSA, Bunn AG, Cao C, Stroeve JC (2013) Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, 3, 581-586.

Zeng H, Jia G, Epstein H (2011) Recent changes in phenology over the northern high latitudes detected from multi-satellite data. *Environmental Research Letters*, 6, 045508.

Zha Y, Gao J, Ni S, Shen N (2005) Temporal filtering of successive MODIS data in monitoring a locust outbreak. *International Journal of Remote Sensing*, 26, 5665-5674.

Zhang G, Zhang Y, Dong J, Xiao X (2013) Green-up dates in the Tibetan Plateau have continuously advanced from 1982 to 2011. *Proceedings of the National Academy of Sciences*, 110, 4309-4314.

Zhang X, Friedl MA, Schaaf CB, Strahler AH, Hodges JCF, Gao F, Reed BC, Huete A (2003) Monitoring vegetation phenology using MODIS. *Remote Sensing Environment*, 84, 471-475.

Zhou LM, Tucker CJ, Kaufmann RK, Slayback D, Shabanov NV, Myneni RB (2001) Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981-1999. *Journal of Geophysical Research*, 106, 20,069-20,083.