Structural comparison of arctic plant communities across the landscape and with experimental warming in Northern Alaska.

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DEDICATION

Dedicated to my husband Adam,

Without whose constant love and encouragement this project would never have been accomplished.

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ABSTRACT

Understanding vegetation change is central to forecasting the impacts of climate change. Percent cover, determined from a point frame method, is commonly used to monitor vegetation change. Cover is influenced by canopy structure which may change with the size (growth) or number (density) of individual plants. The overarching objective of this project was to document the relationship between vegetation cover and traits representing plant growth and density and determine if these relationships changed with warming. We used regressions and analysis of covariance to detect which of several traits was most strongly related to cover in vegetation at a wet and a dry site as well as across a grid covering a range of community types in Northern Alaska. The wet and dry sites also included a warming experiment. We found that graminoid cover was positively correlated with proxies for plant growth (canopy height and leaf length) at the wet and dry sites but was negatively correlated with density across the grid. This signified an inverse relationship between growth and density. Shrub cover was not correlated with any of the selected traits at the wet site, but was correlated with inflorescence length and canopy height at the dry site. Across the grid evergreen shrub cover correlated with density while deciduous shrub cover correlated with canopy height. Experimental warming significantly altered the relationships between vegetation traits and cover, particularly at the dry site, resulting in varying relationships between cover and traits in control versus warmed plots. Furthermore, correlations between cover and vegetation traits for growth forms were not always consistent with those of their constituent species. These results demonstrate that cover is related to canopy structure which differs across species and community types, and may change with warming. Continued research at the landscape level is needed to provide a better understanding of the implications of observed changes in plant cover in response to climate warming.

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CHAPTER I: INTRODUCTION

Overview of Climate Change Impacts

Climate change and its effects on ecosystems and biological processes are a rising concern within the scientific community and have been since the mid-twentieth century. The most striking responses to warming have been detected in polar regions, as these areas have experienced among the highest increases in average annual temperatures (Figure 1) (Cubasch et al. 2013). The tundra biome is considered to be more vulnerable to changing global climate patterns because of its short growing season, colder temperatures, and limited nutrient supply (Callaghan et al. 2005; Anisimov et al. 2007). Monitoring the response of arctic ecosystems to climate change is especially critical for understanding long-term consequences on resource availability and cycling, as well as community structure. Overall warming trends across arctic regions have been observed, although recent decreases in temperature have also been recorded in some locations (Hinzman et al. 2005). Research shows an overall increasing trend in precipitation in the Arctic, with some local variation (Curtis et al. 1998). Observed effects of warming in the Arctic include thawing of sea ice and permafrost, changing precipitation and surface hydrology patterns, a longer growing season associated with earlier snowmelt, decreased snow cover, and altered distributions of plants and animals (Curtis et al. 1998; Hinkel et al. 2001; Callaghan et al. 2005; Hinzman et al. 2005; Hill and Henry 2011).

Warming trends over the last century have undoubtedly contributed to the reduced mass of glaciers and sea ice, particularly in North America and Russia, which is coupled with a rise in sea levels over this period (Hinzman et al. 2005; Cubasch et al. 2013). Examples of this are a 30% reduction in total glacial length of the Grand Union glacier on Alaska’s Seward Peninsula between 1950 and 1990 (Calkin et al. 1998) and the thinning of the Greenland ice sheet (Jones et al. 2000). This thinning has resulted in a greater flow volume of freshwater into the Arctic Ocean and contributed to rising sea levels and increasing coastal erosion (Arendt et al. 2002; Brown et al. 2003). Warming has also resulted in the degradation of discontinuous permafrost in low and sub-arctic regions (Osterkamp and Romanovsky 1999; Callaghan et al. 2005). This degradation has led to increased thermokarst topography and the destabilization of forests near the taiga-tundra tree line (Hinzman et al. 2005). Increased soil temperatures and active layer thickness, along with soil drying trends resulting from surface water drainage are associated with the thawing of upper layers of permafrost. Drying trends leading to increased fire frequency in the tundra may influence the distribution of vegetation (Barrett et al. 2012). Such hydrological changes have been shown to impact the flow of surface streams and rivers, in addition to facilitating the drainage of some thaw lakes (Yoshikawa and Hinzman 2003; Hinzman et al. 2005).

Another significant impact of climate warming on global ecosystems is the lengthening of the growing season, most notably in the Arctic, resulting from earlier snowmelt and onset of spring, which has been documented by several studies in recent decades (Holben 1986; Myneni et al. 1997; Shabanov et al. 2002). Earlier snowmelt and onset of the growing season have led to increased growth of vegetation in addition to shifts in the range limits (Parmesan and Yohe 2003; Chen et al. 2011) and phenological development of both plant and animal species (Myneni et al. 1997; Arft et al. 1999). In the Arctic, timing of events such as leaf bud burst and first flowering date (FFD) of vegetation has been shown to advance with warming, with little to no effect on the cessation of growth at the end of the growing season (Arft et al. 1999). Similar patterns have also been recorded within alpine areas (Wipf et al. 2009) and even in temperate regions (Fitter and Fitter 2002). A study of nearly 400 plant species from central England showed that the FFD occurred 4.5 days earlier from 1991-2000 than during the period from 1954-1990 (Fitter and Fitter 2002). Another study determined that not only are vegetation flowering times affected by climate warming, but the activity of pollinators is also largely impacted (Hegland et al. 2009). This is apparent in studies documenting recent advances in the first arrival times of insect pollinators and migrating birds (Roy and Sparks 2000; Gordo and Sanz 2005; Gordo and Sanz 2006; Bartomeus et al. 2011). A global meta-analysis by Parmesan and Yohe (2003) of greater than 1,700 species showed an overall migration of species toward polar regions and higher elevations at a rate of 6.1 km per decade, consistent with the earlier commencement of spring. Other range shifts have been documented for various types of vegetation, particularly shrubs, as well as for avian and insect species (Benson et al. 2000; Sturm et al. 2001; Fitter and Fitter 2002; Hegland et al. 2009; Bartomeus et al. 2011). Such alterations in the phenology and range distributions of species are byproducts of climate change that have the potential to significantly alter ecosystem structure and function (Parmesan and Yohe 2003).

Vegetation and Climate Change Research

Plant communities are valuable for studying the effects of climate change because they drive energy and nutrient distribution to other trophic levels and thus impact the functioning of the ecosystem as a whole, particularly in arctic regions (Anisimov et al. 2007; Bret-Harte et al. 2008). Vegetation plays a major role in numerous ecosystem processes which are expected to be altered by climate warming, including carbon cycling, energy balance, and habitat quality. The balance between primary production and ecosystem respiration impacts the net carbon exchange within an ecosystem and is partially dependent on the hydrology of the region (Hinzman et al. 1991; Oechel et al. 2000; Oberbauer et al. 2007). Warming generally results in increased net loss of CO_2, particularly in dry ecosystems, although the magnitude of CO_2 change may be ecosystem-dependent (Oberbauer et al. 2007). Changes to vegetation structure or composition within a community may alter ecosystem carbon exchange (Johnson et al. 2000; Welker et al. 2004; Oberbauer et al. 2007). Additionally, vegetation community assembly impacts ecosystem energy balance, contributing to changes in albedo. Shrub and tree line expansion in the low Arctic is projected to decrease albedo and create a positive feedback to future warming (Chapin 2003; Callaghan et al. 2005; Barrett et al. 2012). Furthermore, the amount and type of vegetation present contributes to overall herbivore forage quality. Many large herbivores in arctic tundra are reliant upon certain vegetation types. For example, large migrating caribou populations depend on the presence of lichens for survival in winter (Ferguson et al. 2001; Callaghan et al. 2005; Hinzman et al. 2005). Therefore, documenting vegetation change will give insight into future shifts in ecosystem structure and function due to warming (Hollister et al. 2005a; Hollister and Flaherty 2010).

Impacts of Climate Change on Plant Communities

Vegetation has been shown to respond to climate change through increased height, cover, biomass, and photosynthetic production, although responses vary by growth forms and species (Chapin and Shaver 1985; Chapin et al. 1996; Hollister 2003; Hudson and Henry 2009; Hudson et al. 2011; Oberbauer et al. 2013). In general, graminoids and shrubs have shown increasing trends in both height and cover, whereas the cover of lichens and bryophytes has decreased in response to warming (Hollister et al. 2005a; Wilson and Nilsson 2009; Elmendorf et al. 2012a). The responses of species with warming typically vary across community types, with the greatest responses being recorded in sites with moderate moisture levels, and in low arctic regions

(Hollister 2003; Walker et al. 2006). Species responses are not always consistent with those of their respective growth forms, signifying the importance of research at the species level (Chapin and Shaver 1985). Changes in biodiversity have also been described for vegetation in arctic regions as a result of climate change, possibly resulting from competitive interactions as species adjust to warmer temperatures (Hollister et al. 2005a; Klady et al. 2011). Early predictions anticipated major declines in biodiversity with climate warming (Callaghan et al. 2005). While some areas have shown short-term declines in biodiversity (Hollister et al. 2005a; Wilson and Nilsson 2009), other more comprehensive analyses have documented no net change in diversity across species and sites worldwide (Vellend et al. 2013).

Methods of Studying Climate Change

Remote sensing and normalized difference vegetation index (NDVI) are technologically-driven methods of studying vegetation and climate change. They are not restricted by time or personnel limitations and have been helpful in identifying widespread trends in vegetation change. Through these methods, patterns of earlier vegetation 'greening' with earlier snowmelt (Myneni et al. 1997; Hinzman et al. 2005; Huemmrich et al. 2010), increased gross ecosystem production (Boelman et al. 2003) and the sensitivity of vegetation to warming across latitudinal gradients (Stow et al. 2003; Bhatt et al. 2010) have been detected, contributing to our overall understanding of climate warming effects at a global scale. Several remote sensing studies have detected the expansion of shrub tundra, consistent with climate change predictions (Silapaswan et al. 2001; Sturm et al. 2001; Hinzman et al. 2005; Bunn and Goetz 2006; Blok et al. 2011). Studies have shown heterogeneous responses of vegetation to climate change across the landscape, although the plethora of causes involved is not well understood (Elmendorf et al.

2012b). While these methods are useful in providing information on general trends, heterogeneous responses are difficult to analyze remotely and should be accompanied by ground-based research (Oberbauer et al. 2013).

Plot-based research methods that simulate climate warming are often utilized in order to provide assessments of vegetation change at a small scale. Active warming methods involve the use of an external heat source which is applied either beneath the soil or at the soil surface in order to maintain a constant heat differential between the treated plots and the controls (Aronson and McNulty 2009). Implementation of active warming typically includes the use of infrared (IR) heat lamps suspended above the plots (Harte et al. 1995) or heating cables which may be placed at, above, or buried beneath the ground’s surface (Fitter et al. 1999). These techniques are typically very time, labor, and cost intensive, and involve a high amount of environmental disturbance (Aronson and McNulty 2009). Passive warming methods work to achieve experimental warming without the use of external heat sources. Instead, they often utilize IR shades, greenhouses, tents, or open top chambers (OTCs) which trap IR radiation as a method of simulating climate warming (Marion et al. 1997; Aronson and McNulty 2009). These methods are beneficial in remote areas or locations that are difficult to access, and have been heavily utilized in the Arctic for decades (Chapin and Shaver 1985; Hollister et al. 2008; Aronson and McNulty 2009). Open-top methods are the most cost effective, and are generally preferred because they allow the access of light, precipitation, pollinators, and herbivores while causing minimal disturbance (Henry and Molau 1997; Marion et al. 1997; Hollister and Webber 2000).

Introduction to Project

Percent cover has long been used as a method of determining arctic vegetation response to climate warming. Because of the short stature of tundra vegetation, point framing methods are commonly used to estimate percent cover. Change in plant cover is impacted by the structure of the plant canopy, which is influenced both by changes in the size of individual plants (growth) and changes in the number of individual plants (density) (Figure 2). Plant traits which relate to growth include leaf length and inflorescence length; both are contributors to the overall height of the vegetation canopy. Increases in leaf and inflorescence length have been documented for forbs, graminoids, and shrubs as a direct result of warming in several arctic experimental studies (Hollister et al. 2005a; Walker et al. 2006; Hudson et al. 2011). Plant density, or abundance, may be influenced by clonal expansion (Jónsdóttir 2011), or by sexual reproduction, which includes total seed production and seedling recruitment (Myers-Smith et al. 2011). Both may be augmented through anthropogenic or natural disturbance which increases the availability of bare ground for seedling establishment and may facilitate increased colonization. Competitive interactions between species as they adjust to changing climatic conditions certainly also play a role in species density (Hollister et al. 2005a; Klady et al. 2011). The balance between growth and density and their respective influences on cover may be critical for predicting the long-term changes that may occur in arctic plant community composition and diversity. Therefore, identifying these underlying processes affecting vegetation cover is necessary to determine the long-term sustainability of predictions for arctic regions with continued warming.

The purpose of this project was to document the relationships between vegetation cover and traits representing vegetation growth and density for dominant growth forms and species across the landscape. Because of the prediction that the long-term warming response will be greater in low arctic regions, and because the low arctic is especially susceptible to shrub expansion (‘shrubification’), it has been suggested that research examining vegetation cover change is most valuable in these regions (Hollister et al. 2005a; Walker et al. 2006; Myers-Smith et al. 2011). This research was therefore conducted across the landscape within a low arctic region of Northern Alaska with the following specific objectives: 1) identify the impact of abiotic variables on cover, 2) pinpoint which traits are related to cover of dominant growth forms and species, 3) determine the impact of experimental warming on these relationships, and 4) examine how these relationships change across the landscape.

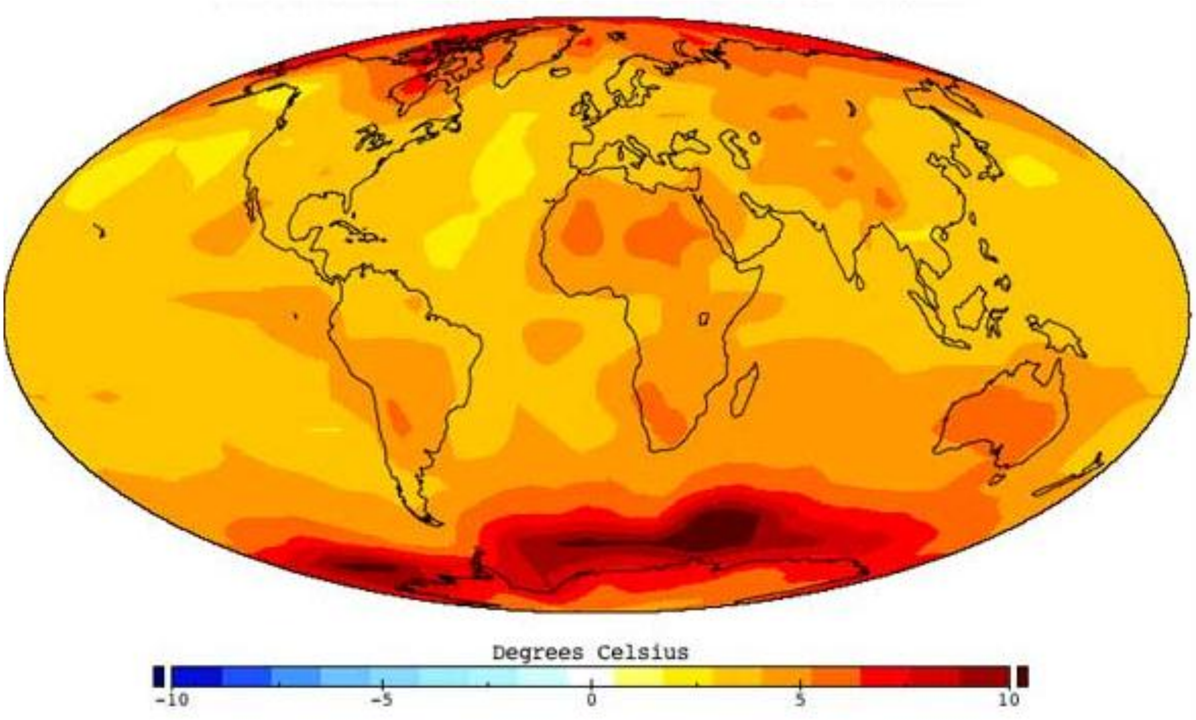


Figure 1: Real and simulated average global surface air temperature increase from 1960 - 2060, obtained from the National Aeronautic and Space Administration (http://www.nasa.gov).

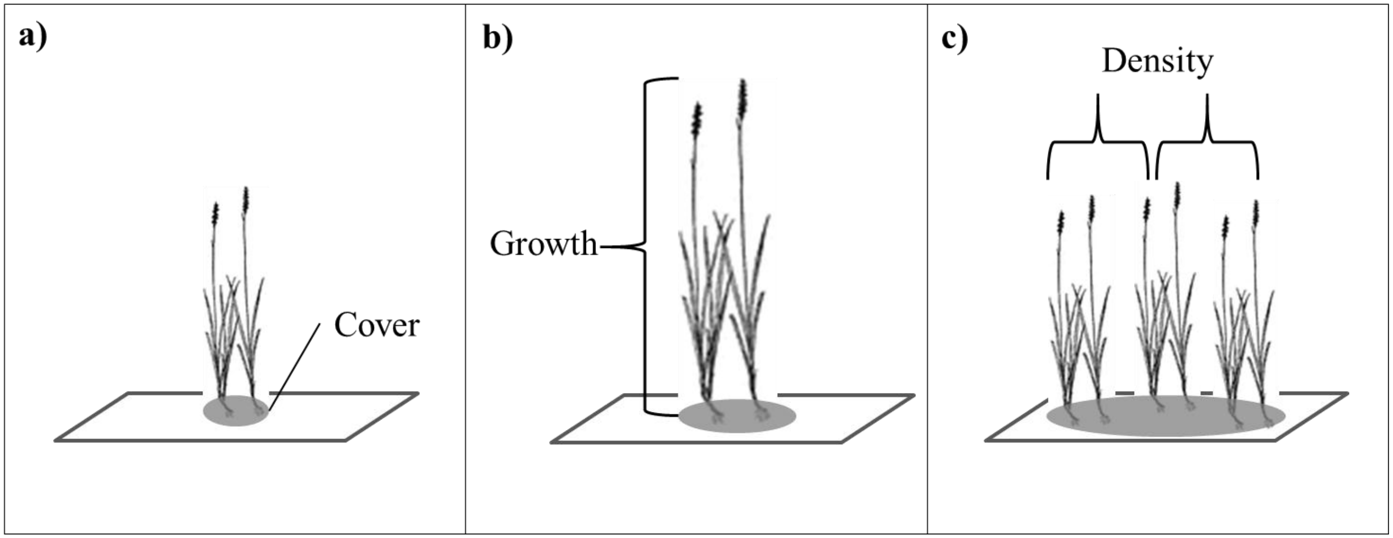


Figure 2: A schematic diagram illustrating **a)** the underlying processes that may impact vegetation cover. Changes in cover may be due to **b)** a change in the size of individual plants (growth) or **c)** due to a change in the number of individual plants (density).

CHAPTER II: PROJECT

Methods

Study Area

Research was conducted on the North Slope of Alaska near Atqasuk (70° 29' N, 157° 20'W). Atqasuk is situated in a low Arctic tundra region about 60 miles south of Barrow, Alaska (71° 17′ N, 156° 47′ W) adjacent to the Meade River and is characterized by thermokarst topography. Average summer temperature in Atqasuk is 9 °C, while average summer precipitation is near 20.8mm (Haugen & Brown 1980). We used two study sites nested within a larger spatial grid to determine the relationships between cover and vegetation traits (Figure 3). The spatial grid (Atqasuk Grid or AG) consisted of 30-1m^2 untreated plots located 100 meters apart across an area of landscape covering approximately 20 hectares. This grid was established in the 1990s through the National Science Foundation's Arctic System Science (ARCSS) program (http://www.arcus.org/ARCSS/index.html), and vegetation surveys were conducted annually beginning in 2010. Here the AG represented a subsample of the larger ARCSS grid which includes approximately 100 plots spread across 1 km^2 (100 hectares). The AG represented a mosaic of community types, and was characteristic of the vegetation cover across the landscape in this region (Figure 4 and personal observation**)**. The two study sites were situated within the grid and represented two ends of the moisture gradient. The dry heath site (Atqasuk Dry or AD) was situated on an elevated ridge characterized by firm, well-drained soils and high occurrences of bare ground and standing dead plant material. Vegetation at the AD site consisted mainly of forbs, graminoids, and evergreen shrubs (Webber 1978; Komarkova and Webber 1980; Hollister 1998; May and Hollister 2012). The wet meadow site (Atqasuk Wet or AW) was located adjacent to a partially-drained thaw lake in an area with poorly drained soils underlain with sand. Vegetation at the AW site consisted mainly of graminoids and bryophytes in addition to deciduous shrubs (Miller et al. 1976; Simpson et al. 2002; Hollister et al. 2005a; Hollister and Flaherty 2010).

Both the AD and AW sites were established in 1996 as part of a long-term warming experiment by the International Tundra Experiment (ITEX), a global collaborative effort to document vegetation response to climate warming (Henry and Molau 1997; Hollister et al. 2005b). Each site consisted of 48 total plots, of which 24 had been randomly designated as experimental plots upon site establishment. Plot designations have remained consistent throughout all years of experimentation. Warming was achieved using 1m^2 open-top chambers (OTCs, Figure 5) to passively warm the air surrounding the vegetation by an average of 0.6 to 2.2 ° C, which has been shown to reflect natural temperature increases resulting from climate warming (Henry and Molau 1997; Hollister and Webber 2000; Hollister 2003). Use of these chambers has been validated as an accurate method of predicting vegetation response to warming (Hollister and Webber 2000). Chambers were placed onto their designated plots as soon after snowmelt as possible (typically around June 15), and were removed after August 15 at the end of the growing season. Chamber dimensions and additional details about their construction are provided by Henry and Molau (1997) and also by Hollister (2003).

Abiotic Variables

We measured soil moisture and temperature, soil bulk density, percent organic matter, and thaw depth at all sites in 2013. Soil moisture (Volumetric Water Content, VWC (%)) was measured repeatedly throughout the growing season using a FieldScout TDR 300 soil moisture meter at a depth of 12 cm. Soil temperatures were recorded using a standard household-grade thermometer. Season averages of these values were used for analysis. Soil samples were collected at 15-20 cm depth between 20 July, 2013 and 21 July, 2013 and oven dried at approximately 105 °C for 8-12 hours or until constant weight was reached to obtain the water content by mass (Gravimetric Water Content, GWC (%)). Both VWC and GWC are widely used and accepted methods of calculating soil moisture. Samples were subsequently weighed, burned at 500 °C for 4 hours, and then re-weighed to calculate percent organic matter using the following formula:

$$\% \text{ Organic Matter} = 100 * (N2\text{-}N3) \div (N2\text{-}N1),$$

where N1 = weight of empty crucible, N2 = weight of crucible + sample before burning, and N3 = weight of crucible + sample after burning (Bilskie 2001; DeAngelis 2007). Bulk density (g/cm^3) was also calculated for our soil samples. We measured soil sample container volume for use in calculating bulk density by filling several of the containers completely with water using a 100mL burette. This volume was then averaged and used as a constant for calculating bulk density. Thaw depth (cm) was recorded for each plot at the end of the field season by inserting a stainless steel graduated rod into the ground until the frozen surface was reached.

Vegetation Variables

All vegetation measurements were recorded from the AW and AD sites, as well as from across the AG in 2012 and 2013, with the exception of cover at the AW and AD sites in 2012. Plants were measured by species, however species were also grouped into vascular plant growth forms and genera (at AG) in order to assess overall vegetation trends. Growth forms assessed in this study included evergreen shrubs, deciduous shrubs, forbs, and graminoids and were analyzed when present within each study site. Species or genera were chosen for analysis based on their dominance within each site and the quality of data available (Table A-1 and A-2, Appendix). At the AW and AD sites, dominant species were determined by their presence in ≥30 plots, and data quality was assessed through consistency between vegetation measures through preliminary analysis. Two deciduous shrub species at the AW site (*Salix pulchra* and *Salix polaris*) were combined into a single group (*Salix* spp.) due to their similar morphologies and because of sampling error for those individual species during the sampling years.

In order to determine whether vegetation cover was influenced more by growth or density, we measured several different vegetation variables. Leaf length, inflorescence length, biomass, and canopy height represented proxies for growth, whereas counts of individual shoots (or *ramets*) provided an estimate of density.

Cover and Canopy height

Vegetation cover and canopy height of live vascular plants were measured in each plot during peak season (July-August) using a point-frame sampling method (Cottam and Curtis 1956; May and Hollister 2012). The point frame grid was 75cm by 75cm with measurement points every 7cm (100 points total). At each contact within the plant canopy we identified and recorded species, live/dead status, and height above ground. Percent cover for each plot was derived by summing the total number of contacts for each species or growth form. Canopy height was determined by calculating the difference between the height of each contact and the ground height for each sampling point.

Leaf and Inflorescence Length

Leaf length and length of inflorescence were measured in each plot at the end of the growing season and represented total season growth. *Leaf length* was the length of the longest basal leaf for graminoids, or the length measured from the base of the petiole to the tip of the longest leaf for shrubs and forbs. Leaf length was measured for 1-3 vegetative individuals of each species within each plot. *Inflorescence length* was measured from the base of the stem to the tip of the inflorescence for the three tallest inflorescences within each plot (Hollister 2003). Individuals used for measuring inflorescence length were different than those used for measuring leaf length. All marked individuals were part of a long-term warming experiment and had been monitored consistently each year following site establishment. Leaf and inflorescence length were recorded at the AW and AD sites for all growth forms, but across the AG for graminoids only.

Biomass

Since we did not directly measure biomass, a proxy for biomass was calculated from end-of-season measurements for graminoids only. Leaf length was multiplied by the number of green leaves for each individual and averaged to yield a biomass proxy for each species per plot.

Density

We measured density of vascular plants at all sites by placing a 10cm x 50cm wooden frame over each plot. Placement of the wooden frame was kept consistent from year to year within plots using wooden stakes (Figure 6). Individual shoots of each species were counted in each of five 10cm^2 sections of the frame and assigned a status: live, dead, juvenile, diseased, or eaten (live included juvenile, diseased, and eaten). Only individuals marked with a ‘live’ status were included in this study. Counts were averaged across all five sections of the frame for each species or growth form, providing a measurement of density for each plot (individuals/10 cm^2).

Statistical Analysis

Each site was analyzed separately to account for between-site variation. Data from all growth forms and species were assessed for a normal distribution using the Shapiro-Wilk normality test prior to analysis and log or square root transformed when necessary to approximate normality. Variance was assessed using Bartlett's test of homoscedasticity. In cases where the assumptions of normality were not met, non-parametric forms of testing were used. For all analyses, we used an alpha level of 0.05 to indicate significance. Statistical operations were performed using R Software for Statistical Computing v. 3.0.2 (2013).

Abiotic Variables

T-tests and one-way ANOVAs were used to quantify differences in abiotic variables between the AW and AD sites and between treatments at each site. When normality assumptions were not met Wilcoxon Rank Sum or Kruskal-Wallis tests were used. We performed canonical correspondence analysis (CCA) using growth form cover and abiotic variables across the AG (2013 data) as a qualitative method of determining which were most strongly correlated with cover (Eidesen et al. 2013). This was done only across the AG because it encompassed the other two sites and provided the best representation of the landscape. We used simple linear regression (SLR) analysis to provide a quantitative assessment of the CCA results. We also used Spearman rank correlations to determine the relationship between the VWC and GWC methods of determining soil moisture content.

Climate Warming

We used one-way analysis of variance (ANOVA) to examine how warming impacted vegetation traits for different growth forms and species at the AD and AW sites in 2012. No warming treatments were applied across the AG, so it was not included in the warming analysis. We used this information to show recent changes that have occurred in the vegetation as a result of warming at these sites, and to supply a baseline for determining the impacts of warming on the relationships between cover and other vegetation variables.

We used multiple linear regressions (MLR) which included 'Treatment' as a variable in order to determine whether warming impacted the relationships between cover and the other vegetation variables. MLR was only used for the most dominant growth forms and species at each site in order to maintain adequate sample sizes for model development with multiple explanatory variables (Cohen and Cohen 1983). Based on the number of explanatory variables in each MLR model, we determined that to be included growth forms and species had to be present in roughly half of the total number of plots for each sampling site, or ≥ 25 (plots) at the AD and AW sites, and ≥ 16 (plots) across the AG. We checked variance inflation (VIF) and variables were removed from analysis if necessary to reduce the effects of multicollinearity. Across the AG we removed leaf length and inflorescence length from the models for all growth forms except *Eriophorum* for this reason. Plant variables were considered to be correlated with cover based upon significant p values (<0.05) combined with R^2 *adjusted* values ≥ 0.10. Final models were determined using Akaike information criterion (AIC) values, and only contained significant variables. MLR analysis showed that warming did impact the relationships between cover and the plant variables, so the analyses were then separated by treatment (control plots versus warmed plots). For all MLR, missing values were removed using the list-wise deletion method where only plots that contained data for each variable were included in analysis (Jones 1996; Howell 2012). Therefore, sample sizes varied for growth forms and species within a particular study site. Because not all measurements were recorded in the same year, MLR were also used to determine if ‘year’ significantly impacted the relationships between cover and vegetation variables. After finding no significant differences, analysis comparing vegetation variables with abiotic variables used measurements from 2013, whereas analysis comparing vegetation variables with cover used measurements from 2012. We used analysis of covariance (ANCOVA) to compare the slopes of the regression lines for each growth form and species between controls and warmed plots to look for a directional influence of warming on relationships between plant variables.

Correlations Between Cover and Vegetation Variables

We then used SLR analysis to determine which of the vegetation variables we measured was most strongly correlated with plant cover for growth forms and species within each site. Regressions were performed for each growth form or species, with cover as the response variable and vegetation variables as explanatory factors. Plant variables were considered to be correlated with cover based upon significant p values (<0.05) combined with R^2 values ≥ 0.10. For all SLR, missing values were removed for cover and each trait being considered using the list-wise deletion method (Jones 1996; Howell 2012). For SLR, cover was square root transformed prior to inclusion in analysis. Spearman rank correlations were used in place of regressions when normality assumptions were not met (i.e. for forbs across the AG).

Community Type

We utilized ANCOVA to compare the slopes of the relationships between vegetation variables and cover across sites to look for an influence of community type (i.e. AD, AW). For this analysis, plots were not distinguished by treatment but were pooled together. The AG was excluded from this analysis. We performed a similar analysis using only control plots from all sites (including the AG), but no significant results were found and normality assumptions were violated, thus they are not reported. The same datasets were used for the ANCOVAs as for the SLR analysis. We also used correspondence analysis (CA) to give a visual representation of the differences in the cover distribution of growth forms across the AW and AD sites and across the AG. All species present in >5 plots within a site were included in the CA, and only data from control plots were used so that direct comparisons could be made with the untreated plots across the AG.

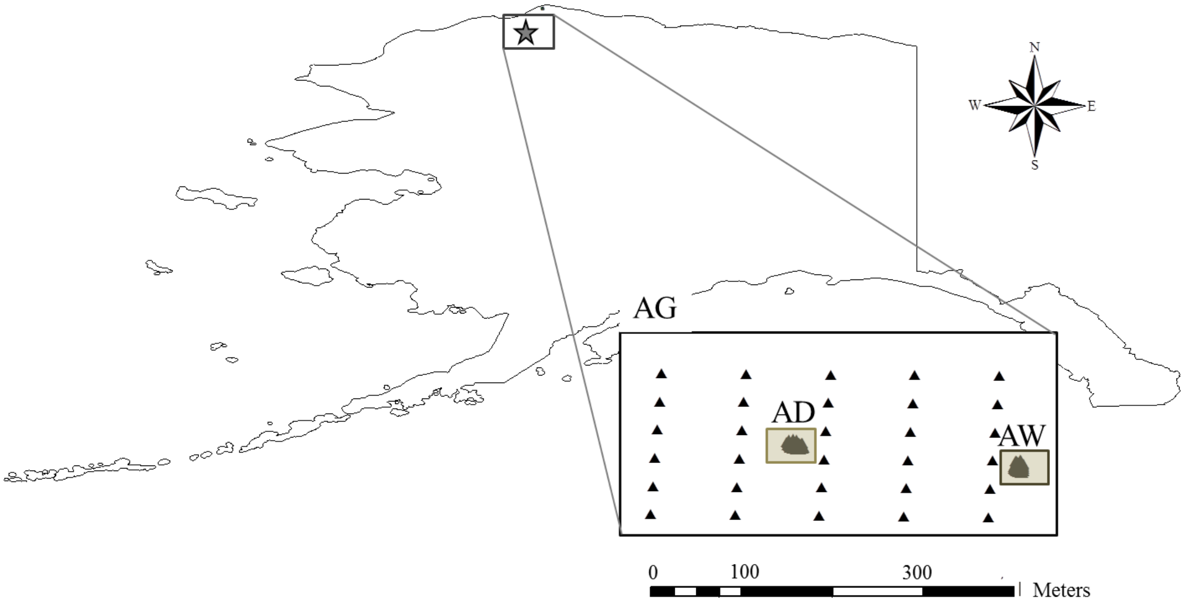


Figure 3: Layout of long-term research sites at Atqasuk on the North Slope of Alaska. The inset area enclosed within the black outline shows the plots (dark triangles) located across the Atqasuk Grid (AG). Dark clustered areas within the grid represent the Atqasuk Dry (AD) site and the Atqasuk Wet (AW) site.

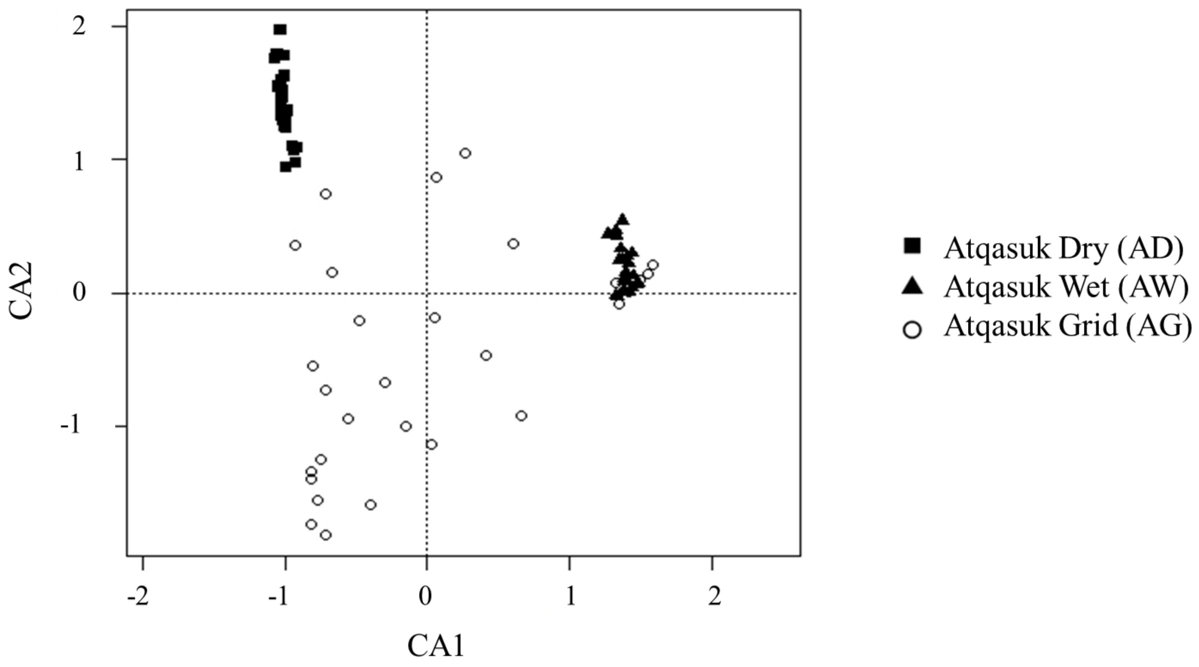


Figure 4: Ordination biplot (CA) showing the distribution of cover for species in control plots for the study sites in Atqasuk, Alaska. The model included five axes which explained 77.1% of the variation. Only the first two axes are shown, which explained 63.7% of the variation. Species were clearly separated between the Atqasuk Dry (AD) and Atqasuk Wet (AW) sites. Percent cover of species across the Atqasuk Grid (AG) was mainly intermediate between the AD and AW sites.

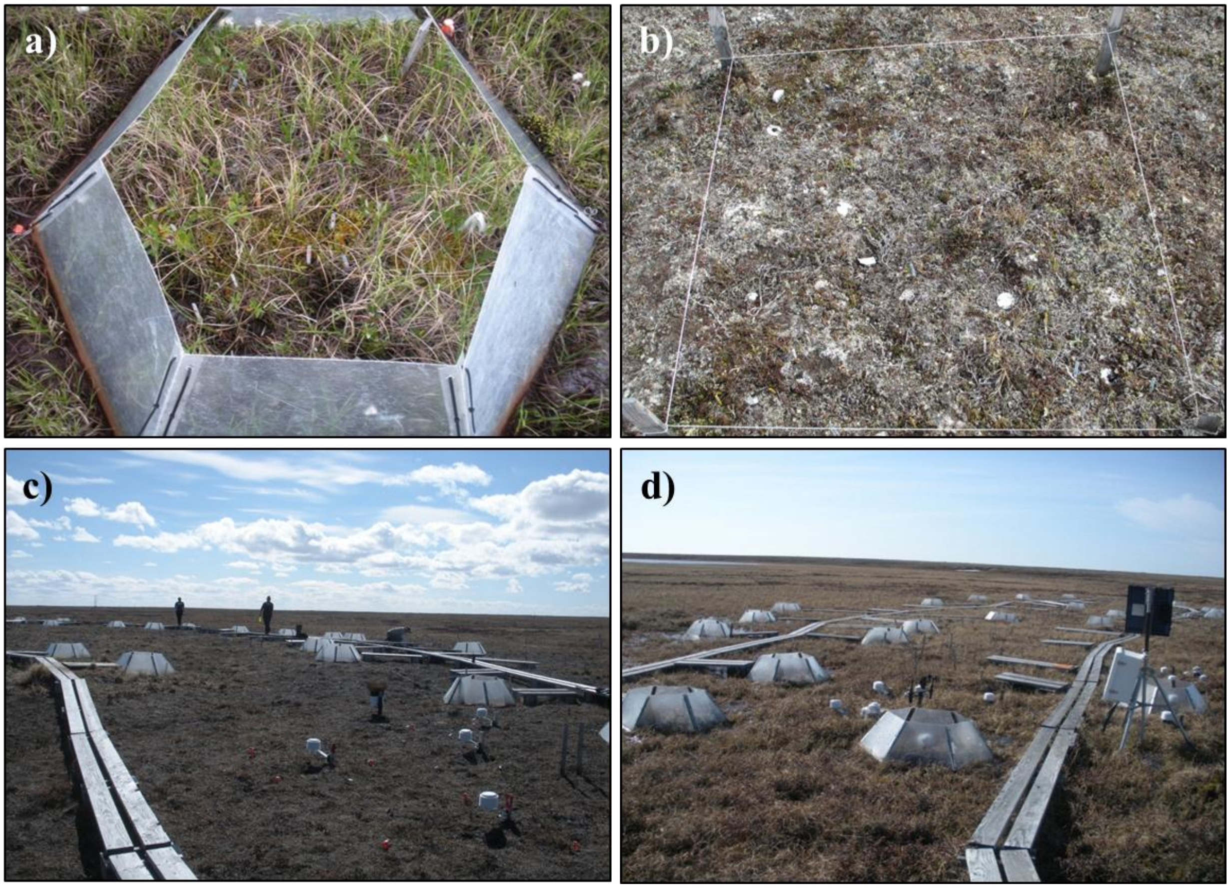


Figure 5: Photographs of **a)** a warmed plot and **b)** a control plot and images of the **c)** Atqasuk Dry (AD) site and the **d)** Atqasuk Wet (AW) site.

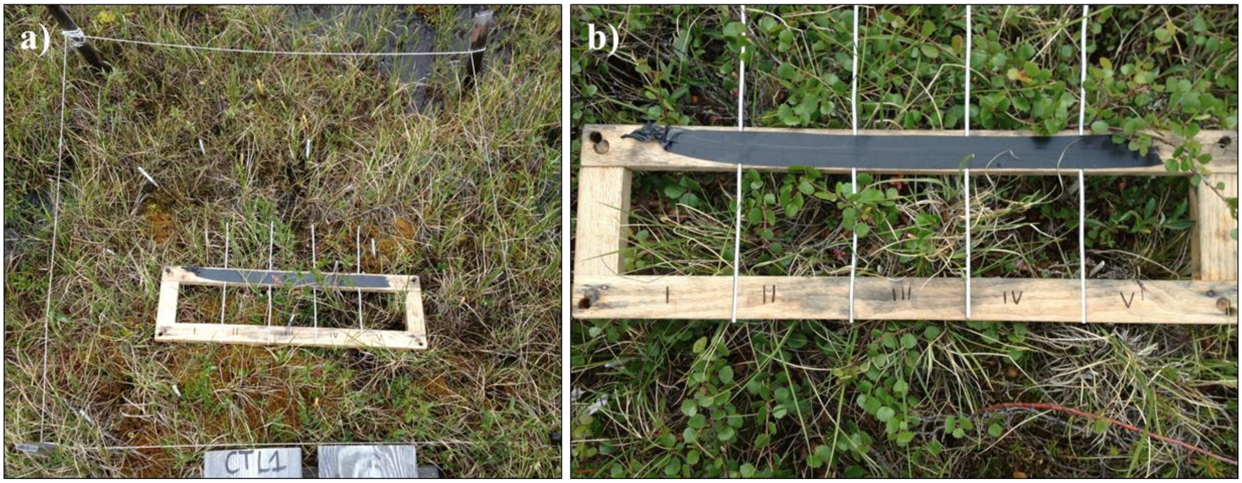


Figure 6: Photograph of the frame used to measure species density within each plot showing **a)** the orientation of the frame within a plot and **b)** a close up of the 10cm x 50cm frame. The frame is divided into five 10cm^2 sections and individual shoots were counted within each section and averaged to estimate the density of each plot.

Results

Abiotic Variables

Abiotic variables differed significantly among the study sites in 2013. Although the two methods of assessing soil moisture content were strongly correlated (*rho* = 0.52), GWC was measured only once during the field season whereas VWC was measured multiple times and more accurately represented natural environmental conditions. Therefore only VWC was used in remaining analyses. Soil temperature and thaw depth were significantly greater at the AD site than at the AW site, while soil moisture (VWC) was significantly greater at the AW site (Figure 7). Mean bulk density, soil moisture, organic matter, and thaw depth across the grid (AG) were significantly different from both the AW and AD sites. Soil temperature (°C) across the AG was significantly different from the temperature at the AD site but not from the AW site (Figure 7). In general, the range of values for abiotic variables across the AG encompassed those at both the AW and AD sites, demonstrating that this grid represented multiple community types. At the AD site, soil moisture in the warmed plots was significantly lower than in the controls (14.19% ± 1.10 and 17.65% ± 1.04, respectively; mean ± standard error; $p = 0.02$ from two-tailed t-test), indicating that warming may have impacted moisture levels at this site.

Ordination results across the AG provided a qualitative illustration to show that different abiotic variables were associated with cover of vegetation growth forms and impacted their distribution across the landscape (Figure 8). From the canonical correspondence analysis (CCA) we identified five axes which explained 45.6 % of the variation in the model. The first two axes were significant (CCA1: $p = 0.001$, CCA2: $p = 0.008$) and explained 39.2% of the variation (Figure 8). The final CCA model was significant and included soil moisture (VWC), bulk density, soil temperature, soil organic matter, and thaw depth ($p < 0.001$). Soil moisture, soil temperature, and thaw depth were most strongly associated with CCA1, whereas soil organic matter and bulk density were most strongly associated with CCA2. Because CCA is a distance-based ordination method, the placement of species groups in relation to one another indicates their degree of similarity or dissimilarity. Both evergreen and deciduous shrubs, along with forbs, had similar environmental requirements which were different from those of graminoids.

As a quantitative way of describing these relationships across the AG, we used regression analysis to determine which of the abiotic variables were most strongly correlated with cover of growth forms and the dominant species groups, *Carex* and *Eriophorum* (Table 1). Soil temperature and moisture were again the two main variables associated with cover of growth forms, consistent with the ordination. Both forms of analysis revealed that cover of shrubs and forbs across the AG was generally greater in areas of low soil moisture, soil temperature, and organic matter, but with high bulk density. Conversely, cover of graminoids was generally greater in areas of high soil moisture, soil temperature, organic matter, and thaw depth. These results demonstrate that abiotic variables impact the cover distribution of vegetation communities across the landscape.

Vegetation Variables

Change in Vegetation Variables Between Sites

For growth forms and species in 2012, we found that there were more significant differences in vegetation variables at the AW site than at the AD site. At the AW site, graminoid cover, canopy height, and leaf length were significantly greater in warmed plots than in controls (Figure 9). The dominant graminoid species *Carex aquatilis* followed the same trends as the graminoids, with cover, canopy height, and leaf length significantly greater in warmed plots

(Table 2). Notably, density of *C. aquatilis* was significantly lower in warmed plots. These increases in growth simultaneous with decreased density indicate an inverse relationship between growth and density for graminoids. Leaf length of *Eriophorum angustifolium* and the proxy for biomass in *E. russeolum* were significantly greater in warmed plots. At the AD site, canopy height of evergreen shrubs was significantly greater and inflorescence length for forbs was significantly lower in warmed plots (Figure 10). Biomass in *Luzula confusa* was significantly greater in warmed plots. No other species at the AD site displayed differences in vegetation variables resulting from treatment in 2012.

Across the grid (AG) we tested for significant differences in vegetation variables of growth forms, *Carex*, and *Eriophorum* between 2012 and 2013. Only graminoid inflorescence length and cover of *Carex* were significantly greater in 2013; no other significant differences were recorded (Figure 11; Table 3).

Correlations between Cover and Vegetation Variables

In general, vegetation variables significantly related to cover of graminoids were representative of the growth of individual plants. At the AW site, leaf length and canopy height, both growth traits, were significantly correlated with cover of graminoids and *C. aquatilis* (Table 4). Cover of *E. angustifolium* and *E. russeolum* at the AW site were not significantly correlated with any of the vegetation variables. At the AD site, cover of graminoids was most strongly correlated with canopy height. Cover of *L. confusa* and *Hierechloe alpina* was associated with leaf length and canopy height, resembling the graminoid growth form. Across the AG, graminoid cover was most strongly related to density, which was inconsistent with the relationships observed at the AW and AD sites. However, cover of the dominant graminoid genus, *Carex*, was strongly correlated with canopy height (a growth trait), although density was also significant.

Cover of the genus *Eriophorum* was most strongly correlated with inflorescence length, likewise a trait representing plant growth.

Vegetation variables significantly related to cover of shrubs differed depending on community type (Table 4). At the AW site, cover of deciduous shrubs (including *Salix* spp.) was not significantly correlated with any of the vegetation variables we measured. Evergreen shrub cover at the AD site was best described by inflorescence length and canopy height, but was inconsistent with the variables correlated to cover of the dominant species *Diapensia lapponica* and *Vaccinium vitis-idaea*, which were strongly correlated with density. Across the AG evergreen shrub cover was most strongly related to density whereas deciduous shrub cover was most strongly related to canopy height. None of the variables were correlated with cover of forbs across the AG.

Of all the vegetation variables, canopy height was more strongly related to overall shrub cover (both evergreen and deciduous) at the AD site than at the AW site, as indicated through ANCOVA (Figure 12). At the AD site canopy height showed a strong positive relationship with shrub cover (positive slope), whereas there was no relationship between canopy height and shrub cover at the AW site. Relationships between the remaining vegetation variables and cover did not differ between sites, as seen by the insignificant slopes (Table 5). For graminoids, intercepts were significantly different, indicating a difference in the size of plants between sites.

Impact of Warming

Warming significantly impacted the relationships between vegetation variables and cover, resulting in some discrepancies between traits that were most correlated with cover in controls and warmed plots, particularly at the AD site (Table 4). This was initially demonstrated through multiple linear regression analysis, as ‘treatment’ was significantly correlated with cover of graminoids at the AW and AD sites, as well as for *C. aquatilis* at the AW site (Table 6). At the AW site warming had only a minor impact on the relationships between cover and vegetation variables (Table 4). Graminoid cover correlated most with canopy height in both the controls and warmed plots, but in the controls leaf length was additionally correlated with cover. Cover of *C. aquatilis* was related most to canopy height, leaf length, and biomass in the warmed plots but only to canopy height in the controls. At the AD site warming had a much more significant impact on the relationships between cover and vegetation variables (Table 4). Variables most strongly correlated with cover differed between controls and warmed plots for nearly all growth forms and species measured at this site. For example, graminoid cover in the controls was most strongly correlated with leaf length, but to canopy height and density in the warmed plots. Similarly, cover of evergreen shrubs was most strongly correlated with canopy height in the controls, but to inflorescence length in the warmed plots. The same variability was observed in each of the dominant evergreen shrub species at the AD site.

The impact of warming specifically at the AD site was also shown through ANCOVA, in which the slopes of the relationships between cover and plant variables were significantly different in graminoids, *L. confusa*, and *H. alpina* (Figure 13; Table 7). For graminoids, the slopes of cover and leaf length differed by treatment, with a strong positive relationship in the controls and little to no relationship in the warmed plots. For *L. confusa*, we found a similar relationship between the slopes of cover and biomass. The slopes of cover and density for *H. alpina* were also significantly different, where density was strongly positively related to cover in the controls but very negatively related to cover in the warmed plots. These significant differences in slopes suggest the same inverse relationship between growth and density in graminoids previously considered at the AW site (Figure 14). This demonstrates that at these sites warming not only impacted which traits were significantly correlated with cover, but also the relationships between plant variables and cover.

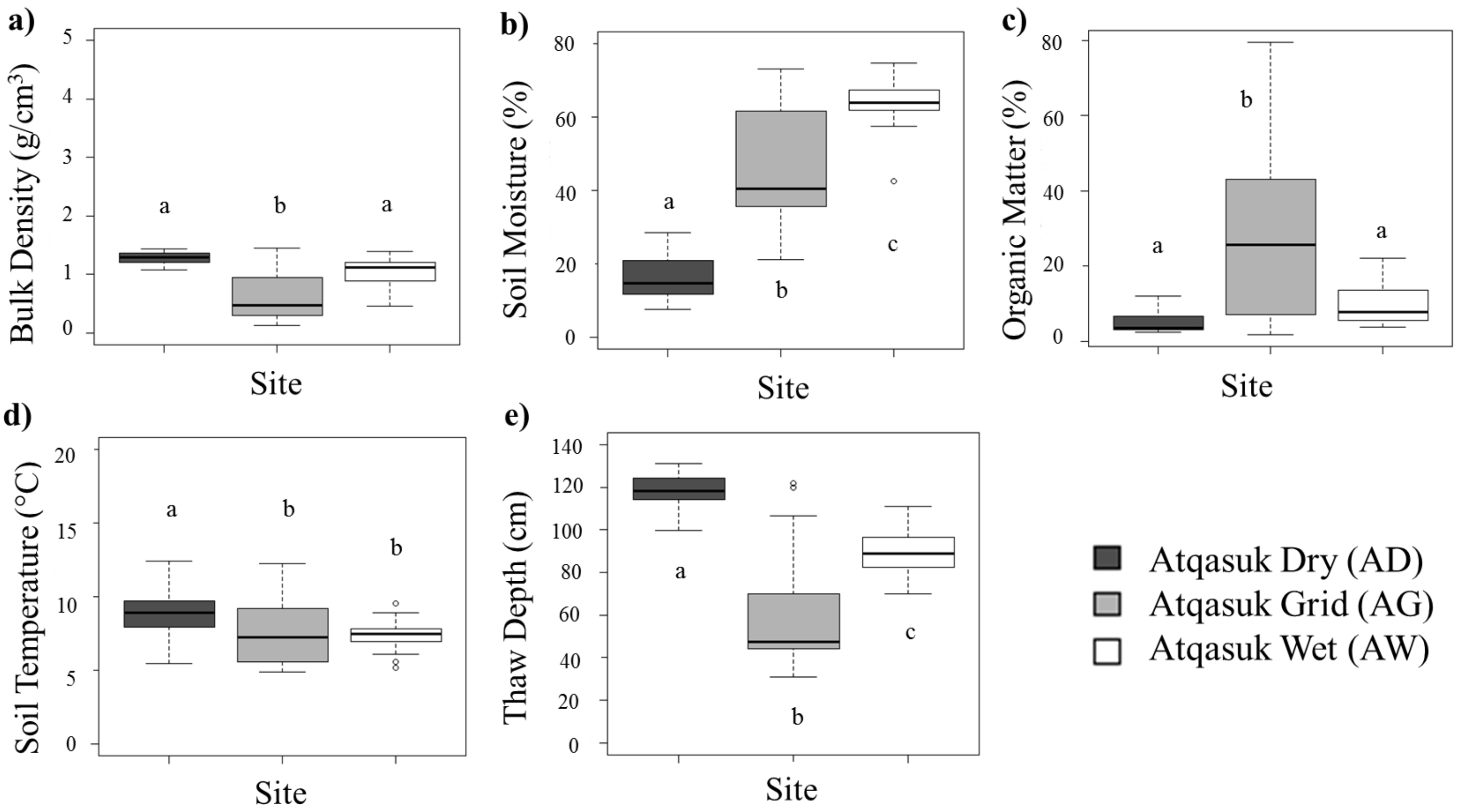


Figure 7: Boxplots showing **a)** bulk density, **b)** soil moisture (VWC), **c)** organic matter, **d)** soil temperature, and **e)** thaw depth at the AD and AW sites and across the AG. Values for the AG generally encompassed a greater range of values for all variables than at the AD or AW sites. Significant differences between sites were determined using the Kruskal Wallis test and *post-hoc* analysis was performed using pairwise t-tests (α = 0.05), significant differences are denoted by different letters.

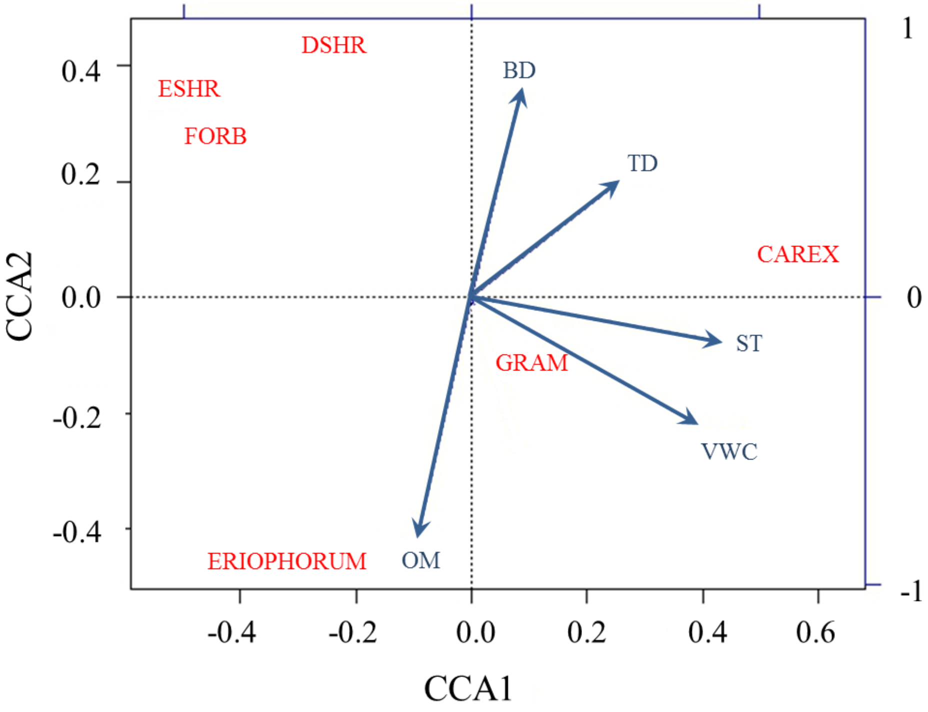


Figure 8: Ordination biplot (CCA) showing growth forms present across the Atqasuk Grid (AG) and their distribution along environmental gradients (CCA axis 1 and 2). GRAM = graminoids, DSHR = deciduous shrubs, ESHR = evergreen shrubs, FORB = forbs, CAREX = species within the dominant genus *Carex*, and ERIOPHORUM = species within the dominant genus *Eriophorum*. Environmental variables included in the final model were bulk density (BD), thaw depth (TD), soil temperature (ST), volumetric soil moisture (VWC), and soil organic matter (OM). Orientation of arrows indicates which axis each variable is most closely associated with and the length of the arrows indicates the strength of the association. The final model was significant (p = 0.001) and included both CCA axis 1 and 2, which accounted for 39.2% of the variation.

Table 1: Relationships between plant cover and abiotic variables across the Atqasuk Grid (AG). Coefficients (C) are from simple linear regressions (R^2) or Spearman Rank correlations (*rho*). Significant values ($\alpha = 0.05$) are shown in bold. Square root transformations were applied to all variables. n = the total number of plots included in analyses.

		Soil Moisture (VWC%)		Soil Temperature (°C)		Soil Organic Matter (%)		Bulk Density (g/cm^3)		Thaw Depth (cm)	
Growth Form/Taxa	n	C	*p* value	C	*p* value	C	*p* value	C	*p* value	C	*p* value
Graminoids[a]	30	0.00	0.80	0.00	0.82	0.06	0.19	0.09	0.10	0.00	0.75
Carex spp.[a]	30	**0.16**	**0.03**	**0.33**	**0.00**	0.03	0.37	0.01	0.59	**0.33**	**0.00**
Eriophorum spp.[a]	30	0.00	0.85	0.05	0.25	**0.39**	**0.00**	**0.31**	**0.00**	0.10	0.09
Deciduous Shrubs[b]	30	**-0.46**	**0.01**	-0.29	0.12	-0.21	0.25	0.15	0.43	0.19	0.32
Evergreen Shrubs[b]	30	**-0.68**	**0.00**	**-0.66**	**0.00**	-0.13	0.50	0.27	0.14	-0.32	0.08
Forbs[b]	30	-0.28	0.14	**-0.36**	**0.05**	-0.31	0.09	0.16	0.38	-0.18	0.33

[a] Linear regressions were performed for graminoids, *Carex* spp., and *Eriophorum* spp.

[b] Spearman Rank correlations were performed for shrubs and forbs due to non-normality

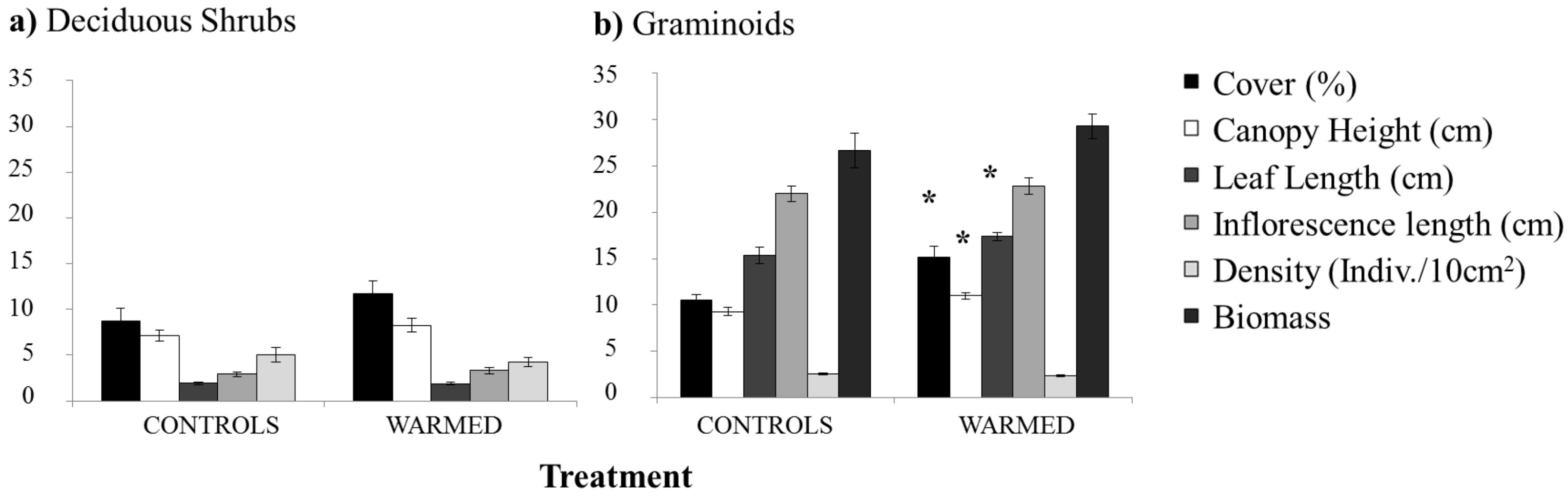


Figure 9: Means (± standard error) of vegetation variables for **a)** deciduous shrubs and **b)** graminoids at the Atqasuk Wet (AW) site. Significant differences were determined using one-way analysis of variance and are denoted using an ‘*’ ($\alpha = 0.05$).

Table 2: Means (±standard error) for vegetation variables by growth form and species at the Atqasuk Wet (AW) and Atqasuk Dry (AD) sites in 2012 for controls (C) and warmed (W) plots. Significance is indicated by *p* values from one-way analysis of variance and significant values are bolded (α = 0.05). NC = No Change. NA = data not recorded. Df = 1 for all. Only plots in which each growth form or species was measured were included in the analysis (n). Test statistics are F values or Kruskal-Wallis chi-squared values.

		Treatment						
Taxa	n	Control		Warmed		Test statistic	*p* value	Trend
				Atqasuk Wet (AW)				
Cover (%)								
Graminoids[c]	48	**10.6**	**±0.5**	**15.1**	**±1.2**	**9.25**	**< 0.01**	**W > C**
Carex aquatilis	48	**24.2**	**±1.8**	**33.0**	**±2.1**	**10.13**	**< 0.01**	**W > C**
Eriophorum angustifolium[c]	46	7.3	±0.8	8.4	±1.1	0.67	0.42	W > C
Eriophorum russeolum[b]	45	5.3	±0.7	5.7	±0.9	0.06	0.81	W > C
Deciduous Shrubs[b]	46	8.8	±1.3	11.7	±1.4	2.93	0.09	W > C
Salix spp.[b]	46	8.7	±1.3	11.7	±1.4	3.17	0.08	W > C
Forbs[c]	12	1.2	±0.2	3.1	±1.3	1.27	0.26	W > C
Canopy Height (cm)								
Graminoids	48	**9.3**	**±0.4**	**11.0**	**±0.4**	**10.35**	**< 0.01**	**W > C**
Carex aquatilis	48	**11.1**	**±0.6**	**13.5**	**±0.5**	**10.12**	**< 0.01**	**W > C**
Eriophorum angustifolium[a]	44	9.5	±0.7	10.4	±0.7	1.14	0.29	W > C
Eriophorum russeolum	42	8.0	±0.6	9.6	±0.8	2.44	0.13	W > C
Deciduous Shrubs[a]	48	7.2	±0.6	8.3	±0.7	1.39	0.25	W > C
Salix spp.[a]	45	7.2	±0.6	8.3	±0.7	1.39	0.25	W > C
Forbs	NA	NA	NA	NA	NA	NA	NA	—

Table 2 (continued):

		Treatment						
Taxa	n	Control		Warmed		Test statistic	*p* value	Trend
				Atqasuk Wet (AW)				
Leaf Length (cm)								
Graminoids[c]	48	**15.4**	**±0.9**	**17.4**	**±0.5**	**6.64**	**0.01**	**W > C**
Carex aquatilis	48	**17.7**	**±0.9**	**20.8**	**±0.7**	**6.89**	**0.01**	**W > C**
Eriophorum angustifolium[c]	42	**18.3**	**±1.2**	**21.0**	**±0.7**	**4.85**	**0.03**	**W > C**
Eriophorum russeolum	37	12.5	±0.9	13.9	±0.8	1.36	0.25	W > C
Deciduous Shrubs	25	2.0	±0.2	1.9	±0.2	0.13	0.73	C > W
Salix spp.	25	2.0	±0.2	1.9	±0.2	0.13	0.73	C > W
Forbs	22	2.6	±0.2	2.8	±0.2	0.25	0.62	W > C
Inflorescence Length (cm)								
Graminoids	47	22.0	±0.9	22.9	±0.9	0.45	0.51	W > C
Carex aquatilis	35	24.2	±1.2	27.4	±1.4	3.22	0.08	W > C
Eriophorum angustifolium	32	18.5	±0.8	20.0	±1.0	1.21	0.28	W > C
Eriophorum russeolum	4	20.5	±0.0	16.2	±1.4	2.29	0.27	C > W
Deciduous Shrubs[c]	33	2.9	±0.3	3.3	±0.3	1.65	0.20	W > C
Salix spp.[c]	33	2.9	±0.3	3.3	±0.3	1.65	0.20	W > C
Forbs	16	9.6	±1.4	11.4	±1.8	0.66	0.43	W > C
Density (individuals/10cm^2)								
Graminoids	48	2.6	±0.1	2.4	±0.1	1.23	0.27	C > W
Carex aquatilis[a]	48	**4.6**	**±0.3**	**3.6**	**±0.2**	**6.04**	**0.02**	**C > W**
Eriophorum angustifolium[c]	42	1.4	±0.1	1.7	±0.1	3.25	0.07	W > C
Eriophorum russeolum[c]	42	2.0	±0.2	2.0	±0.2	0.00	0.99	NC
Deciduous Shrubs[a]	40	5.0	±0.8	4.3	±0.5	0.45	0.51	C > W
Salix spp.[b]	40	5.0	±0.8	4.3	±0.5	0.45	0.51	C > W
Forbs	10	1.8	±0.5	2.2	±0.5	0.48	0.51	W > C
Biomass (proxy)								
Graminoids[a]	48	26.6	±1.9	29.3	±1.3	2.48	0.12	W > C
Carex aquatilis[a]	48	29.7	±3.1	34.6	±3.1	1.67	0.20	W > C
Eriophorum angustifolium	42	36.3	±3.6	42.8	±2.7	2.14	0.15	W > C
Eriophorum russeolum[a]	37	**14.6**	**±1.5**	**18.4**	**±1.6**	**4.31**	**0.05**	**W > C**

Table 2 (continued):

		Treatment						
Taxa	n	Control		Warmed		Test statistic	p value	Trend
				Atqasuk Dry (AD)				
Cover (%)								
Graminoids[c]	46	5.3	±0.5	6.7	±1.5	0.00	0.95	W > C
Hierechloe alpina	31	4.5	±0.7	4.7	±0.7	0.06	0.80	W > C
Luzula confusa[b]	40	5.8	±0.8	5.7	±0.9	0.00	0.98	C > W
Evergreen shrubs	48	8.9	±0.8	10.2	±0.9	1.34	0.25	W > C
Diapensia lapponica[c]	34	4.5	±0.7	3.5	±0.6	2.09	0.15	C > W
Vaccinium vitis-idaea[b]	46	10.6	±1.4	8.5	±1.1	1.55	0.22	C > W
Deciduous Shrubs	8	3.1	±0.8	4.1	±1.5	0.38	0.56	W > C
Forbs[b]	17	2.5	±0.6	3.1	±0.7	0.27	0.61	W > C
Canopy Height (cm)								
Graminoids[a]	46	5.5	±0.4	6.5	±0.5	2.09	0.16	W > C
Hierechloe alpina	30	6.7	±0.6	7.7	±0.6	1.41	0.25	W > C
Luzula confusa	37	4.3	±0.4	4.5	±0.4	0.08	0.77	W > C
Evergreen shrubs	48	**1.6**	**±0.1**	**2.0**	**±0.1**	**6.19**	**0.02**	**W > C**
Diapensia lapponica[a]	30	1.3	±0.3	1.0	±0.2	0.55	0.47	C > W
Vaccinium vitis-idaea[a]	44	0.9	±0.1	1.1	±0.1	2.23	0.14	W > C
Deciduous Shrubs	7	1.1	±0.1	1.2	±0.2	0.02	0.90	W > C
Forbs[a]	14	3.5	±1.3	2.5	±0.9	0.90	0.36	C > W
Leaf Length (cm)								
Graminoids	48	9.7	±0.6	10.1	±0.6	0.23	0.63	W > C
Hierechloe alpina[c]	31	10.9	±0.5	11.8	±1.0	0.59	0.44	W > C
Luzula confusa	47	7.2	±0.3	8.1	±0.4	2.92	0.09	W > C
Evergreen shrubs[a]	48	2.5	±0.2	2.2	±0.1	2.83	0.10	C > W
Diapensia lapponica[c]	39	0.5	±0.0	0.5	±0.1	0.18	0.67	W > C
Vaccinium vitis-idaea	48	2.6	±0.1	2.6	±0.1	0.02	0.89	W > C
Deciduous Shrubs[a]	8	1.5	±0.2	2.2	±0.5	1.96	0.21	W > C
Forbs	22	4.7	±0.7	4.5	±0.7	0.02	0.88	C > W

Table 2 (continued):

Taxa	n	Treatment				Test statistic	*p* value	Trend
		Control		Warmed				
Atqasuk Dry (AD)								
Inflorescence Length (cm)								
Graminoids	46	22.3	±0.9	21.3	±1.2	0.45	0.51	C > W
Hierechloe alpina	31	26.7	±0.9	27.0	±1.4	0.04	0.84	W > C
Luzula confusa	38	19.6	±0.6	19.1	±0.9	0.23	0.63	C > W
Evergreen shrubs	48	4.3	±0.1	4.5	±0.2	0.68	0.41	W > C
Diapensia lapponica[b]	42	4.2	±0.2	4.0	±0.2	0.93	0.34	C > W
Vaccinium vitis-idaea	37	3.7	±0.2	3.8	±0.2	0.19	0.67	W > C
Deciduous Shrubs	9	2.9	±0.6	1.9	±0.2	1.79	0.22	C > W
Forbs	17	11.9	±1.0	9.3	±0.6	2.01	0.18	C > W
Density (individuals/10cm^2)								
Graminoids[a]	46	3.5	±0.3	3.4	±0.4	0.14	0.71	C > W
Hierechloe alpina	21	3.5	±0.3	3.7	±0.4	0.14	0.71	W > C
Luzula confusa[a]	37	3.7	±0.4	3.5	±0.6	0.46	0.50	C > W
Evergreen shrubs[a]	48	11.5	±1.3	14.3	±1.4	2.40	0.13	W > C
Diapensia lapponica[a]	31	13.9	±2.6	11.7	±1.6	0.16	0.70	C > W
Vaccinium vitis-idaea[a]	48	7.4	±0.8	5.6	±0.4	2.42	0.13	C > W
Deciduous Shrubs	5	6.3	±3.0	10.8	±9.8	0.29	0.63	W > C
Forbs[c]	10	**1.0**	**±0.0**	**1.4**	**±0.2**	**5.54**	**0.02**	**W > C**
Biomass (proxy)								
Graminoids	48	11.1	±1.0	12.6	±1.0	1.13	0.29	W > C
Hierechloe alpina[a]	31	9.7	±1.6	11.6	±1.6	0.89	0.35	W > C
Luzula confusa[a]	47	**6.5**	**±0.5**	**9.8**	**±1.1**	**6.77**	**0.01**	**W > C**

[a] Log transformed
[b] Square root transformed
[c] Kruskal-Wallis chi-squared values presented

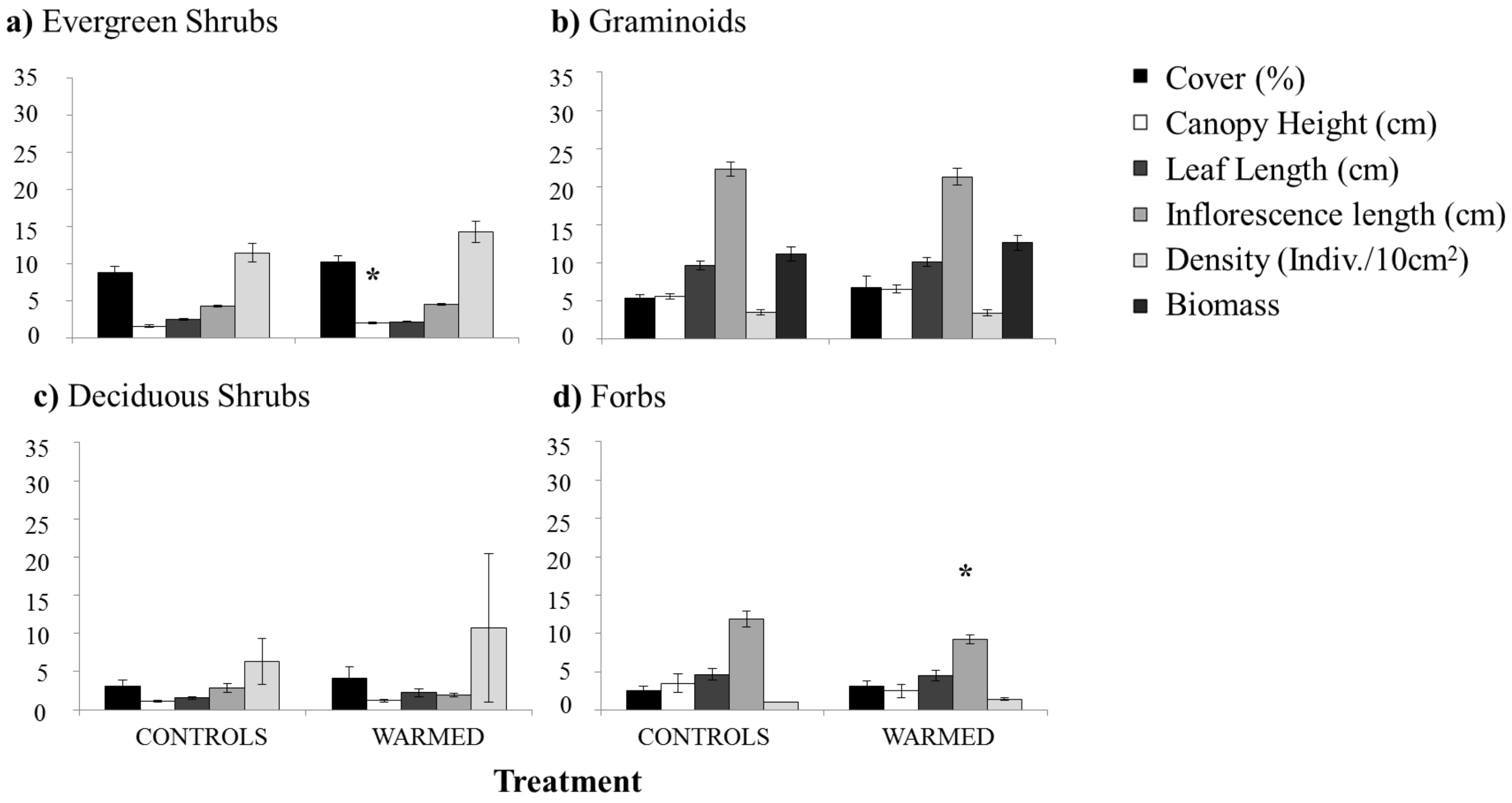


Figure 10: Means (± standard error) of vegetation variables for **a)** evergreen shrubs, **b)** graminoids, **c)** deciduous shrubs, and **d)** forbs at the Atqasuk Dry (AD) site. Significant differences were determined using one-way analysis of variance and are denoted using an '*' (α = 0.05).

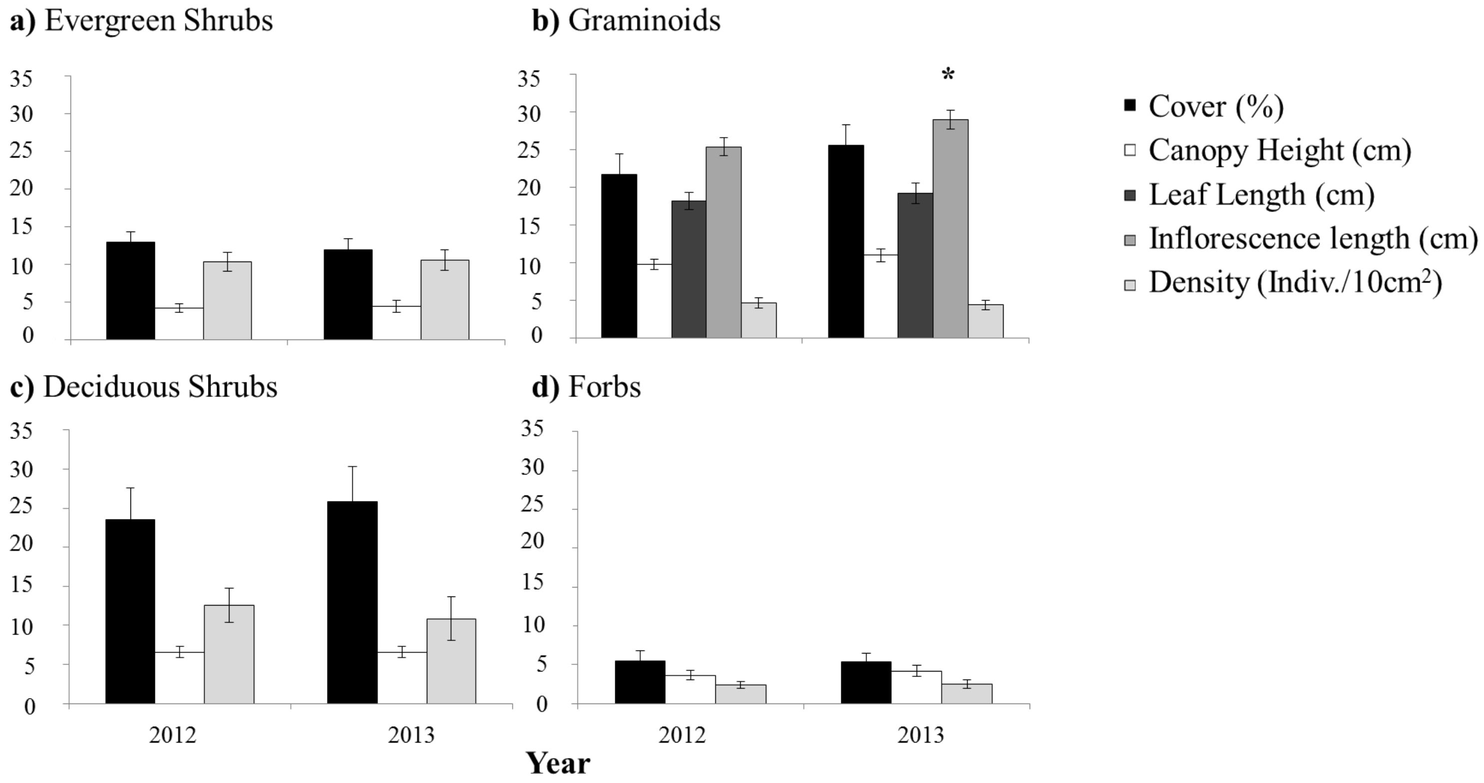


Figure 11: Means (± standard error) of vegetation variables for **a)** evergreen shrubs, **b)** graminoids, **c)** deciduous shrubs, and **d)** forbs across the Atqasuk Grid (AG). Significant differences were determined using one-way analysis of variance and are denoted using an ‘*’ (α = 0.05).

Table 3: Means (±standard error) for vegetation variables by growth form and species across the Atqasuk Grid (AG) from 2012 - 2013. Significance is indicated by *p* values from one-way analysis of variance and significant values are bolded (α = 0.05). NC = No Change. NA = data not recorded. Df = 1 for all. Only plots in which each growth form or species was measured were included in the analysis (n). Test statistics are F values or Kruskal-Wallis chi-squared values.

				Year					
Taxa	n	2012		n	2013		Test statistic	*p* value	Trend
Cover (%)									
Graminoids[b]	30	21.7	±2.8	30	25.6	±2.7	1.32	0.26	2013 > 2012
Carex spp.	27	**18.5**	**±2.1**	**27**	**26.2**	**±3.0**	**4.44**	**0.04**	**2013 > 2012**
Eriophorum spp.[c]	25	30.3	±5.8	24	28.1	±4.3	0.06	0.81	2012 > 2013
Evergreen Shrubs	22	13.0	±1.4	22	12.0	±1.4	0.23	0.64	2012 > 2013
Deciduous Shrubs[b]	20	23.6	±4.0	20	25.9	±4.5	0.20	0.66	2013 > 2012
Forbs[c]	16	5.5	±1.3	16	5.4	±1.1	0.07	0.79	2012 > 2013
Canopy Height (cm)									
Graminoids	30	9.8	±0.7	30	11.0	±0.8	1.22	0.28	2013 > 2012
Carex spp.	26	11.6	±0.8	27	12.5	±1.0	0.49	0.49	2013 > 2012
Eriophorum spp.[a]	24	8.6	±0.7	24	9.6	±0.9	0.36	0.55	2013 > 2012
Evergreen Shrubs[a]	20	4.2	±0.6	20	4.4	±0.8	0.02	0.88	2013 > 2012
Deciduous Shrubs[a]	20	6.6	±0.7	21	6.6	±0.7	0.01	0.94	NC
Forbs[a]	15	3.7	±0.6	14	4.2	±0.7	0.30	0.59	2013 > 2012
Leaf Length (cm)									
Graminoids[a]	30	18.2	±1.1	30	19.2	±1.4	0.19	0.66	2013 > 2012
Carex spp.	28	20.5	±1.1	26	21.3	±1.0	0.31	0.58	2013 > 2012
Eriophorum spp.[c]	21	16.1	±1.4	22	17.3	±1.8	0.12	0.72	2013 > 2012
Evergreen Shrubs	NA	NA	NA	NA	NA	NA	NA	NA	–
Deciduous Shrubs	NA	NA	NA	NA	NA	NA	NA	NA	–
Forbs	NA	NA	NA	NA	NA	NA	NA	NA	–

Table 3 (continued):

Taxa	n	2012		n	2013		Test statistic	*p* value	Trend
Inflorescence Length (cm)									
Graminoids	27	**25.4**	**±1.2**	**26**	**29.0**	**±1.3**	**4.21**	**0.05**	**2013 > 2012**
Carex spp.	20	26.1	±1.3	18	30.6	±2.0	3.50	0.07	2013 > 2012
Eriophorum spp.	15	23.8	±1.8	16	26.8	±1.8	1.39	0.25	2013 > 2012
Evergreen Shrubs	NA	NA	NA	NA	NA	NA	NA	NA	–
Deciduous Shrubs	NA	NA	NA	NA	NA	NA	NA	NA	–
Forbs	NA	NA	NA	NA	NA	NA	NA	NA	–
Density (individuals/10cm^2)									
Graminoids[c]	29	4.7	±0.7	29	4.3	±0.6	0.20	0.66	2012 > 2013
Carex spp.	25	3.0	±0.3	25	2.9	±0.2	0.02	0.89	NC
Eriophorum spp.	21	7.6	±1.9	24	6.1	±1.1	0.65	0.42	2012 > 2013
Evergreen Shrubs[a]	21	10.4	±1.3	21	10.6	±1.4	0.02	0.89	2013 > 2012
Deciduous Shrubs[a]	16	12.6	±2.2	17	10.9	±2.8	0.89	0.35	2012 > 2013
Forbs[c]	15	2.4	±0.5	15	2.5	±0.6	0.02	0.90	2013 > 2012

[a] Log transformed
[b] Square root transformed
[c] Kruskal-Wallis chi-squared values presented

Table 4: Correlations between cover and vegetation variables using simple linear regression coefficients (R^2) for growth forms and species at the Atqasuk Wet (AW) and Atqasuk Dry (AD) sites as well as across the Atqasuk Grid (AG). Control and warmed plots were regressed together and also separately. Significance is indicated by *p* values and significant values are shown in bold ($\alpha = 0.05$). n = the total number of plots included in analyses after removing missing values. NA = data not recorded. Plots were only included in the analysis if the taxa (growth form or species) was measured. The total possible number of plots at the AW and AD site was 48 and 30 at the AG. Cover was square root transformed for all regressions.

Table 4 (continued):

	Leaf Length			Inflorescence Length			Canopy Height			Density			Biomass		
Growth Form/Taxa	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value
Atqasuk Wet (AW)															
Graminoids	48	**0.13**	**0.01**	47	0.02	0.31	48	**0.37**	**0.00**	48	0.00	0.74	48	0.06	0.09
Controls	24	**0.16**	**0.05**	24	0.00	0.78	24	**0.34**	**0.01**	24	0.02	0.56	24	0.04	0.34
Warmed	24	0.10	0.14	23	0.03	0.44	24	**0.31**	**0.01**	24	0.00	0.94	24	0.06	0.24
Carex aquatilis	48	**0.23**	**0.00**	35	0.06	0.15	48	**0.42**	**0.00**	48	0.00	0.93	48	**0.16**	**0.01**
Controls	24	0.09	0.15	19	0.00	0.88	24	**0.47**	**0.00**	24	0.11	0.12	24	0.05	0.30
Warmed	24	**0.23**	**0.02**	16	0.05	0.43	24	**0.21**	**0.02**	24	0.01	0.73	24	**0.25**	**0.01**
Eriophorum angustifolium	40	0.02	0.36	32	0.06	0.18	44	0.01	0.47	41	0.08	0.07	40	0.03	0.27
Controls	20	0.01	0.63	16	0.00	0.81	22	0.00	0.76	21	0.15	0.08	20	0.02	0.55
Warmed	20	0.03	0.48	16	0.13	0.16	22	0.01	0.60	20	0.03	0.45	20	0.04	0.41
Eriophorum russeolum †	36	0.07	0.12	NA	NA	NA	42	0.04	0.21	40	0.08	0.08	36	0.02	0.45
Controls	19	0.15	0.10	NA	NA	NA	21	0.09	0.17	21	0.06	0.29	19	0.00	0.91
Warmed	17	0.03	0.49	NA	NA	NA	21	0.03	0.49	19	0.10	0.20	17	0.09	0.25
Deciduous Shrubs	26	0.09	0.13	32	0.04	0.29	45	0.00	0.82	40	0.06	0.11	NA	NA	NA
Controls	17	0.10	0.21	17	0.01	0.67	21	0.11	0.14	19	0.05	0.38	NA	NA	NA
Warmed	9	0.20	0.23	15	0.04	0.50	24	0.00	0.74	21	0.14	0.10	NA	NA	NA
Salix spp.	26	0.12	0.09	31	0.04	0.27	45	0.00	0.75	40	0.07	0.11	NA	NA	NA
Controls	17	0.15	0.13	16	0.01	0.67	21	0.12	0.12	19	0.05	0.36	NA	NA	NA
Warmed	9	0.20	0.23	15	0.04	0.50	24	0.00	0.74	21	0.14	0.10	NA	NA	NA

Table 4 (continued):

	Leaf Length			Inflorescence Length			Canopy Height			Density			Biomass		
Growth Form/Taxa	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value
							Atqasuk Dry (AD)								
Graminoids	46	0.03	0.21	45	0.01	0.51	46	**0.24**	**0.00**	44	0.07	0.09	46	0.02	0.33
Controls	23	**0.28**	**0.01**	23	0.11	0.12	23	0.15	0.07	21	0.04	0.38	23	0.09	0.16
Warmed	23	0.00	0.96	22	0.01	0.63	23	**0.27**	**0.01**	23	**0.21**	**0.03**	23	0.00	0.86
Hierechloe alpina	26	**0.18**	**0.03**	29	0.09	0.12	30	0.07	0.14	19	0.00	1.00	26	0.03	0.44
Controls	14	0.03	0.55	15	**0.38**	**0.02**	15	**0.29**	**0.04**	10	0.25	0.14	14	0.03	0.56
Warmed	12	**0.40**	**0.03**	14	0.00	0.85	15	0.00	0.93	9	0.31	0.12	12	0.02	0.66
Luzula confusa	39	**0.12**	**0.03**	35	0.11	0.06	37	0.07	0.10	32	0.02	0.41	39	0.00	0.81
Controls	21	0.11	0.14	18	0.05	0.36	20	0.07	0.25	17	0.00	0.95	21	0.13	0.11
Warmed	18	0.17	0.09	17	0.14	0.14	17	0.08	0.29	15	0.11	0.22	18	0.08	0.27
Evergreen Shrubs	48	0.04	0.18	48	**0.20**	**0.01**	48	**0.19**	**0.00**	48	0.06	0.10	NA	NA	NA
Controls	24	0.12	0.09	24	0.01	0.70	24	**0.25**	**0.01**	24	0.08	0.19	NA	NA	NA
Warmed	24	0.02	0.55	24	**0.44**	**0.00**	24	0.11	0.11	24	0.03	0.45	NA	NA	NA
Diapensia lapponica	27	0.01	0.67	31	0.08	0.13	30	**0.20**	**0.01**	24	**0.25**	**0.01**	NA	NA	NA
Controls	12	0.18	0.17	14	0.01	0.79	14	0.26	0.06	9	**0.46**	**0.05**	NA	NA	NA
Warmed	15	0.07	0.34	17	0.13	0.15	16	0.13	0.18	15	0.11	0.22	NA	NA	NA
Vaccinium vitis-idaea	46	**0.15**	**0.01**	37	0.03	0.27	44	0.06	0.10	46	**0.37**	**0.00**	NA	NA	NA
Controls	22	0.07	0.25	21	0.10	0.17	21	**0.27**	**0.02**	22	**0.33**	**0.01**	NA	NA	NA
Warmed	24	**0.25**	**0.01**	16	0.01	0.74	23	0.03	0.43	24	**0.47**	**0.00**	NA	NA	NA

Table 4 (continued):

	Leaf Length			Inflorescence Length			Canopy Height			Density			Biomass		
Growth Form/Taxa	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value	n	R^2	*p* value
Atqasuk Grid (AG)															
Graminoids	30	0.00	0.84	27	0.09	0.14	30	0.07	0.17	29	**0.24**	**0.01**	NA	NA	NA
Carex spp.	27	0.11	0.09	20	0.14	0.11	26	**0.32**	**0.01**	25	**0.22**	**0.02**	NA	NA	NA
Eriophorum spp.	21	0.01	0.65	15	**0.49**	**0.01**	24	0.03	0.46	21	0.11	0.15	NA	NA	NA
Deciduous Shrubs	NA	NA	NA	NA	NA	NA	20	**0.21**	**0.04**	16	0.23	0.06	NA	NA	NA
Evergreen Shrubs	NA	NA	NA	NA	NA	NA	20	0.08	0.22	21	**0.64**	**0.00**	NA	NA	NA
Forbs	NA	NA	NA	NA	NA	NA	14	0.02	0.59	14	0.01	0.73	NA	NA	NA

[†] Inflorescence length was not included as a variable in regressions for *E. russeolum* due to insufficient data for that trait.

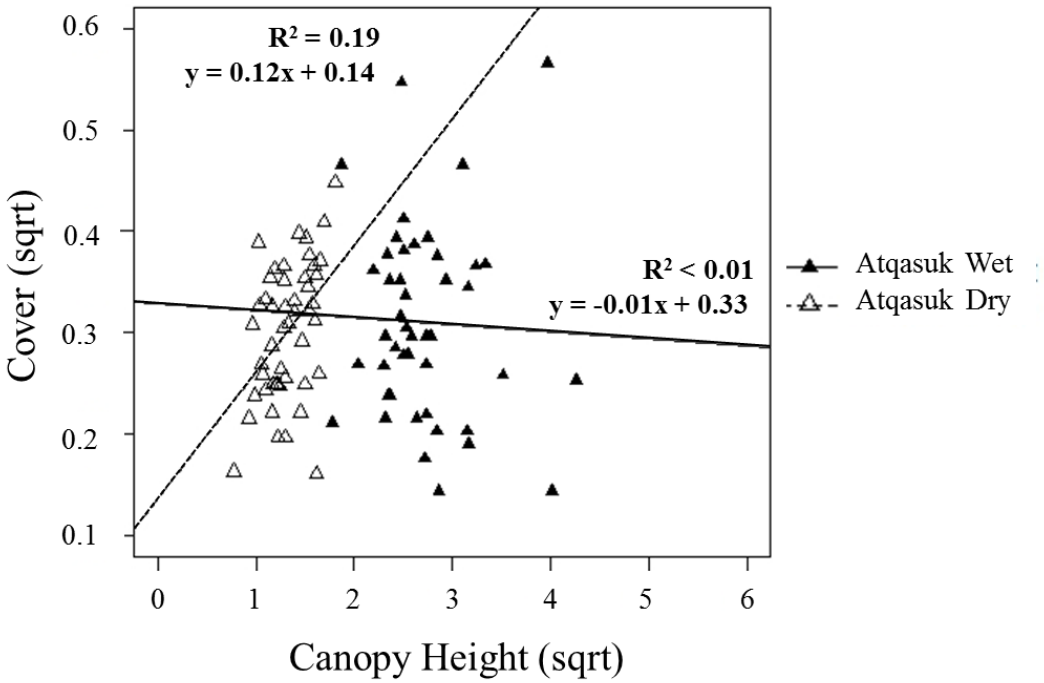


Figure 12: Significant difference in slopes of shrub cover versus canopy height (p = 0.02) from analysis of covariance between the Atqasuk Dry (AD) site and the Atqasuk Wet (AW) site. All values are square root (sqrt) transformed.

Table 5: Coefficients from analysis of covariance between cover and vegetation variables for growth forms and species between the Atqasuk Wet (AW) and Atqasuk Dry (AD) sites. If the slopes were not significantly different, we proceeded to test for differences in intercepts. Only coefficients for growth forms and species with significant differences or with nearly significant differences are shown ($\alpha = 0.05$). Variables for which a significant difference was found are indicated by *p* values and are shown in bold. All values are square root transformed.

	Slope		Intercept		Slope	Intercept
Growth Form/Trait	AW	AD	AW	AD	*p* value	*p* value
Graminoids						
Leaf Length	0.05	0.03	0.14	0.13	0.47	**<0.001**
Inflorescence Length	0.02	-0.01	0.26	0.27	0.25	**<0.001**
Canopy Height	0.13	0.08	-0.06	0.04	0.15	**0.01**
Density	-0.02	0.05	0.39	0.15	0.29	**<0.001**
Shrubs						
Inflorescence Length	0.05	0.17	0.23	-0.06	0.07	0.06
Canopy Height	-0.01	0.13	0.33	0.14	**0.02**	0.67

Table 6: Multiple linear regressions between cover (C) and the following vegetation variables: (leaf length (LL), inflorescence length (IL), canopy height (CH), density (DD), and treatment (TR). Analyses were performed for the dominant growth forms and species at the Atqasuk Wet (AW) and Atqasuk Dry (AD) sites and across the Atqasuk Grid (AG) using data collected in 2012. The *p* values shown represent the final significant models, and variables are listed in order of significance (by *p* values). Significant traits are bolded ($\alpha = 0.05$). n = number of plots included in the regression analysis after missing values were removed. Plots were only included in the analysis if the taxa (growth form or species) was measured. Cover was square root transformed for all regressions.

Growth Form/Taxa	n	Multiple Linear Regressions Final model equations (C = slope_1 + slope_2... + intercept)	R^2 (adj.)	*p* value	Variables Strongly Correlated with Cover
Atqasuk Wet (AW)					
Graminoids	47	C = **0.016089CH** + **0.038485TR** + 0.172838	0.42	<0.001	**Canopy height**, **Treatment**
Carex aquatilis	35	C = **0.018396CH** + **0.056172TR** + (-0.004248IL) + 0.004033LL + 0.307902	0.46	<0.001	**Canopy height**, **Treatment**, Inflorescence length, Leaf length
Eriophorum russeolum	35	C = **-0.009957LL** + **0.034351DD** + **0.008576CH** + 0.223576	0.22	0.01	**Leaf length**, **Density**, **Canopy height**
Atqasuk Dry (AD)					
Evergreen Shrubs	48	C = **0.02994IL** + **0.03438CH** + 0.10723	0.25	<0.001	**Inflorescence length**, **Canopy height**
Vaccinium vitis-idaea	35	C = **0.016247DD** + **0.041413LL** + **0.055625CH** + 0.024439	0.46	<0.001	**Density**, **Leaf length**, **Canopy height**
Graminoids	43	C = **0.013337CH**+ (-0.002658IL) + (-0.022500TR) + 0.219526	0.18	0.01	**Canopy height**, Inflorescence length, Treatment
Atqasuk Grid (AG)					
Graminoids	26	C = **0.019045DD** + 0.372208	0.18	0.02	**Density**
Carex spp.	19	C = 0.02658DD + 0.00885CH + 0.01115	0.28	0.03	Density, Canopy height
Eriophorum spp.	14	C = **0.030355IL** + (**-0.015548LL**) + 0.102682	0.60	<0.01	**Inflorescence length, Leaf Length**
Deciduous Shrubs	16	C = **0.019476CH** + 0.005147DD + 0.034322	0.37	0.02	**Canopy height,** Density
Evergreen Shrubs	19	C = **0.011574DD** + 0.241160	0.59	<0.001	**Density**

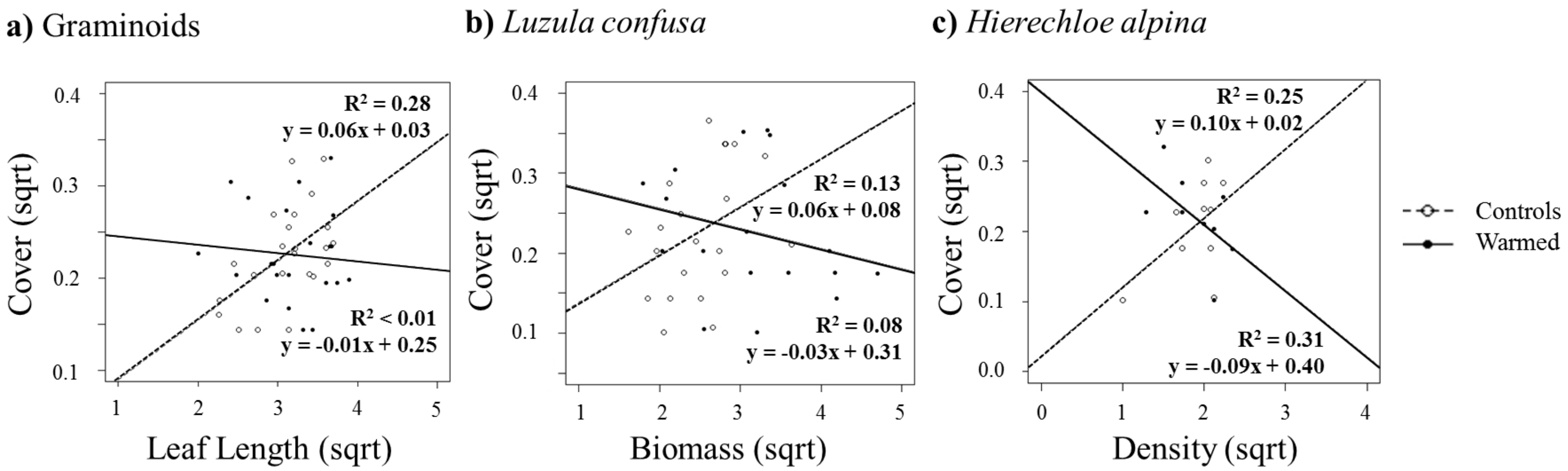


Figure 13: Significant differences in slopes of **a)** graminoid cover versus leaf length (p = 0.03), **b)** *L. confusa* cover versus biomass (p = 0.05), and **c)** *H. alpina* cover versus density (p = 0.03) at the Atqasuk Dry (AD) site. Results are from analysis of covariance between treatments. All values are square root (sqrt) transformed.

Table 7: Coefficients from analysis of covariance between cover and vegetation variables for growth forms and species in controls and warmed plots at the Atqasuk Dry (AD) and Atqasuk Wet (AW) sites. If the slopes were not significantly different, we proceeded to test for differences in intercepts. Only coefficients for growth forms and species with significant differences or with nearly significant differences are shown (α = 0.05). Variables for which a significant difference was found are indicated by *p* values and are shown in bold. All values are square root transformed.

		Slope		Intercept		Slope	Intercept
Site/Growth Form	Trait	Warmed	Control	Warmed	Control	*p* value	*p* value
				Atqasuk Wet (AW)			
Graminoids	Leaf Length	0.07	0.03	0.09	0.21	0.35	**0.01**
	Inflorescence Length	0.02	-0.01	0.28	0.35	0.50	**<0.001**
	Density	-0.01	0.04	0.40	0.26	0.68	**0.00**
	Biomass	0.03	0.01	0.23	0.27	0.47	**0.00**
Carex aquatilis	Leaf Length	0.11	0.05	0.07	0.28	0.28	**0.04**
	Inflorescence Length	0.03	-0.01	0.40	0.51	0.51	**0.01**
	Density	-0.03	0.08	0.62	0.31	0.21	**0.00**
	Biomass	0.04	0.02	0.36	0.40	0.34	**0.01**
Salix spp.	Leaf Length	0.18	0.14	0.09	0.09	0.81	**0.04**
				Atqasuk Dry (AD)			
Graminoids	Leaf Length	-0.01	0.06	0.25	0.03	**0.03**	0.94
Hierechloe alpina	Inflorescence Length	-0.01	0.07	0.27	-0.16	0.07	0.92
	Density	-0.10	0.10	0.40	0.02	**0.03**	0.71
Luzula confusa	Biomass	-0.03	0.06	0.31	0.08	**0.05**	0.98
Evergreen Shrubs	Inflorescence Length	0.24	0.04	-0.19	0.21	0.07	0.44

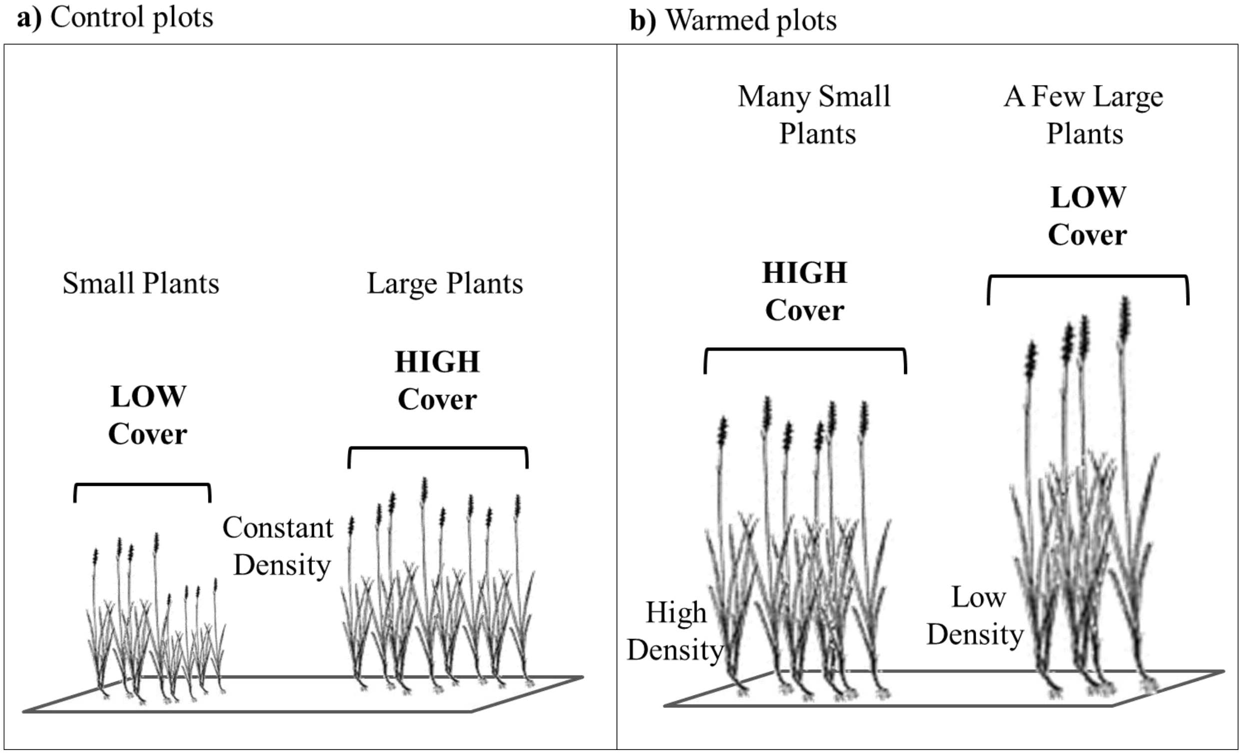


Figure 14: A schematic diagram illustrating the inverse relationship between growth and density observed in graminoids at both the Atqasuk Wet (AW) and Atqasuk Dry (AD) sites for **a)** normal environmental conditions (control plots) and **b)** experimentally warmed conditions (warmed plots).

Discussion

Cover Correlates with Different Vegetation Variables Depending on Growth Form

Our results report changes occurring mainly in shrubs and graminoids, and suggest that these growth forms are the most responsive to climate warming in this low arctic region. This is supported by previous research which has shown that graminoids and shrubs are more sensitive to warming than forbs, particularly in the low arctic (Hollister et al. 2005b; Klady et al. 2011) and may eventually dominate the tundra ecosystem as a result of increased nutrient availability with warming (Bret-Harte et al. 2008).

Graminoids

Graminoids have been shown to be one of the most responsive growth forms to experimental warming, particularly in wet sites, which corresponds to our observation of significant increases in growth with warming at the AW site (Walker et al. 2006; Elmendorf et al. 2012a). We found that graminoid cover at the AW site and the AD site was most strongly related to traits representing the growth of individual plants rather than density (Figure 15). At the AW site, traits relating to plant growth (canopy height and leaf length) increased with warming. Furthermore, *C. aquatilis* decreased in density with warming at this site, presenting strong evidence that the increase in cover was due to increased plant size. Previous research on arctic community dynamics has shown similar increases in canopy height of graminoids resulting from the increased growth of individual plants with warming (Hollister et al. 2005b; Walker et al. 2006). In a study published by Hollister and Flaherty (2010) the above-ground biomass of graminoids increased over several years of experimental warming in Barrow, Alaska. A synthesis of 61 experimental warming studies across a range of sites and community types also showed that warming can be detrimental to graminoid abundance, since graminoid cover is typically more highly associated with cooler and wetter tundra (Elmendorf et al. 2012b). One explanation for such an overwhelming growth response within this growth form is that particularly in wet tundra sites, graminoid density is high (Elmendorf et al. 2012b) and the recruitment and establishment of new individuals (which may contribute to density) may be restricted due to a lack of available bare ground for seed establishment (Hollister et al. 2014). In warmed conditions where the temperature limitation to growth is removed, plants in this type of community may respond mainly by expanding upward (Walker et al. 2006).

It is likely that the graminoid growth form was impacted mainly by dominant constituent species such as *C. aquatilis*. At the AW site, *C. aquatilis* was the only species that consistently demonstrated a change with warming that paralleled changes occurring within the graminoid growth form. While other graminoid species at the AW site exhibited a few significant changes, they were not consistent with the overall growth form, further demonstrating that at the AW site *C. aquatilis* had the most significant impact on its growth form and was likely driving these results. Similarly, across the AG cover of both graminoids and *Carex* was highly influenced by density, a trait that was not evident in *Eriophorum*, the other dominant graminoid. Similar findings have been found in previous studies (Henry and Molau 1997; Hollister and Flaherty 2010).

At both the AW and AD sites, regression results for graminoids and constituent species showed that either canopy height or leaf length were the traits most strongly related to cover. This provides evidence that the importance of growth to cover was consistent between these two differing community types. These findings initially appeared to be inconsistent with the results from across the AG, where density was most strongly related to cover for graminoids. However, from the warming experiment we found evidence of an inverse relationship between growth and density of graminoids, which may clarify these findings. At the AW site *C. aquatilis* increased in growth while decreasing in density. This relationship may become more apparent in the overall growth form across a larger landscape area such as the AG where multiple community types are considered, which could explain the apparent inconsistency across this larger area. Another possible explanation is that species may behave differently within a particular community type than when the 'sum' of the relationships between cover and plant variables is considered across a broader landscape, which has been documented previously (Elmendorf et al. 2012a). Studying relationships between vegetation variables within individual communities such as the AD or AW site is beneficial for determining how gradients such as soil moisture impact plant growth. However, further investigation of these relationships across a landscape may ultimately be more relevant for developing broad-scale climate change predictions.

Shrubs

The traits most strongly influencing shrub cover (both evergreen and deciduous) differed by community type (Figure 15). Deciduous shrub cover was not well correlated with vegetation variables at the AW site, and the variables most strongly related to evergreen shrub cover at the AD site showed a great deal of distinction. Across the AG the variables most correlated with shrub cover also differed by growth form (deciduous or evergreen). Previous research has documented differences in shrub cover depending on the community type (Myers-Smith et al. 2011). Because the variables we measured showed few to no significant differences for shrubs with warming, it is apparent that at these sites shrubs may be less responsive overall to warming than graminoids. Recent studies by Elmendorf et al. (2012a, b) noted that deciduous shrubs increased in abundance with warming, particularly in plots exhibiting warm, wet conditions, while evergreen shrubs varied in their response based on moisture regime. Because of the varied and significant impacts of increasing shrub abundance in arctic tundra, it will be important to consider the expansion patterns of individual shrub types across various temperature and moisture gradients in order to strengthen predictions about future shifts in distribution (Myers-Smith et al. 2011).

Shrub canopy height was related more strongly to overall shrub cover (combined evergreen and deciduous) at the AD site than at the AW site. This was supported by the fact that deciduous shrub cover at the AW site was not well correlated with any plant traits, but the variables correlated with cover of evergreen shrubs at the AD site were canopy height and inflorescence length, which contribute to plant canopy structure. Variables that would enhance canopy height (such as inflorescence length) may be particularly influential for vegetation with a smaller stature, as at the AD site.

Experimental Warming Impacts Correlations between Cover and Vegetation Variables

Past research has shown that warming impacts herbaceous growth forms more strongly and consistently than woody growth forms (Arft et al. 1999). Other studies have suggested that the correlations between physical plant traits and above-ground to below-ground biomass ratios may differ with warming (Hollister and Flaherty 2010). Increases in plant growth once thought to be an initial transient response to a changing climate may actually be sustained with long-term warming (Hudson et al. 2011). Results from our warming experiment at AW and AD are consistent with the changes recorded at these sites since the late 1990s (Hollister et al. 2005a; May and Hollister 2012), indicating that these responses likely are representative of a long-term sustained response.

Experimental warming significantly altered the relationships between vegetation variables and cover in our study, particularly at the AD site. We found that growth forms and species at the AD site were highly impacted by warming in the relationships between cover and vegetation variables, which was exemplified in the significantly different slopes for graminoids, *L. confusa*, and *H. alpina*. For graminoids and *L. confusa*, growth traits (leaf length and biomass, respectively) were more strongly correlated with cover in the control plots than in the warmed plots, suggesting an inverse relationship between growth and density (Figure 14). It is possible that small-scale variations in microclimate and abiotic factors have a greater influence on growth of certain plant functional types in the controls because different types of vegetation are adapted for different micro-climate conditions (Walker et al. 1989; Hector et al. 1999; DeMarco et al. 2011; Myers-Smith et al. 2011). Under normal environmental conditions such as the control plots, different individuals within a species may exhibit plasticity in their growth depending upon the available resources. In this way some plants may be larger and some may be smaller, contributing to higher and lower percent cover, respectively. Because the growth of tundra plants is especially limited by temperature, the addition of experimental warming results in increased growth for nearly all vascular plants. On one hand high percent cover with experimental warming may be explained by the increased growth of plants that were initially larger under normal conditions, resulting in fewer large plants as smaller individuals are competitively excluded (low density). It has been shown that warming facilitates vertical plant growth and overall closure of the canopy as growth increases (Elmendorf et al. 2012b). Conversely, individuals that were initially smaller under normal conditions would not grow as large but the density would remain the same, resulting in low percent cover relative to their larger counterparts. While competition and its impacts on a community were not directly measured in this study, similar findings have been published showing that plant-plant interactions have significant effects on community composition and assemblage (Hollister et al. 2005a; Klady et al. 2011; le Roux et al. 2013).

For *H. alpina*, density had a strong positive relationship with cover in the control plots, but a strong inverse relationship with cover in the warmed plots. In this case under natural environmental conditions such as the control plots an increase in plant density corresponded with an increase in cover. Therefore, high percent cover may be explained by the presence of many individual plants as opposed to large individual plants in the control plots. However in experimentally warmed conditions, this relationship suggests that increased plant density corresponds with decreased cover, which is inconsistent with the relationship between growth traits and cover that was previously described for graminoids and *L. confusa* at this site. However, this anomaly may be explained by the water stress conditions documented at the AD site both in this study and in previous studies (May and Hollister 2012). Under experimentally warmed conditions, many individuals may be present (high density) but the lack of water availability would restrict them to a small size, leading to low percent cover. Conversely, individual plants which grow large due to warming eventually exclude smaller plants through competition for water, resulting in higher percent cover from a few large individuals. While it is likely that the water stress conditions at this site provide sufficient explanation for these results, further investigation is suggested to explore these relationships. Other abiotic factors, such as the location and elevation of the AD site may have also negatively impacted the vegetation in the warmed plots. Due to their frequent location on elevated ridges, dry heath communities may be more vulnerable to harsh environmental conditions such as high winds and lower winter snow cover, leading to greater susceptibility to warming (Oberbauer et al. 2013). Environmental disturbance may also significantly impact the way in which differing vegetation types respond to warming. The AD site is known to be frequently disturbed by caribou throughout the winter months, which may influence growth of vegetation during the growing season.

Abiotic Variables Influence Vegetation Cover

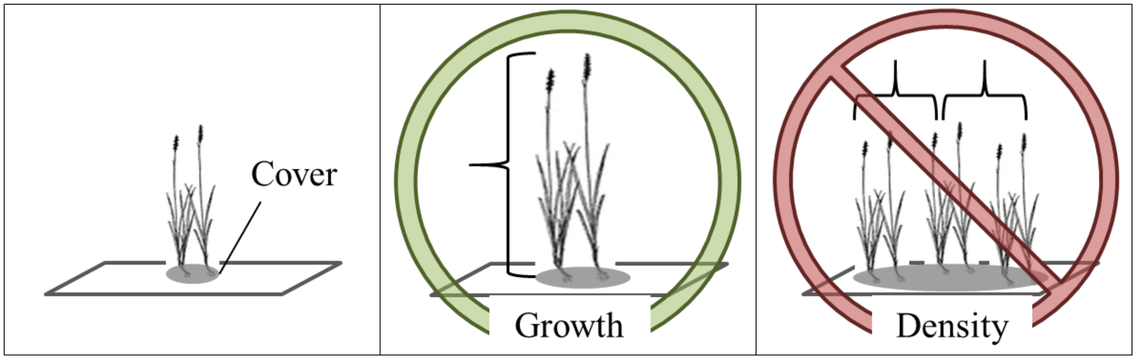
The significant relationships we observed between vascular cover and abiotic variables show that cover is also impacted by the conditions of the surrounding environment (Lantz et al. 2010; Elmendorf et al. 2012b). Our results show that soil temperature and moisture were the variables most commonly related to vascular plant cover across the landscape. It has been well established that vegetation community assembly across the tundra landscape is based on abiotic conditions such as soil moisture and temperature (Berdanier and Klein 2011), as well as active layer thickness (i.e. thaw depth) which is influenced by climate warming (Kane et al. 1991; Hinkel et al. 2001). Several previous studies have also found that abiotic conditions strongly influence the growth and reproduction of tundra plants (Chapin 1985; Chapin et al. 1995). Organic matter quality and snow accumulation can have major impacts on microclimate conditions and nitrogen (N) mineralization during the growing season (DeMarco et al. 2011). While abiotic variables certainly influence plant growth patterns and distribution, they may be secondary in importance to plant-plant interactions (Klady et al. 2011; le Roux et al. 2013). While this study was concerned primarily with the influence of the environment on vegetation growth patterns, there is evidence that vegetation composition also alters soil abiotic conditions such as temperature and moisture in Arctic and alpine environments, contributing to small-scale heterogeneity across the landscape (Aalto et al. 2013). The presence of certain types of vegetation may serve to mediate the response of abiotic variables and soil communities to climate change (Lamb et al. 2011; Aalto et al. 2013).

Correlations for Growth Forms Inconsistent with Correlations for Species

This study emphasizes the importance of making predictions based on the responses of individual species in place of more generalized grouping schemes such as growth form. We observed that correlations between cover and vegetation variables for growth forms were not always consistent with those of their constituent species, in part because the aggregate growth form mean values used were highly influenced by dominant species but did not necessarily pertain to every species. At AW, *C. aquatilis* was the only species that mirrored the changes in graminoids with warming, likely due to its dominance at the site. Conversely, at AD, a significant increase in canopy height of evergreen shrubs was not mirrored by any of the study species within that growth form. Basing conclusions solely on the growth form results therefore underrepresents the response of individual species, and may underestimate the overall vegetation response to warming (Chapin and Shaver 1985; Hudson et al. 2011). Species within a growth form do not necessarily share morphology or physiology, often resulting in heterogeneous responses to the same treatment (Chapin et al. 1995). For example, evergreen shrub species are morphologically diverse, with some having a lower, more prostrate structure and others being more errect (Hollister 2003; May and Hollister 2012). This heterogeneity leads to complications in making predictions about cover changes, as most of the current global assessments are applied to vegetation at the growth form level (Elmendorf et al. 2012b). Chapin et al. (1996) pointed out that plant functional types or growth forms traditionally used by ecologists are useful in predicting overall vegetation response to environmental changes, but are not as effective for predicting shifts in plant distributions. Other factors not measured here such as community composition, diversity, colonization rates, and species-specific nutrient storage and use strategies all likely affect the vegetation cover patterns that we can expect to see with a warmer climate (Chapin et al. 1996). Because it is often impossible to perform vegetation analysis without some grouping strategy, it may be beneficial to determine a new method other than combining species by growth form, as has been suggested previously (Hollister et al. 2014). Grouping by functional type, which takes into account the physiological properties of the vegetation, may be a more appropriate method.

Caution should be used in interpreting the relationships we documented between cover and traits for shrubs. Inconsistencies in shrub growth patterns may be an artifact of the grouping methods we employed throughout this study. Deciduous shrubs at the AW site consisted of the two dominant species of willows (*Salix polaris* and *Salix pulchra*) as well as a dwarf birch (*Betula nana*), whereas at the AD site they included only *Salix phlebophylla*. Evergreen shrubs at the AD site included *Cassiope tetragona*, *Ledum palustre*, *Diapensia lapponica*, and *Vaccinium vitis-idaea*. Across the AG, *B. nana*, *L. palustre,* and *V. vitis-idaea* dominated the shrub growth forms (Appendix). These different species, although often grouped together for comparisons by growth form, were very morphologically diverse and their inherent differences may have significantly altered the overall growth form results. Moreover, not all growth forms were present within each site, making direct comparisons between sites difficult. For example, evergreen shrubs were absent at the AW site, while deciduous shrubs were infrequent at the AD site. Of all the sites, shrub species richness was greatest across the AG, which was the only location where multiple species within each shrub growth form were present (Appendix). It is also possible that the traits we measured for shrubs at the AW site did not accurately capture which specific growth mechanisms were most influential to cover, which could be a derivative of grouping the two willows into a single species group (*Salix* spp.). The grouping of two species that exhibit morphological differences may present some ambiguities in the interpretation of the results.

a) Graminoids



b) Shrubs

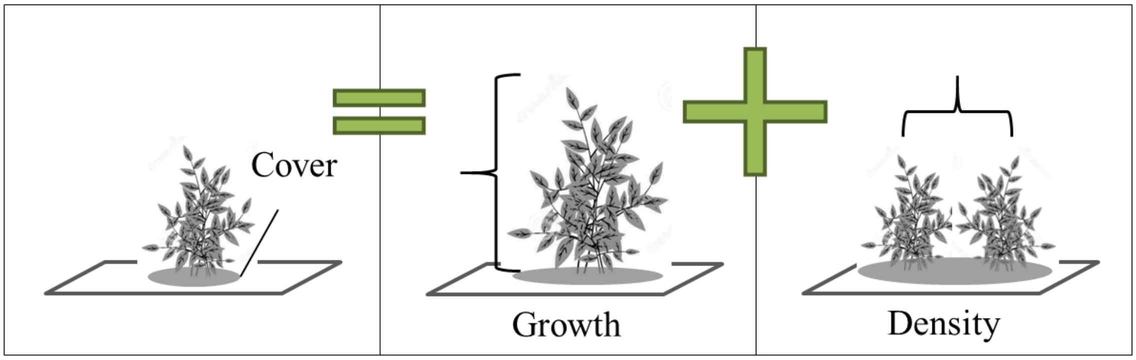


Figure 15: A schematic diagram illustrating the underlying processes impacting vegetation cover for **a)** graminoids and **b)** shrubs at the sites in Atqasuk, Alaska. Cover of graminoids was most strongly related to growth of individual plants, whereas the processes impacting cover of shrubs varied by community type.

CHAPTER III: CONCLUSION

Climate warming has far-reaching consequences on many aspects of global ecosystem functioning, including carbon budgets, energy transfer, hydrology, and plant community dynamics. The Arctic presents a valuable frontier for climate change research, as the most significant changes have been observed and are predicted to continue in these regions due to the temperature limitations to ecosystem functioning. Vegetation communities are particularly important, because they influence energy distribution to other trophic levels and play a major role in carbon cycling, energy balance, and habitat quality, all of which have been shown to be affected by prolonged climate warming. Although percent cover has long been a common method of documenting vegetation change with warming, the underlying processes influencing cover change for different growth forms and species are unclear. The balance in the factors contributing to canopy structure such as the size of individual plants (growth) and the number of individual plants (density) may be critical in determining the predictability of future change. In this study we examined the relationships between cover and vegetation variables relating both to plant growth and density. We found that the vegetation variables influencing cover differed by growth form and species across community types, and with experimental warming. We show that the cover of graminoids was influenced more by growth of individual plants rather than density at the AW and the AD sites. Although across the grid cover of graminoids was most strongly correlated with density, cover of the dominant graminoid *Carex* was strongly correlated with canopy height, which relates to plant growth. Thus there appears to be an inverse relationship between growth and density of graminoids at these sites. Cover of shrubs (both evergreen and deciduous) was influenced by different traits depending on community type. Vegetation variables correlated with cover at the AD site varied with warming, while at the AW site warming resulted in consistent directional responses. Leaf length in graminoids, biomass in *L. confusa*, and density in *H. alpina* were more strongly correlated with cover in the control plots than in the warmed plots at this site, providing further evidence of an inverse relationship between traits representing growth and density. Additionally, we found that abiotic variables were important for determining the distribution of cover for various growth forms and species. Shrubs and forbs seem to have different environmental requirements than graminoids, which influences the cover distribution of these dominant growth forms across the landscape. We also found that the responses of individual species were often quite different from their associated growth forms, along with the relationships between cover and the vegetation variables. For example, at the AW site *C. aquatilis* was the only species that reflected the same changes as were apparent in graminoids with warming. At the AD site the vegetation variable most strongly correlated with cover for evergreen shrubs was inflorescence length, whereas the most strongly related variables for *D. lapponica* and *V. vitis-idaea* were density. This provides evidence that changes in the relationships between vegetation cover and other traits as a result of warming is species specific. Therefore, great caution should be used when attempting to apply findings across broad growth forms or functional groups. We suggest that predictions regarding vegetation cover response to continued climate warming are made on a species by species basis, and that the specific factors driving cover for each are taken into careful consideration in order to improve the accuracy of future predictive models. Continued research at the landscape level is suggested to further investigate these patterns as the manner in which vegetation responds to climate warming will have far-reaching ecosystem consequences.

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APPENDIX

Table A-1: Vascular species present at the Atqasuk Dry (AD) and Atqasuk Wet (AW) sites in 2012. Abundance is the % cover averaged across all plots in which the species was present. Species used in analysis are bolded. n = the total number of plots included in analyses.

Species Present	n	Abundance	Family	Growth Form
		Atqasuk Dry (AD)		
Antennaria friesiana	1	1.03	Asteraceae	Forb
Artemisia borealis	2	4.36	Asteraceae	Forb
Carex bigelowii	10	11.17	Cyperaceae	Graminoid
Cassiope tetragona[‡]	45	5.46	Ericaceae	Evergreen Shrub
Diapensia lapponica	**34**	**4.48**	**Diapensiaceae**	**Evergreen Shrub**
Hierechloe alpina	**31**	**4.48**	**Poaceae**	**Graminoid**
Ledum palustre[‡]	47	12.80	Ericaceae	Evergreen Shrub
Luzula arctica	2	1.03	Juncaceae	Graminoid
Luzula confusa	**40**	**5.80**	**Juncaceae**	**Graminoid**
Minuartia obtusiloba	5	3.33	Caryophyllaceae	Forb
Polygonum bistorta	13	2.78	Polygonaceae	Forb
Salix phlebophylla	8	3.09	Salicaceae	Deciduous Shrub
Trisetum spicatum	29	5.45	Poaceae	Graminoid
Vaccinium vitis-idaea	**46**	**10.60**	**Ericaceae**	**Evergreen Shrub**
		Atqasuk Wet (AW)		
Betula nana	3	11.34	Betulaceae	Deciduous Shrub
Carex aquatilis[†]	**48**	**24.21**	**Cyperaceae**	**Graminoid**
Dupontia fisheri	23	1.61	Poaceae	Graminoid
Eriophorum angustifolium	**46**	**7.32**	**Cyperaceae**	**Graminoid**
Eriophorum russeolum	**45**	**5.26**	**Cyperaceae**	**Graminoid**
Luzula wahlenbergii	2	2.06	Juncaceae	Graminoid
Pedicularis sudetica	8	1.28	Scrophulariaceae	Forb
Polygonum viviparum	4	1.03	Polygonaceae	Forb
Salix polaris	**35**	**6.47**	**Salicaceae**	**Deciduous Shrub**
Salix pulchra	**43**	**10.40**	**Salicaceae**	**Deciduous Shrub**

[†] *C. aquatilis* at AW includes *C. rotundata* and *C. rariflora* due to their low individual abundance

[‡] *C. tetragona* and *L. palustre* were not used for species analysis due to data consistency concerns

Table A-2: Vascular species present with their abundances across the Atqasuk Grid (AG) in 2012 and in 2013. Abundance is the % cover averaged across all plots in which the species was present. Species present in < 3 plots for any given year were removed from analysis due to their low abundance. n = the total number of plots included in analyses.

	n		Abundance			
Species Present	2012	2013	2012	2013	Family	Growth Form
Andromeda polifolia	3	9	2.83	4.38	Ericaceae	Evergreen Shrub
Betula nana	12	13	33.10	35.69	Betulaceae	Deciduous Shrub
Carex aquatilis	21	18	18.74	29.59	Cyperaceae	Graminoid
Carex bigelowii	11	10	13.12	19.18	Cyperaceae	Graminoid
Cassiope tetragona	12	15	10.06	8.80	Ericaceae	Evergreen Shrub
Dupontia fisheri	2	0	1.01	0.00	Poaceae	Graminoid
Empetrum nigrum	2	2	6.19	5.15	Empetraceae	Evergreen Shrub
Eriophorum angustifolium	6	5	7.63	8.76	Cyperaceae	Graminoid
Eriophorum russeolum	9	8	10.98	23.18	Cyperaceae	Graminoid
Eriophorum vaginatum	19	17	34.16	33.53	Cyperaceae	Graminoid
Ledum palustre	18	18	14.80	13.75	Ericaceae	Evergreen Shrub
Luzula arctica	2	2	1.03	1.03	Juncaceae	Graminoid
Luzula confusa	3	2	9.28	16.49	Juncaceae	Graminoid
Luzula wahlenbergii	1	1	1.03	1.03	Juncaceae	Graminoid
Pedicularis lapponica	2	2	4.12	2.58	Scrophulariaceae	Forb
Pedicularis sudetica	1	4	2.06	1.80	Scrophulariaceae	Forb
Petasites frigidus	0	1	0.00	1.03	Asteraceae	Forb
Polygonum bistora	1	2	6.19	6.19	Polygonaceae	Forb
Potentilla hyparctica	1	0	1.03	0.00	Rosaceae	Forb
Polygonum viviparum	0	1	0.00	1.03	Polygonaceae	Forb
Pyrola grandiflora	1	1	3.09	3.09	Pyrolaceae	Forb
Ranunculus pallasii	1	1	3.06	2.06	Ranunculaceae	Forb
Rubus chamaemorus	12	10	5.93	6.29	Rosaceae	Forb
Salix polaris	7	6	10.15	13.75	Salicaceae	Deciduous Shrub
Salix pulchra	9	8	14.20	19.20	Salicaceae	Deciduous Shrub
Trisetum spicatum	6	6	13.06	8.42	Poaceae	Graminoid
Vaccinium vitis-idaea	20	20	13.55	14.07	Ericaceae	Evergreen Shrub