DOCUMENTING TUNDRA PLANT COMMUNITY CHANGE IN NORTHERN ALASKA

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Master of Science

By

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To

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No part of the world can be truly understood without knowledge of its garment of vegetation, for this determines not only the nature of the animal inhabitants but also the occupations of the majority of human beings. -Ellsworth Huntington

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ABSTRACT

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Warming in the Arctic has been documented and is expected to continue. This project investigates responses of tundra plant communities to warming at four sites in northern Alaska. Each site consisted of 24 experimentally warmed plots and 24 control plots. The design of the research allowed comparisons between the responses of the vegetation to warming with changes occurring in the control plots over time. First the method used to monitor vegetation was validated. The point frame method used included only the uppermost and lowermost encounter of a plant below each grid point compared to the typical procedure where every contact is recorded. The top and bottom method underrepresented the species cover for between 29 to 44% of the taxa depending on the site however this method was nearly equal as the all contact method in its ability to detect a response to warming and to estimate aboveground biomass. Therefore the top and bottom only method was used to document vegetation change occurring naturally and due to experimental warming over 15 years with emphasis on the consistency of the response over time and across locations. Changes between years in the control plots were generally larger than were observed in experimentally warmed plots, however changes between years were mostly in different directions and the changes were not consistent across locations. Responses to experimental warming were generally larger initially and diminished over time. The number of taxa that responded consistently over time, although relatively few, was greater in response to warming (22 taxa) than that observed in the control plots (8 taxa). However, the response to experimental warming in early years of the experiment was a poor predictor of later years (24 out of 83 taxa). In conclusion, the top and bottom contact only method of point frame sampling was found to be effective at monitoring community responses and the response of tundra vegetation to warming was found to be heterogeneous across time and space.

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Chapter I: Introduction

I.1 Arctic (Tundra Environment)

The Arctic is defined as the region that is north of the Arctic Circle $(66^{\circ}21^{\circ})$ latitude). Arctic regions are mostly covered by tundra and polar desert landscapes, both are often underlain by permafrost which can lead to abrupt changes in vegetation cover (ACIA, 2004; Billings and Mooney, 1968; Bliss, 1962; Savile, 1972).

Arctic conditions are often harsh, characterized by months of darkness during the winter and with continuous daylight in the summer (ACIA, 2004). Summers are cool and short while winters are long with very cold temperatures making plant growing seasons short (Bliss, 62; Savile, 1972). Temperatures during growing seasons are often just above 0^oC and frequently drop below freezing during the night (Chapin and Shaver, 1985; Savile, 1972). Light intensity at high latitudes is lower compared to more temperate regions, however continuous light during the summer compensates for low intensity making total radiation comparable to temperate regions (Bliss, 1962; Billings and Mooney, 1968; Ledrew and Weller, 1978). Soil temperatures are affected by light presence as it quickly warms soil temperatures in area with sparse vegetation (Billings and Mooney, 1968).

Arctic soils can be unstable due to intense and often uneven frost action causing polygons and frost scars in the landscape (Bliss, 1971). These landscape formations

contribute to the spatial heterogeneity of plant communities (Sigafoos, 1952). Due to a plant canopy buffering effect soils can remain thawed later into the fall and even after cooling air temperatures halt aboveground vegetation metabolic processes (Chapin and Shaver, 1985).

Low atmospheric inputs of nitrogen, essentially no weathering of parent material, and low levels of microbial activity cause soils to be very nutrient limiting (Bliss, 1971; Chapin and Shaver, 1985; Russell, 1940; Savile, 1972). Frozen soils also impede drainage and enhance surface flow (Bliss, 1973; Russell, 1940). When these difficult conditions are alleviated plants often respond quickly. This is demonstrated around animal carcasses and old campsites that infuse the immediate area with nutrients can cause increased growth for years (Savile, 1972).

In addition to freezing soils, snow and ice also play a role in making Arctic conditions harsh. Abrasion caused by sustained winds along with snow and ice cause direct, mechanical injuries to plants (Bliss, 1962; Savile, 1972). Drifting snow also contributes to arctic landscape heterogeneity by filling in and protecting low areas while exposing higher areas. This uneven distribution of snow leads to an uneven distribution of water in the spring during snowmelt (Bliss, 1962).

Warming temperatures have been documented in the Arctic for the last century and have increased over recent decades (ACIA, 2004; Cattle and Crossley, 1995; IPCC, 2007). Short growing seasons and harsh conditions make Arctic regions difficult for

plants to grow however these factors also make the Arctic sensitive to climate fluctuations (ACIA, 2004; Chapin and Shaver, 1985; IPCC, 2007).

I.2 Arctic Plant Communities

Arctic plants have many adaptations that allow for them to survive such low temperatures, such as short stature, growing in dense clumps, and shallow root systems that are confined to the active layer (Bliss 1956; Bliss 1962; Chapin and Shaver 1985; Savile 1972; Warren and Wilson 1957). Adaptations in metabolic processes also allow for growth at low temperatures and protection from damage (Billings and Mooney 1968; Bliss 1962; Savile 1972). Photosynthesis rates have been shown to greatest between 10- 15° C while other adaptations such as leaf shape and sun tracking in genera such as *Papaver* add in keeping internal temperatures warm (Johnson and Tieszen 1973; Mölgaard 1982; Tieszen 1973; Wager 1941). Flowers are often large and brightly colored to attract pollinators that are often scarce and scattered (Bliss 1971). Flower buds are also often held for long periods and developed close to the ground to protect from freezing before elongating for pollination (Bliss 1962; Bliss 1971; Chapin and Shaver 1985; Billings and Mooney 1968; Sorenson 1941).

Desiccation is a continuous challenge as winds are often strong and for much of the year water is in an unusable form. Some plants are able to commence growing early in the season when they are still protected by a layer of snow (Savile 1972). In order to prevent excessive water loss many arctic plants have developed pubescence on leaves and buds to lower air circulation (Bliss 1971; Savile 1972). Plants are often densely clumped

and confined to low lying areas to protect against wind and snow sheer (Bliss 1962; Savile 1972; Warren and Wilson 1959).

Life cycle adaptations also help arctic plants survive and reproduce under harsh conditions. Annuals are rare in Arctic systems because short growing seasons and limited nutrient reserves make it difficult for them to complete their life cycles (Billing and Mooney 1968; Savile 1972). In order to prevent loss of reserves many plants are evergreen and have slow rates of growth (Billings and Mooney; Bliss 1971; Johnson and Tieszen 1976; Savile 1972). Often nutrient reserves are used to sustain early season growth and are recouped later in the growing season when photosynthesis rates are higher (Shaver and Billings 1976; Savile 1972). Neighboring plants grow and develop simultaneously to increase pollination and decrease herbivory rates (Bliss 1956). Vegetative reproduction is very common and in many cases is the primary method of spreading due to high degrees of variation in flowering rates (Bliss 1962; Bliss 1971; Savile 1972). Flowering rates are influenced by conditions present in previous years and often plants are self pollinated due to landscape heterogeneity and rare pollinators (Sorenson 1960; Bliss 1962).

Arctic plant communities are often spatially heterogeneous due to widely varying conditions and there is a large reduction in species diversity with increasing latitude (Bliss 1962). Around 900 species have limited ranges in the Arctic with around 200 being circumpolar and because of similar conditions between systems there is much species overlap between alpine and arctic regions (Billings and Mooney 1968; Bliss 1973). The

low Arctic regions are often dominated by vascular plants, while high Arctic regions are dominated by bryophytes and lichens where at high latitudes biomass of these two growth forms can be several times that of vascular plants. (Billings and Mooney 1968; Chapin and Shaver 1985). Bryophytes tend to dominate moister areas and lichens tend to dominate drier areas (Bliss 1971). Arctic plant communities are often simple in structure and in early successional stages due to a history of frequent glacial advances and retreats (Savile 1972).

The simplicity of communities in the Arctic coupled with adaptations to harsh growing conditions causes them to be vulnerable to perturbations, such as those associated with climate change (Bliss 1973). Higher temperatures spur increased growth rates in Arctic plants (Arft et al 1999; Bliss 1962; Chapin et al 1995). Shrub abundance has increased in recent years at higher latitudes where they were previously at a disadvantage (Tape et al, 2006). Also, increased temperature and the subsequent higher evaporation rates areas that are moist will begin to dry making conditions more difficult for bryophytes (Chapin et al 1995).

I.3 International Tundra Experiment (ITEX)

This project is a part of a larger project called the International Tundra Experiment (ITEX). ITEX is a circumpolar, network of researchers from over 11 countries (Figure I.1). The focus of ITEX is primarily the investigation of Arctic plants species response to increases in temperature in the immediate environment (Webber and Walker 1991). All sites within the project achieve some kind of temperature warming

scheme, with most by using small open top warming chambers. Experimental observations in all sites focus on the effect of warming on plant growth, phenological development, and community responses to warming (Molau 1993; Molau and Mölgaard 1996). Data collected within the ITEX network is then pooled in order to monitor the effects of warming temperatures across the entire biome.

I.4 Layout and goals of this project

This thesis is the continuation of a project started by Dr. Patrick Webber in 1994, and is currently continued and maintained by Dr. Robert Hollister. There are four study sites that were established between 1994 and 1996. All of the sites are located in northern Alaska, with two sites near Barrow, Alaska $(70^{\circ}29^{\circ}N, 157^{\circ}25^{\circ}W)$ and two sites near Atqasuk, Alaska (71°18'N, 156°40'W). Each site consists of 24 experimentally warmed and 24 control plots. Warming is achieved using open-top, fiberglass, hexagonal chambers that are placed over each plot every year shortly after snowmelt. Within each site an array of observations are made weekly including phenological observations of growth and flowering.

This thesis will focus on community measure observations made at 3 samplings (1995-96, 2000, and 2007-08) using a point frame method. Chapter II will focus on validating the top and bottom only method of point frame measurement (Molau and Mölgaard 1996). Specifically the relationship between this widely used method and an all contact method to determine any difference between estimates in the two types of measurement and in their ability to detect warming responses. Chapter III will focus on

how control plots change over time and how communities in warmed plots respond to increased temperatures, both across time and across the landscape. Furthermore, this chapter will investigate how the warming response changes over time in the experiment and the ability to use this response to predict the conditions in a community at some point in the future.

A

B

Figure I.1 Symbol (A) and map (B) of the original International Tundra Experiment (ITEX) study sites. Site 13 is Barrow, Alaska (Molau and Mölgaard 1996).

Chapter II: Validation of a Simplified Point Frame Method to Detect Change in Tundra Vegetation

II.1 Introduction:

Vegetation change is an area of interest because plant community composition reflects how the ecosystem functions as a whole. Arctic vegetation change is of particular interest as it is expected to experience the greatest amount of warming of any region (ACIA 2005; IPCC 2007). Warming in the Arctic has been documented for over a century, however this trend has become more pronounced in the $20th$ century (Cattle 1995; IPCC 2007). Plant communities in the Arctic are adapted to cool, short growing seasons and long, cold winters (Wilson 1959; Bliss 1962; Billings 1968). As a result, communities in this region can be affected by even small increases in temperature (Chapin and Shaver 1985; Arft et al 1999; Hollister et al 2005). Vegetation changes can impact how Arctic communities function, i.e. nutrient cycling, growth rates, and phenological progressions (Sorensen 1941; Chapin and Shaver 1985; Arft et al 1999). Warming can lead to increases in vascular plant cover, in particular an increase of graminoids and shrubs, both in expansion within regions (Hobbie and Chapin 1998; Hollister et al 2005; Walker et al 2006; Wilson and Nilsson 2009) and expansions into new regions (Stow et al 2004; Chapin et al 2005; Tape et al 2006). Increases in these

growth types can negatively affect others, such as bryophytes and lichens, further altering how the community functions (Epstein et al 2004; Wahren et al 2005; Joly et al 2009).

There are several of methods by which changes in plant communities are monitored. The point intercept method is often favored in short stature communities and there are many variations of this method used (Levy 1927; Walker 1996; Booth et al 2006). This method has also been used in many recent long-term vegetation monitoring studies because it is non-destructive and allows for exact resampling of vegetation; however, all contact methods of point framing cover estimation have their own set of drawbacks as they often are labor intensive and time consuming, leading to lower spatial and temporal replication. The International Tundra Experiment (ITEX) network uses a time saving modification to the point frame method that simplifies data collection by sampling only the uppermost and lowermost contacts at every point on the grid in each plot (Walker 1996) as opposed to the traditional sampling of every contact. This modification of the point frame method is commonly used and has been cited by over 20 studies for assessing changes in arctic tundra communities. The main use of this method is to monitoring how warming affects plant communities (Hollister et al 2005; Walker et al 2006). Several studies have also applied this simplified point frame method to monitoring how plant communities are affected by other physical environment changes such as soil pH (Gough et al 2000), permafrost depth (Schuur et al 2006), snow depth (Wahren et al 2005), and grazing (Kitti and Forbes 2006; Soppela et al 2006; Zhou et al

2006; Kitti et al 2009). Despite its wide use, there have been no studies to assess its ability to accurately detect community change.

This study investigates the effectiveness of the top and bottom contact only method (TB method) of point framing as outlined in the ITEX manual (Walker 1996) by comparing its results to the more time and labor intensive traditional method of sampling all contacts (AC method) at each point on the point frame grid. Our investigation included three types of comparisons. First, we determined if there was a difference between the two methods in estimates of plant cover and diversity. Second, we investigated the ability of the TB method to detect plant community responses to experimental warming as effectively as the AC method for all types of cover and diversity indices. Finally, we assessed the ability of the TB method to estimate aboveground plant biomass compared to the AC method.

II.2 Methods:

II.2.1 Site Descriptions

Our study included four sites established between 1994 and 1996 in two regions in Northern Alaska. The two regions were located near Barrow, AK $(70^{\circ}29^{\circ}N,$ $157^{\circ}25'$ W) and 100km south near Atqasuk, AK (71 $^{\circ}18'$ N, 156 $^{\circ}40'$ W). Within both regions a wet and dry site was monitored. The Barrow region has a mean July temperature of 3.7° C (Brown et al 1980). The Barrow Dry site is situated on a well drained beach ridge above a drained thaw lake with moderately well drained xeric Pergelic Cryaquept soils underlain with fine silt, sand and gravel. The Barrow Wet site is

in a frequently inundated zone between the dry site beach ridge and a drained lake basin with poorly drained histic Pergelic Cryaquept soils underlain with fine silt. Thaw depth in the Barrow typically ranged from 50-100cm at the end of the growing season, with the Dry Site having thicker active layers (Hollister et al 2006). The Atqasuk region has a mean July temperature of $9^{\circ}C$ (Haugen and Brown 1980). The Atqasuk Dry site is situated on a well drained, ridge above a thaw lake with well drained pergelic cryosamment soils underlain with aolian sand. The Atqasuk Wet site is located in a frequently inundated meadow at the edge of a partially drained thaw lake with poorly drained histic pergelic cryaquept soils underlain with aolian sand and silt. Thaw depth in Atqasuk ranged from 90 to 110cm at the end of the growing season, with the Atqasuk Dry Site having thicker active layers (Hollister et al 2006). Topographic changes within each of the sites are small $\langle 0.5m \rangle$ however even small variation is associated with significant changes in soil moisture and plant community composition (Britton 1957; Engstrom et al 2005; Engstrom et al 2008).

All four sites consisted of 24 control and 24 warmed $\sim 1 \text{m}^2$ plots (192 plots total). Experimental warming was achieved using hexagonal open-top chambers (OTCs) that were installed shortly after snowmelt and removed at the end of the growing season each year. The Barrow Dry site was established in 1994, the Barrow Wet site in 1995, and both Atqasuk sites in 1996. The OTCs were constructed of Sun-Lite HPTM fiberglass and installed according to the guidelines outlined in the ITEX manual (Molau and Mölgaard 1996). OTCs have been shown to warm air temperatures at the sites by an

average of 0.6 to 2.2° C over the summer (Hollister et al 2006). Furthermore, OTCs have been shown to be effective at simulating the response of the plant community to a warm year and are believed to be a reasonable analog of climate change (Hollister and Webber 2000).

II.2.2 Point Frame Method

All plots were sampled between mid-July and early August; the Atqasuk sites were sampled in 2007 and the Barrow sites in 2008. Sampling was done using the nondestructive point frame method outlined by Walker (1996). A 100 point grid that was leveled above the canopy in each plot using permanent markers which allow for the grid to be reinstalled in the same position and orientation year after year. The grid was 75cm by 75cm with measurement points every 7cm .

At each point on the grid a graduated ruler was lowered to the first contact within the plant canopy. At each contact the taxon, live/dead status and height were recorded. Height for each contact was calculated as the difference between each contact and the ground measurement. When multiple contacts occurred, each was recorded in the same manner down to ground level. As a result of the difficulty of identifying some plants to species, we grouped and analyzed species by secure taxa as outlined by Hollister (2003). Vascular plants were identified to species (with the exception of a few species) while bryophytes and lichens were grouped together by narrow growth forms (i.e. acrocarpus moss) due to the difficulty and time constraints.

II.2.3 Biomass Collection

Six $1m²$ biomass plots were established outside each of the four sites in order to investigate the accuracy of estimating biomass for both point frame methods. Biomass plots were selected based on visual estimates to best represent plant communities within the pre-existing sites and were within 10m of each site. Prior to collecting biomass the plots were point framed as outlined above.

Biomass was clipped at ground level and brought back to the lab to be sorted and weighed. Sorting of plants was done by secure taxa outlined above. Aboveground biomass of bryophytes was collected by cutting the live photosynthetic layer off of the non-photosynthetic dead layer. Samples were dried at 60° C for up to 48 hours and weighed.

II.2.4 Analysis

Data collected was filtered into the two types of methods for comparison. For the AC method all contacts at each grid point were used. For the TB method outlined by the ITEX manual (Molau and Molgaard, 1996) the intermediate contacts were removed. All data collected was managed in a relational database using Microsoft Access. The cover of each taxon was estimated by summing all of the live contacts of each taxa within each plot. Taxa were also grouped together by narrow and broad growth forms (i.e. bryophyte and acrocarpus moss) outlined by Hollister (2003). Live and dead plant cover estimates were calculated by summing all of the live contacts (regardless of taxa) and all of the dead contacts respectively for each plot. Diversity indices used for analysis were species richness and Shannon index. All indices were calculated based on the live cover of all

taxa (described above) of each plot using PC-ORD 4.0 (McCune and Mefford 1999). The cover of each taxa and diversity indices were calculated for each plot and then reported as averages.

Three sets of one-way analyses of variance (ANOVA) were run using the cover estimates for each taxon or the diversity indices for each plot in SAS 9.1.3 (SAS Institute, 2005). The first set of ANOVAs compared cover estimates from the AC method with these from the TB method to determine if there were differences. These analyses did not distinguish between warmed and control plots. A second set of ANOVAs were run using only results from the AC method in order to identify differences between the warmed and control plots. A third set of ANOVAs were run using only results from the TB method to identify differences between warmed and control plots. The results from the ANOVAs of the second and third sets were then compared to determine if there was a difference between the two sampling methods (AC and TB) in their ability to detect changes in cover due to warming.

Linear regressions were used to compare the number of contacts of each taxon with its aboveground biomass using SAS 9.1.3 (SAS Institute 2005). Two regressions were performed for each taxon; one used the number of contacts from the TB methods and the other used the number of contacts from the AC method. Data for vascular plant species are only presented when the species was present in four or more of the six plots per site where biomass was recorded (as described above). Regressions were compared using their R^2 values and statistical significances.

II.3 Results:

II.3.1 Total Live and Dead Cover

Average live cover ranged from 130 to 201% across the four sites and differences between the AC and TB method for live and dead cover were significant in all cases, except for Barrow Dry site dead cover which had a borderline significance (p=0.079; Table II.1). In other words, the TB method underrepresented the cover of living biomass between 7 and 34% depending on the site. However, the ability to detect treatment response was the same for the AC and TB method for dead cover across all sites when using statistical significances as the measure. The ability to detect treatment response was the same for live cover in the Wet sites but not the Dry sites. The Atqasuk Dry site AC method detected a significant difference $(p=0.042)$ and the TB method only detected a borderline significant difference (p=0.099), while the Barrow Dry site AC method did not detect a response ($p=0.461$) and the TB method detected a response ($p=0.010$).

II.3.2 Estimation of Diversity

The TB method identified significantly less diversity than the AC method at all sites except Atqasuk Dry site; however, there was no significant difference in species richness with either method. The two sampling methods showed no difference in their ability to detect treatment responses for either diversity indices at all sites. Both sampling methods showed that there was no significant treatment response at Atqasuk and a decrease in diversity at Barrow.

II.3.3 Estimation of Cover

The trends in cover differences between the AC and TB methods were similar for all four of the sites (Table II.2). All sites had a large frequency of instances (29 to 44% of the sampled taxa within the sites) in which the magnitude of missing cover estimated with the TB method was significant. Differences between methods were significant in at least 4 broad growth forms for all sites with the Barrow Dry site having all broad growth forms different. Despite the differences between the two methods being significant, the magnitude of cover missed by the TB method was less than 1% for forbs and nonvascular plants and less than 16% for graminoids and shrubs. The ability to detect a treatment response was the same for the AC and TB method for the cover of all taxa at all sites except for one case out of the 208 observed. The only case was forbs at the Barrow Dry site where the AC method detected a response (p=0.043) but the TB method did not $(p=0.071)$.

II.3.4 Estimation of Biomass

In order to evaluate the ability of the AC and TB method to estimate aboveground biomass in a plot we compared the r^2 values for the linear regression between cover and biomass (Table II.3). We found that r^2 values were similar between the two methods, with all but 2 taxon comparisons being within 0.1 and more than 70% of taxa having r^2 values that were within 0.05 between both methods. Of the 12 instances where the r^2 values varied by more than 0.02, 6 were higher for the AC method and 6 were higher for the TB method. Both methods were reasonably accurate in predicting biomass with 15

taxa having r^2 values above 0.75. Biomass estimation for graminoids had the highest and most frequently significant r^2 values of all growth forms (r^2 =0.61-0.86). Conversely, forbs had the lowest and least number of significant r^2 values (r^2 =0.05-0.66). Regression r^2 values were adequate for deciduous (r^2 = 0.70-0.88) and evergreen shrubs (r^2 = 0.75-0.76) in the Barrow Dry and Atqasuk Wet sites. In the Atqasuk Dry site values were much lower for evergreen shrubs (r^2 =0.15-0.17) and deciduous shrubs were not present in the biomass plots. The Barrow Wet site did not include any shrubs of either type. The ability to estimate lichen biomass based on cover was low in the Atqasuk Dry site $(r^2=0.20)$ and fairly high in the Barrow Dry site $(r^2=0.88)$. Regression r^2 values for bryophytes were high in both the Atqasuk and Barrow Dry sites $(r^2=0.71-0.99)$ however they were lower in the Barrow Dry site $(r^2=0.24)$

II.4 Discussion:

There were many differences in vegetation cover and diversity indices between the two point frame sampling methods examined in this study. Despite the underrepresentation of cover by the TB method compared to the AC method, the ability of the TB method to detect vegetation change was nearly equal. In fact there were only three cases where the two methods differed in their ability to detect change in cover, total live cover at the Barrow Dry and Atqasuk Dry sites and forbs cover at the Barrow Dry site. This is likely because most of the contacts lost when using the TB method are contacts of taxa that are redundant in the plots, allowing the responses to still be detected. This redundancy was also the reason that despite excluded contacts in the TB method

there was no significant reduction in species richness despite a small but significant decline in the Shannon index. Community responses to warming reported here were similar to previously published literature with shrub and graminoid cover increasing and decreasing in forbs, lichens, and bryophytes in most sites (Chapin et al, 1995; Arft et al, 1999; Hollister et al, 2005; Walker et al 2006). The only site that showed a decrease in shrub and graminoid cover was the Atqasuk Dry site, with this decrease likely being as result of increased water stress. Diversity also followed the trends of previous literature with all indices decreasing with warming across all four sites (Chapin et al, 1995; Wahren et al, 2005; Hollister et al, 2005).

The AC and TB methods were nearly equal in their ability to estimate aboveground biomass. In fact, there were no differences in number of statistical significant regressions between the two methods. It is surprising that cover estimates from the AC method did not predict biomass better than the TB method. It is likely that this is because the sites are relatively short statured and often there is little difference in cover estimates of the two methods.

Graminoids were the growth form with the most statistically significant and highest r^2 values due to the similarity in their morphology across taxa within the group. Forbs had the lowest and least number of significant r^2 values due their varied morphology. This is acceptable due to graminoids and shrubs making up the majority of cover and biomass in the four sites sampled with forbs making up only a small amount. This does not hold true in the Atqasuk Dry site however where evergreen shrubs vary

from dense, erect morphology (*Cassiope tetragona*) to a smaller, more prostrate morphology (*Vaccinium vitis-idaea*). Biomass regression r² values were consistent with those reported in other findings for graminoids and shrubs across all sites, except the Atqasuk Dry site (Shaver et al, 2001). As previously mentioned, deciduous and evergreen shrubs in the Atqasuk Dry site had r^2 values that were significantly lower than those in previous findings, likely due to a high degree of variability in the morphology of shrubs in the site. Differences in r^2 values for nonvascular plants between sites is likely as result of some sites having nearly full ground cover while in others the cover is more patchy.

There should be caution when implementing the TB method over the AC method. In communities that have a complex canopy or with high LAI the TB method clearly under represents the cover of taxa that occupy the middle layers of the canopy. This makes it a poor choice for sampling community structure. It is best suited for vegetation surveys targeted at measuring vegetation change. Morphological variations between treatments could also skew aboveground biomass and point frame contact correlations resulting in inaccurate biomass estimations. The TB method is justified for use in communities with LAI of 2 or less (Shaver et al, 2001; Campioli et al 2009) however is less likely to work in communities with LAI above 2 (Zhou et al, 2006; Campioli et al, 2009; Zhao et al, 2010). In relatively open tundra communities, like those examined in this study, the TB method worked well. On inspection the intermediate contacts omitted were mostly repetition with the uppermost contact. Areas with more advanced layering

may result in inaccurate estimations due to the exclusion species that inhabit middle canopy layers (Klein et al, 2004).

Our results show that the TB method is similar to the AC method in detecting plant community responses to warming in the tundra. Differences between the two methods were small and did not affect the TB methods ability detect plant community change. One of the major benefits of using the TB method to sample plant communities is the time investment required, as the AC method is much more time intensive, both in field and from a data management and analysis perspective. The TB method is accurate in detecting plant community response to warming. We therefore conclude that the TB method, as outlined in the ITEX manual, is a valid and reasonable approach that yields accurate and sound results.

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Table II.1: Estimates of live cover, dead cover, and diversity indices in warmed and control plots at the four sites. Values represent average cover in the control plots as determined by the all contact method (Cover AC); the difference in the estimate of the cover in the average plot between the all contact and the top and bottom only method (Difference/Method TB); and the average difference between the warmed and the control plots when estimated by the all contact method (Difference/Treatment/ AC) and top and bottom only method (Difference/Treatment/TB). Statistical tests were performed with one factor ANOVAs ($*=p$ value < 0.05).

		Difference		
	Cover	Method	Treatment	
	AC	TВ	AC	TВ
Atgasuk Dry site				
Live	142.18	$-10.51*$	$-10.08*$	-6.46
Dead	38.02	$-6.90*$	4.46	4.83
Richness	9.26	-0.02	-0.91	-0.89
Shannon	1.78	0.00	-0.02	-0.02
Atgasuk Wet site				
Live	201.18	$-69.51*$	$15.71*$	13.42*
Dead	57.06	$-28.16*$	11.38	-0.08
Richness	6.40	-0.01	-0.55	-0.57
Shannon	1.02	$-0.04*$	0.00	-0.01
Barrow Dry site				
Live	141.42	$-10.07*$	-2.29	$-6.71*$
Dead	41.20	-3.50	17.46*	14.96*
Richness	8.66	-0.03	$-3.02*$	$-3.01*$
Shannon	1.72	$-0.01*$	$-0.24*$	$-0.23*$
Barrow Wet site				
Live	136.66	$-16.77*$	-7.75	-6.75
Dead	80.10	$-36.90*$	$21.13*$	13.38 *
Richness	10.75	-0.02	-1.45	-1.51
Shannon	1.81	$-0.03*$	$-0.15*$	$-0.15*$

Table II.2: Average cover estimates of taxa (growth form or species) in the warmed and control plots at the four sites. Values represent average cover in the control plots as determined by the all contact method (Cover AC); the difference in the estimate of the cover in the average plot between the all contact and the top and bottom only method (Difference Method TB) and its statistical significance; and the average difference between the warmed and the control plots when estimated by the all contact method (Difference Treatment AC) and top and bottom only method (Difference Treatment TB) and its statistical significance. Statistical tests were performed with one factor ANOVAs (*=p value< 0.05).

Table II.2 continued…

Table II.2 continued…

Table II.2 continued…

¹ *Carex aquatilis/stans, Carex rariflora, Carex rotundata*. 2 *Stellaria laeta, Stellaria humifusa*.

³ *Cerastium beeringinum,Cerastium jenisejénse*.

⁴ *Carex aquatilis/stans, Carex subspathacea*. 5 *Eriophorum russeolum, Eriophorum scheuchzeri*.

⁶*Calamagrostis holmii, Hierochloe pauciflora, Poa arctica*
Table II.3: Linear regressions between aboveground biomass (BM) and cover estimates (C) of each taxa at the four sites calculated from the all contact method (AC Method) and top and bottom only method (TB Method). Only species and growth forms that were sampled in at least 4 often 6 biomass plots are presented. *=p<0.05.

		AC Method		TB Method			
Taxon		C/BM	r ²	C/BM	r^2		
		Atqasuk Dry site					
Evergreen Shrub	6	BM=1.5c+12.7	0.15	BM=1.6c+12.1	0.17		
Cassiope tetragona	5	BM=0.7c+32.2	0.01	BM=2.2c+18.7	0.07		
Diapensia lapponica	4	BM=4.1c+10.6	0.58	BM=4.1c+10.6	0.58		
Vaccinium vitis-idaea	6	BM=0.7c+5.0	0.16	BM=0.9c+4.1	0.18		
Graminoid	6	BM=1.2c-1.5	$0.72*$	BM=1.2c-1.2	$0.61*$		
Lichen	6	BM=4.3c+8.7	0.20	BM=4.3c+8.7	0.20		
		Atqasuk Wet Site					
Deciduous Shrub	5	BM=1.6c-3.7	0.76	BM=3.2c-12.4	0.70		
Graminoid	6	BM=0.5c+0.6	$0.80*$	BM=0.7c+0.5	$0.81*$		
Single Graminoid	6	BM=0.5c+0.6	$0.80*$	BM=0.7c+0.5	$0.81*$		
Eriophorum angustifolium	5	$BM = 0.2c + 0.7$	$0.95*$	$BM = 0.3c + 0.5$	$0.96*$		
Bryophyte	6	$BM = 0.8c + 0.4$	0.76	$BM = 0.8c + 0.1$	0.74		
		Barrow Dry site					
Deciduous Shrub	6	BM=2.6c-36.9	$0.84*$	BM=2.7c-37.2	$0.88*$		
Salix rotundifolia	6	BM=2.6c-36.9	$0.84*$	BM=2.7c-37.2	$0.88*$		
Evergreen Shrub	4	BM=2.9c+15.6	0.76	BM=3.2c+15.8	0.75		
Cassiope tetragona	4	BM=2.9c+15.6	0.76	BM=3.2c+15.8	0.75		
Graminoid	6	BM=0.7c+0.5	$0.78*$	BM=0.9c+0.2	$0.78*$		
Bryophyte	5	BM=14.8c+64.5	0.24	BM=14.8c+64.5	0.24		
Lichen	6	BM=0.2c-8.1	$0.88*$	BM=0.2c-8.1	$0.88*$		
		Barrow Wet site					
Forb	6	BM=0.4c-0.2	$0.66*$	$BM = 0.4c + 0$	$0.60*$		
Erect Forb	6	BM=0.5c-0.6	$0.94*$	BM=0.5c-0.6	$0.95*$		
Mat Forb	6	$BM = 0.2c + 0.8$	0.03	$BM = 0.1c + 1.5$	0.00		
Stellaria spp.	6	$BM = 0.2c + 0.8$	0.03	$BM = 0.1c + 1.5$	0.00		
Graminoid	6	BM=0.6c-1.0	$0.80*$	BM=0.8c-1.3	$0.86*$		
Single Graminoid	6	BM=0.6c-1.0	$0.80*$	BM=0.8c-1.3	$0.86*$		
Carex aquatilis comp.	6	$BM = 0.5c + 2.3$	0.11	BM=1.1c-5.1	0.43		
Dupontia fisheri	6	BM=0.4c+0.5	$0.83*$	$BM = 0.6c + 0.1$	$0.67*$		
Bryophyte	6	BM=2.3c-8.1	$0.99*$	BM=2.3c-8.1	$0.99*$		

Chapter III: Heterogeneous response to warming of tundra vegetation

III.1 Introduction:

Over the past several decades the subject of global climate change has been increasingly studied. Across the globe much of the focus has been on Arctic regions as they are among the most vulnerable regions to warming temperatures. Warming in the Arctic has been long documented and has been increasing at even faster rates in recent decades (Cattle 1995; IPCC 2007). Arctic plant communities are of particular interest for several reasons. Small changes in environmental conditions can have large effects on the plant community (Arft et al 1999; Chapin et al 1995; Walker et al 2006). These changes in plant community dynamics have been associated with alterations in ecosystem function and nutrient cycling (Cable et al 2009; Hobbie and Chapin 1998; Shaver and Chapin 1991). Plant communities are also the base of a truncated arctic food web and alterations to community structure can have far reaching consequences as they are often food sources for many migratory bird and mammal species (Joly et al 2010; Sorenson et al 2008; Tape et al 2010). Finally, shifts in community dynamics and changes in ecosystem function have the potential of shifting Arctic tundra ecosystems from a carbon sink to a source (Oechel et al 1993) that could lead to a positive feedback to climate change.

Many studies have been conducted to examine how plant communities respond to environmental changes, such as increased temperatures and nutrient availability (Arft et

al 1999; Jagerbrand et al 2006; Walker et al 2006). Yet most studies span five years or less and thus are unable to address whether or not plant community responses are maintained in the long term. A few studies have been done that address the tundra vegetation changes that occur after prolonged periods of environmental changes. These studies have given insights into how plant communities shift beyond the initial responses to changes in their environment (Chapin et al 1995; Hollister et al 2005). Despite these insights, few studies have attempted to predict plant community composition at some point in the future. These studies have focused on predicting community biomass production (Bret-Harte et al 2008) or using computer modeling to predict community type at a landscape scale (Epstein et al 2004), however have not attempted to predict individual species and growth form cover.

This study is a continuation of vegetation sampling at four sites in Northern Alaska began in the 1990s as part of the International Tundra Experiment (ITEX). There are two goals of this study. First, to determine the effects of experimental warming on plant community dynamics over a 13-15 year time span and to evaluate if the changes in plant communities associated with this experimental warming are consistent with the natural trends. Second, to evaluate if the observed response of plant community to experimental warming in early years can be extrapolated to predict plant community composition in later years. We examined aspects in which plant communities respond to natural trends and experimental warming across time: 1) cover, 2) canopy height, and 3) shifts in species diversity. Based on previous studies and latitudinal trends we expect

taller species and growth forms to increase in cover and shorter species and growth forms to decrease in cover in response to increased temperatures. Live and dead cover, along with canopy height, should increase as a result of increased growth, while there should be a shift from a more open canopy to a more closed one. We also expect there to be a decrease in species diversity and a shift in dominance from nonvascular to vascular plants, especially graminoids and shrubs. Community responses in early years are expected to be poor predictor of community composition in later years due to community makeup being influenced by competition and dominance in later years instead of initial increases in plant growth rates in early years.

III.2 Methods:

III.2.1 Site Descriptions

Four sites located in Northern Alaska were sampled in this study. Two sites were located near Barrow, AK $(70°29'N, 157°25'W)$ and two sites approximately 100km south near Atqasuk, AK (71^o18'N, 156^o40'W). The sites near Barrow include a dry (BD) and wet (BW) site, both having a mean July temperature of 3.7° C. In Barrow snowmelt occurs in early-mid June, with a thaw depth of 50 to 100cm in the summer. The BD site is situated on a well drained beach ridge above a drained thaw lake dominated by *Cassiope tetragona*, *Salix rotundifolia*, and *Luzula confusa*. The BW site is in a frequently inundated transitional zone between the beach ridge of the dry site and a drained lake basin, and is dominated by *Carex stans*, *Dupontia fisheri*, and *Eriophorum spp*. The Atqasuk sites also include a dry (AD) and wet (AW) site, both having a mean

July temperature of 9° C. Snowmelt in Atqasuk occurs in late May, with a thaw depth of 90 to 110cm in the summer. The AD site is on a well drained ridge above a thaw lake and is dominated by *Cassiope tetragona*, *Luzula confusa*, and *Hierochloe alpina*. The AW site is located at the edge of a thaw lake in a frequently inundated meadow and is dominated by *Carex aquatilis*, *Eriophorum angustifolium*, and *Salix pulchra*. Topographic changes are small $\langle 0.5m \rangle$ at the sites, however even small differences may be associated with significant shifts in plant community composition and soil moisture (Komarkova and Webber 1980; Webber 1978).

The four sites were established between 1994 and 1996 and each consisted of 48 1m² plots, 24 control and 24 warmed. Warming was achieved using hexagonal open-top chambers (OTCs) constructed of Sun-Lite HPTM fiberglass according to the guidelines in the ITEX manual (Molau and Molgaard 1996). OTCs were installed every year shortly after snowmelt and removed at the end of the growing season. OTCs have been shown to warm the surface air temperature an average of 0.6 to 2.2° C (Hollister et al 2006) and are accurate in simulating climate change in the tundra (Hollister and Webber 2000). Temperature data was collected at a height of 2m at the AD and BD sites using Campbell weather stations.

III.2.2 Point Frame Method

All four sites were sampled three separate times (1995-97, 2000, and 2007-08) according to the non-destructive point frame method outlined by Walker (1996). A 75 cm^2 100 point grid with measurement points every 7 cm was leveled above the plant

canopy using permanent markers that allow for the same orientation year after year. At each point on the grid a graduated ruler was lowered to the first contact with the plant canopy and then to the lowermost contact at that point. This shortcut, omitting intermediate contacts, has been shown to be effective at detecting vegetation change in tundra communities (see Chapter II). At each contact the taxon, live/dead status, and height was recorded. Some taxa were difficult to identify to species in situ and were therefore grouped into the closest secure taxon as outlined by Hollister (2003). Taxa were also grouped into Broad Growth Forms (i.e. Bryophytes) and Narrow Growth Forms (i.e. Acrocarpus Moss) for additional analysis of growth form trends.

III.2.3 Data Analysis

All cover estimates were calculated by summing all contacts from each grouping examined (taxon, live contacts, dead contacts, vascular plant cover and nonvascular plant cover). All encounters of equipment (i.e. individual tags) and feces were removed from the dataset before analysis (<1% total cover). Litter was defined as dead pant matter that was unattached and on the ground. Canopy height for each point was calculated by taking the difference between the uppermost plant contact and the ground contact. Average canopy heights were calculated from the 100 canopy heights in each plot. Maximum canopy height was calculated using only the tallest canopy height in each plot. The maximum canopy height per plot of the most common species was calculated for species that were present in more than 10 plots per treatment within each site.

Diversity indices analyzed were species richness and Shannon index. Both were calculated per plot based on cover estimates of all live taxa using the computer program PC-ORD 4.0 (McCune and Mefford 1999). All values reported are site averages for each treatment. All statistical tests in this study were done using SAS 9.1.3 (SAS Institute 2005). For each statistical test ANOVA with a Tukey post hoc test was run. All results were considered statistically significant with a Type 1 error probability of 5% or less.

Site and treatment averages were used to calculate changes through time (Figure III.1). Changes in control plots between samplings 1 and 2 (*As*) were calculated as the difference between control plots at sampling 1 and sampling 2. Changes in control plots between samplings 2 and 3 (*At*) were the difference between control plots at samplings 2 and 3. The warming response at sampling 1, 2, and 3 (W1, W2, W3) were calculated as the difference between warmed and control plots at sampling 1, 2, and 3 respectively. Warming responses were also partitioned into changes in the warmed plots relative to the observed changes in the control plots from sampling 1 to 2 (*Ws*) and from sampling 2 to 3 (*Wt*). For each change across years, both in controls and in warming response, the difference between the initial and final condition was analyzed using an ANOVA. For example, when testing the warming response at sampling 1, it is the difference between community condition in control (C1) and warmed (E1) plots at sampling 1.

Change across years and in response to warming were also scaled to account for differences in duration of time between samplings. This was done by reducing the raw community change by the number of treatment years. This per-year-change was then

multiplied by the number of years between sampling 2 and 3 for each site. For example, the changes in control plots between samplings 1 and 2 (A_s) at the Atqasuk Dry site is calculated $A_s = ((C2-C1)/4)^*$ 7. The change across time in the control plots (A_s, A_t) and in response to warming (*Ws*, *Wt*) were then compared to determine if the change across both times were consistent. There was considered to be a change if there was a more than 1% difference between A_s and A_t (or W_s and W_t) or if either significantly changed. Change was only calculated for taxa or growth forms that had greater than 1% cover in any of the samplings.

III.2.4 Predictions

The ability of the early response to warming observed to predict community conditions in the experimental plots at sampling 3 (E3) were assessed (Figure III.2). This was done by summing the scaled warming responses with the observed changes in control plots between samplings 2 and 3 (*At*) and the community condition in the warmed plots at sampling 2 (E2). The change in the control plots between sampling 2 and 3 (A_s) was added in order to account for changes occurring in the ambient environment over this time period. For example the prediction for the initial warming response (W1) is calculated, $W1 = E2 + W_i + A_t$. W1 and W_s were further combined to produce a prediction based the overall warming response through sampling 2 (W2). All prediction values were compared to the observed experimental plots at sampling 3 (E3) using an ANOVA with a Tukey post-hoc analysis; results were considered statistically significant with a Type 1 error probability of 5% or less.

III.3 Results:

III.3.1 Temperature

There was large variation in July temperature at both Atqasuk and Barrow throughout the duration of this study (Figure III.3). Temperatures during the summers when the vegetation samplings were done also varied greatly. Both regions showed slightly increasing temperature over the duration of the study, although neither trend was statistically significant.

III.3.2 Community Change

Changes in live, dead, and litter cover in control plots over time (A_s, A_t) varied between sites and were generally much larger than the response to warming across all sites (Table III.1). Changes in live and dead cover in control plots were inconsistent over time for all sites, however changes in litter cover were consistent in two sites (AD and BW). Warming responses (*Ws*, *Wt*) varied between sites for all three cover types yet were more consistent over time. Live cover at the Atqasuk sites responded consistently over time, yet in different directions, while dead cover at the Barrow sites consistently increased. All sites except BW had litter cover that responded consistently, yet in different directions, over time in response to warming.

Changes in vascular and nonvascular plant cover in the control plots over time varied across time and sites (Table III.1). Changes in the control plots (A_s, A_t) were generally much larger than in response to warming (*Ws*, *Wt*) across all sites. Changes in vascular plant cover in control plots (*As*, *As*) were significant at all sites, except for the

BD site between samplings 2 and 3; all changes were inconsistent over time with Atqasuk sites decreasing initially but increasing later while Barrow sites increased initially and decreased later. Nonvascular plant cover changes in control plots were also all significant, except at the AD site changes between samplings 2 and 3. All the significant changes were an increase in nonvascular cover between sampling 1 and 2 and a subsequent decrease between samplings 2 and 3. Warming responses (*Ws*, *Wt*) in both vascular and nonvascular plant cover varied between sites and generally changed over time with only the AW vascular plant cover and BD nonvascular plant cover changing consistently over time.

Changes in species richness in control plots over time (A_s, A_t) varied in direction and magnitude between sites but were in most cases greater in magnitude in early years than in later years (Table III.1) and were either inconsistent over time or did not change. Changes in species richness in response to warming (*Ws*, *Wt*) were nonsignificant. Only the BD site had a consistent change in species richness in response to warming, a nonsignificant decrease over time. Changes in the Shannon index in the control plots over time (A_s, A_t) were small and nonsignificant except at the BW site, which decreased in early years (A_s) . The only consistent change was a nonsignificant decrease at the AW site. Warming responses (*Ws*, *Wt*) measured by the Shannon index were small and nonsignificant except at the BD site which increased in later years.

Changes in canopy height over time were generally greater in the control plots than in the response to warming (Table III.2). Changes in maximum plot canopy height over time in control plots were similar at the Atqasuk sites; both decreased in early years (A_s) and increased in later years (A_t) . At the Barrow sites, the changes in maximum plot canopy height were also similar over time; they both consistently increased, however only the increase in early years was significant. Average canopy height consistently decreased over time in the control plots at all sites, except the BW site which increased (A_s) and then decreased (A_t) over time. Warming responses in maximum canopy height and average canopy height were nonsignificant except for a decrease in maximum canopy height at the AD site in early years (*Ws*) and an increase in average canopy height at the AW site in later years (W_t) . Changes in the height of individual taxa over time were generally larger in the control plots than in response to warming at all sites. Most changes were inconsistent over time. Graminoids showed the largest changes in height over time in the control plots and in response to warming and were the only taxa that responded consistently over time; the consistent responses of graminoids were toward an increase in height over time.

Changes in cover over time were generally much greater in the control plots than in response to warming (Table III.3). However in 71 of the 80 taxa that were abundant enough to comment on, the change observed in the control plots was inconsistent over time (Table III.3, Table III.4). The only taxa in which the change observable in the control plots was consistent were a decrease in lichens, especially foliose and fruticose lichens, at the AD site; a nonsignificant increase in sphagnum moss at the AW site; a nonsignificant increase at the BD site; and a nonsignificant decrease in forbs and a

nonsignificant increase in lichens at the BW site. The change in cover in response to warming was generally also inconsistent over time, however there were many more taxa that did respond consistently to warming than was observed in the control plots over time. At the AD site *Luzula confusa*, leafy liverworts, lichens, fruticose lichens consistently decreased in response to warming over time, however only the decrease in leafy liverworts in later years (*Wt*) was significant. At the AW site *Salix pulchra*, graminoids, sedges, *Carex aquatilis*, pleurocarpus moss, and sphagnum moss consistently increased over time, however only graminoids and sedges in early years (*Ws*) and pleurocarpus moss in later years (*Wt*) were significant. At the BD site *Cassiope tetragona*, graminoids, grasses, and Poa spp. consistently increased over time while lichens, foliose lichens, and fruticose lichens consistently decreased over time, however only the warming response in graminoids throughout the study $(W_s$ and W_t) and grasses, Poa spp., lichens, foliose lichens and fruticose lichens in early years (*Ws*) were significant. At the BW site grasses, pleurocarpus moss, lichens and foliose lichens consistently decreased over time, however only lichens and foliose lichens in later years (*Wt*) was significant.

Species composition change, represented by the Euclidean distance of the change in cover of all taxa, at all sites show that community responses in control and warmed plots were not consistent in magnitude over the duration of the experiment (Table III.5). Changes in the control plots were larger in earlier years however throughout the experiment these control plot changes were generally larger than the response to warming

at all sites. All sites also show that the response to warming is larger in earlier years (*Ws*) and was less in later years (*Wt*).

III.3.3 Assessment of Predictions

The warming response measured at sampling 2 (W2) was the only predictor that was able to statistically predict maximum canopy height and average canopy height in experimental plots at sampling 3 at all sites (Table III.7). The warming response at sampling $2 \, (W_s)$ reasonably precise at predicting maximum and average canopy height as it only misjudged height by 0.4 to 4cm for maximum canopy height and by 0.1 to 0.6cm for average canopy height across sites. When predicting maximum canopy heights of taxa and growth form the warming response measured at sampling 2 (W2) was a better predictor across all sites (27 out of 43 cases were statistically the same) however it still misjudged height by 0.1 to 5.6cm. Warming response between samplings 2 and 3 relative to the changes in control plots (W_t) was the second best predictor (24 out of 43 cases) and the warming response at sampling 1 (W1) was the worst predictor (9 out of 43 cases).

The ability of the warming response measured at sampling 1 (W1), warming response between samplings 2 and 3 relative to changes in control plots (*Ws*), and warming response measured at sampling 2 (W2) to predict individual growth form and taxa E3 cover was site and taxa specific (Table III.8). The warming response measured at sampling 2 was the best overall statistical predictor of taxa and growth form cover at sampling 3 (116 out of 155 cases). The initial warming response and the warming response between sampling 2 and 3 relative to changes in the control plots were almost

equal (84 and 85 out of 155 cases respectively). Of the taxa and growth form covers that responded either inconsistently or consistently to warming the warming response measured at sampling 2 had the most cases that were not statistically different from the cover observed in experiment plots at sampling 3 (56 out of 83 cases) compared the warming response measured at sampling 1 (W1) (48 cases) and the warming response between samplings 2 and 3 relative to changes in control plots (48 cases) (Table 9). The warming response measured at sampling 2 had the most cases where predictions were within 1-5% of the cover in experimental plots at sampling 3 (29 cases) while the warming response measured at sampling 1 (W1) had the least (20 cases). Alternatively, the warming response measured at sampling 1 (W1) had the most predictions that were within 1% of cover in experimental plots at sampling 3 (24 cases) compared to the warming response between samplings 2 and 3 relative to the changes in the control plots (12 cases) and the warming response measured at sampling 2 (22 cases).

III.4 Discussion:

Temperature trends in Barrow and Atqasuk regions followed similar trends to those found elsewhere in high latitude regions (IPCC 2007; Serreze et al 2000; Stafford et al 2000). Both regions had variability in mean July temperatures between years with a small increasing trend across the duration of the study. While this trend was not statistically significant, it was consistent with documented trends (earlier snowmelt and warmer summers) in the region (Hinzman et al 2005; Stone et al 2002). Placements of sampling times were in years with July temperatures that were both above and below the

average. The amount of variability between years may explain some of the inconsistencies in plant community responses across time.

Overall the changes in control plots between the samplings were larger than responses to warming. This may due to differences in temperature between samplings being larger than the differences between controls and warming treatments. Confounding effects possibly have led to variations in responses between years, such as differences in summer precipitation amounts, winter snow depths, or snow melt dates (Cooper et al 2011; Walker et al 1994). These outside factors may prove helpful in the future when incorporated into investigations about arctic plant community changes (Phoenix and Lee 2004).

Community responses to warming were larger in early years of manipulation and declined over time. This is possibly due to an initial release from temperature restraints that cause a surge in growth which cannot be maintained over longer time periods. This abrupt warming response may have cause a significant increase in live shoot growth that would be difficult to maintain in the long term (Chapin et al 1995). A release of air temperature constraints may result in available soil nutrients being used up within the first years of warming. After the initial phase plants may only be able to uptake nutrients as they slowly become available with further soil thawing (Shaver and Jonasson 1999). Later community responses are likely to be the result of differences in plant competitive ability especially their ability to utilize available resources resulting in shifts in abundance rather than changes in growth rates (Walker et al 2006). Overall canopy

heights and covers responded in similar fashions that have been found in the past (Chapin et al 1995; Hollister et al 2006; Jagerbrand et al 2006). As expected, taller species showed an overall increase in cover in response to warming while shorter species showed an overall declined in cover. This is most likely to be a result of competition shifts as the environment becomes more favorable for taller growth forms (such as graminoids and shrubs) allowing them to out compete the shorter mosses, lichens, and forbs (Graglia et al 2001). This trend was consistent with the overall closing of the canopy however both trends were muted in the AD site as a probable result from soil moisture being lower in the sandy substrate and plants becoming water stressed. Live cover increased in control throughout the study, yet decreased in response to warming within years.

Responses to warming and changes in control plots were generally heterogeneous across sites and over time. This is likely due to conditions in each region being different in regards to precipitation and temperature (Cooper et al 2011; Walker et al 1994). The suite of taxa at each site also effects interactions and how the community will respond as a whole. Variations in conditions and species establishment histories across the landscape influence the competitive ability of each individual taxon (Gould and Walker 1999).

Both changes in control plots and in response to warming were heterogeneous through time and across the landscape. Despite changes in control plots being larger, responses to warming were more consistent. This is likely due to some plants, such as graminoids and shrubs, being consistent drivers of the community in their response to warming compared to the more erratic conditions in the control plots. More gradual

warming in later years of the experiment may allow the plants to slowly increase growth rates while maintaining sufficient reserves for long term sustained growth. Dead cover increased throughout the study and within samplings as a result of warming treatments. This is consistent with previously accepted ideas of arctic plants holding their dead leaves in the canopy (Bliss 1962; Savile 1972). Another alternative may be due to increased growth in the early years of the experiment and the resulting growth senescing then being retained as standing dead. Contrary to what we expected, species diversity did not change or decreased slightly across the study and within samplings in response to warming treatments. This is likely due to some species finding increased temperatures more favorable for growth while others fail to utilize conditions, however it may take long periods of time for these community dynamic shifts to fully manifest themselves (Valpine and Harte 2001). The increase in cover of some taxa and decrease of others may have led to the overall no net changes in the community with regards to some diversity indices. Some indices may also be holding steady as a result of replacement as the environmental conditions allow new species to move into the area while others disappear or become less abundant (Walker et al 2006). This is most likely the case in the BD site as some species such as *Vaccinium vitis-idaea* become present in the warming treatments. Microclimate differences within sites could also allow for conditions between plots to vary enough that a species may be successful in some plots and not others (Hudson and Henry 2009).

For predicting plant community conditions in warmed plots at the final sampling of the study both initial warming responses and warming responses between sampling 1

and 2 were often inaccurate. The difference between these predictors and the experimental plots shows that community responses continued to change over time. The overall warming response through sampling 2 was a slightly better predictor than initial warming response overall and this ability as a better predictor further illustrates the slowing warming effect during the later years of the study. Differences in plant community response over time and the often conflicting ways that taxa and growth forms responded to warming contributes to the difficulty in predicting communities in the future. At several sites the taxa within growth forms increased while others decreased resulting in a muting effect to warming responses. This disparity in how taxa within growth forms respond may be able tracked more accurately by regrouping taxa by other attributes, such high/low arctic status or early/late flowering plants. These different schemes could group plants that respond similarly together and making it easier to predict changes in response to changing environmental conditions.

Figure III.1: Diagram of the experimental analytical design with the sampling design.

Reasons for Difference and calculations of values

Ambient Change (A,, A,)

Secondary ambient change due to succession, disturbance or climate fluctuations between samplings 1 and 2

Tertiary ambient change

due to succession, disturbance or climate fluctuations between samplings 2 and 3

Warming Response (W1, W2, W3) Warming Response (W_i , W_s , W_t) Difference between experimentally warmed and control plots at sampling 1 to changes in control plots due to direct short-term plant-environment

relationships (e. g. change in size) $W1 = E1-C1$ if $L = 0$ $W1-W$

Landscape

due to random differences in microtography and species establishment histories

Difference between experimentally warmed and control plots at sampling 2

due to changes in the plant community between control and warmed plots at sampling₂ W2

$$
W2 = E2-C2
$$

W. E₂ $W2 = W_i + W_s$

Difference between experimentally warmed and control plots at sampling 3 due to changes in the plant community between control and warmed plots at

Partitioned

Initial warming response relative due to direct short-term plant-environment

relationships (e. g. change in size)

Secondary warming response relative to changes in control plots

due to the accumulation of direct effects and indirect changes in interactions with other species and the environment (e. g. change in numbers) between samplings 1 and 2

 $W_s = (E2-E1)-(C2-C1)$

Tertiary warming response relative to changes in control plots

due to the accumulation of direct effects and indirect changes in interactions with other species and the environment $(e, g, change in)$ numbers) between samplings 2 and 3

Figure III.2 Diagram of the theoretical reasons for plot differences and the calculations of differences between plots through time.

Figure III.3: Diagram demonstrating the calculations of predictive values for warmed plots at sampling 3 (E3). Values calculate from past data (A) were scaled (B) and then summed with the changes in control plots between samplings 2 and 3 and the community condition in warmed plots at sampling 2 (C).

Figure III.4: Trends in mean July temperature for Atqasuk and Barrow across the duration of the experiment. Barrow temperatures are denoted by X's (R^2 =0.017, p=0.31) and Atqasuk temperature data by open diamonds (R^2 =0.005, p=0.29). The years vegetation was sampled is denoted with a box (S1, S2, and S3). In Atqasuk the samplings were; 1997 for Sampling 1, 2000 for Sampling 2, and 2007 for Sampling 3. In Barrow the samplings were; 1995 (Barrow Dry site) and 1996 (Barrow Wet site) for Sampling 1, 2000 for Sampling 2, and 2007 for Sampling 3.

Table III.1: Change in community indices over time in control plots and in response to warming. Control and experimentally warmed plot values are presented at sampling 1, sampling 2, and sampling 3 (C1, C2, C3, E1, E2, and E3). Warming responses were analyzed as the differences between control and experimental plots at all three samplings (W1, W2, W3). Control plot responses to ambient environmental changes were analyzed as the changes between samplings 1 and 2 (*As*) and between samplings 2 and 3 (*At*). Warming responses were partitioned into changes in warmed plots relative to changes in the control plots between samplings 1 and 2 (*Ws*), and between samplings 2 and 3 (*Wt*). Comparisons of responses to ambient environmental changes $(A_s$ and A_t) and warming responses $(W_s$ and W_t) were categorized as no change (N) , inconsistent change (I) , and consistent change (C) over time (see methods for details). The values representing the changes over time were scaled to 7 years in the Atqasuk sites and 8 years in the Barrow sites to facilitate comparisons; however statistical significance is based on the unscaled values. ANOVAs were used to calculate statistical significance (*=p-value<0.05). Species diversity indices are based on vascular plants only. Sites are the Atqasuk Dry (AD) and Wet (AW) sites, and the Barrow Dry (BD) and Wet (BW) sites.

											Scaled		
	C1	E1	W1	C ₂	E ₂	W ₂	C ₃	E3	W3	A_{s}	A_t	W_{s}	W_t
Live Cover													
AD	112.50	121.67	9.17	100.67	100.75	0.08	102.58	96.13	-6.45	-41.42	3.35 1	-15.90	-6.54 C
AW	124.88	120.92	-3.96	121.17	122.92	1.75	127.96	141.38	13.42	-12.98	11.89 [*] l	9.99	11.67 C
BD	71.88	72.58	0.70	121.38		106.42 -14.96	99.04	92.42	-6.62	198.00	-29.78 * I	-20.89 [*]	8.33 1
BW	105.88	104.17	-1.71	137.33	121.58 -15.75		85.21	78.42	-6.79	125.83	-83.40 [*] I	-22.47	8.96
Dead Cover													
AD	14.50	17.96	3.46	7.13	10.96	3.83	27.00	31.83	4.83	-25.81	34.78	0.66	1.00
AW	36.13	41.42	5.29	43.79	48.54	4.75	27.71	27.63	-0.08	26.83	-28.15 [*] l	-0.95	-4.83
BD	15.08	19.17	4.09	11.88	17.67	5.79	33.25	48.21	14.96	-12.83 ²	28.50	2.28	9.17 \degree C
BW	37.00	40.75	3.75	36.54	45.04	8.50	72.58	85.96	13.38	-1.83	57.67	7.60	4.88 C
Litter Cover													
AD	22.04	20.75	-1.29	11.42	12.50	1.08	9.83	13.21	3.38	-37.19	-2.77 C	4.16	2.29 C
AW	8.38	9.42	1.04	4.08	4.21	0.13	9.71	3.67	-6.04	-15.02 [*]	9.84 [*] l	-1.6	-6.17 C
BD	10.08	12.50	2.42	8.00	9.38	1.38	12.33	12.38	0.05	-8.33	5.78 [*] I	-1.39	-1.33 C
BW	0.67	0.04	-0.63	9.38	13.46	4.08	26.92	24.71	-2.21	34.83	28.07 °C	7.53	-6.29 [?] I

Table III.2: Change in canopy height over time in control plots and in response to warming. Values for plant species are based on the maximum height recorded per plot for only those species present in at least 10 plots per treatment per year. Control and experimentally warmed plot values are presented at sampling 1, sampling 2, and sampling 3 (C1, C2, C3, E1, E2, and E3). Warming responses were analyzed as the differences between control and experimental plots at all three samplings (W1, W2, W3). Control plot responses to ambient environmental changes were analyzed as the changes between samplings 1 and 2 (A_{*s*}) and between samplings 2 and 3 (*At*). Warming responses were partitioned into changes in warmed plots relative to changes in the control plots between samplings 1 and 2 (*Ws*), and between samplings 2 and 3 (*Wt*). Comparisons of responses to ambient environmental changes $(A_s \text{ and } A_t)$ and warming responses $(W_s \text{ and } W_t)$ were categorized as no change (N) , inconsistent change (I), and consistent change (C) over time (see methods for details)The values representing the changes over time were scaled to 7 years in the Atqasuk sites and 8 years in the Barrow sites to facilitate comparisons; however statistical significance is based on the unscaled values. ANOVAs were used to calculate statistical significance ($*=p$ -value < 0.05).

											Scaled		
	C1	E1	W1	C ₂	E ₂	W ₂	C ₃	E3	W ₃	A_{s}	A_t	W_{s}	\textit{W}_{t}
							Atgasuk Dry Site						
Maximum	9.6	11.7	2.1	7.0	6.4	-0.6	12.7	14.9	2.2	-9.0	9.9 ¹	-4.8	$2.8 \quad $
Average	1.9	1.8	-0.1	1.7	1.6	-0.1	1.3	1.4	0.1	-0.7	-0.8^{\degree} C	0.0	0.2 N
Evergreen Shrub	2.1	1.6	-0.5	2.3	1.8	-0.5	1.8	1.6	-0.2	0.5	-0.9 \degree I	0.1	0.3 N
Cassiope tetragona	3.7	2.7	-1.0	2.8	2.5	-0.3	4.1	2.7	-1.4	-3.0	$2.2 \quad $	1.0	-1.1
Diapensia lapponica	1.5	0.7	-0.8	2.4	1.8	-0.6	0.7	0.5	-0.2	3.0^*	-2.9	0.4	0.5 N
Ledum palustre	2.1	1.9	-0.2	2.4	2.0	-0.4	1.8	2.9	1.1	0.9	-1.0	-0.3	1.5
Vaccinium vitis-idaea	1.2	1.4	0.2	1.5	1.1	-0.4	0.5	0.2	-0.3	1.2	$-1.8^?$	-0.9	0.1 N
Graminoid	6.3	7.1	0.8	3.9	4.5	0.6	7.6	8.2	0.6	-8.6	6.5 ¹	-0.3	-0.1 N
Carex bigelowii	6.4	6.3	-0.1	4.8	4.8	0.0	9.0	6.5	-2.5	-5.5	7.3^{\degree} I	0.2	-2.4
Hierachloe alpina	7.7	10.6	2.9	5.2	5.3	0.1	11.9	12.1	0.2	$-8.7^?$	11.7 [*] l	-4.5	0.1
Luzula arctica	1.4	3.6	2.2	0.0	2.2	2.2	1.1	1.4	0.3	-4.8 [*]	1.9 [*] $\overline{}$	-0.1	-1.9
Luzula confusa	5.6	6.5	0.9	5.0	3.8	-1.2	7.5	9.6	2.1	-2.4	4.5	-3.1	$3.2 \quad \square$
Trisetum spicatum	10.6	8.7	-1.9	4.4	6.4	2.0	8.6	11.2	2.6	-22.0	7.3 ^{\degree} l	6.3	0.6

¹ *Calamagrostis holmii, Hierochloe pauciflora, Poa arctica*

Table III.3: Change in taxa absolute cover over time in control plots and in response to warming. Control and experimentally warmed plot values are presented at sampling 1, sampling 2, and sampling 3 (C1, C2, C3, E1, E2, and E3). Warming responses were analyzed as the differences between control and experimental plots at all three samplings (W1, W2, W3). Control plot responses to ambient environmental changes were analyzed as the changes between samplings 1 and 2 (*As*) and between samplings 2 and 3 (*At*). Warming responses were partitioned into changes in warmed plots relative to changes in the control plots between samplings 1 and 2 (*Ws*), and between samplings 2 and 3 (*Wt*). Comparisons of responses to ambient environmental changes $(A_s$ and A_t) and warming responses $(W_s$ and W_t) were categorized as no change (N) , inconsistent change (I), and consistent change (C) over time (see methods for details) for taxa with more than an average of 1% cover in sampling 1. The values representing the changes over time were scaled to 7 years in the Atqasuk sites and 8 years in the Barrow sites to facilitate comparisons; however statistical significance is based on the unscaled values. ANOVAs were used to calculate statistical significance $(*\text{-}p\text{-}value<0.05)$.

¹ *Calamagrostis holmii, Hierochloe pauciflora, Poa arctica*

			Ambient	Warmed				
	N		C-	$C+$	N		C-	C+
Site								
Atqasuk Dry	0	17	3	0	$\overline{2}$	13	5	0
Atgasuk Wet	0	13	0	$\mathbf{1}$	$\mathbf{1}$	7	0	6
Barrow Dry	1	23	0	$\mathbf{1}$	3	15	3	4
Barrow Wet	$\mathbf{1}$	19	1	2	0	19	4	0
Growth Form								
Deciduous Shrub	0	5	0	0	0	4	0	1
Evergreen Shrub	0	7	0	0	$\mathbf{1}$	5	0	$\mathbf{1}$
Forb	$\mathbf{1}$	12	1	1	0	14	0	0
Graminoid	1	27	0	0	2	17	3	6
Bryophyte	0	16	0	$\mathbf{1}$	$\mathbf{1}$	12	3	$\mathbf{1}$
Lichen	0	5	3	$\overline{2}$	$\overline{2}$	1	7	O
Total	2	71	4	4	6	54	13	9

Table III.4: Summary of the consistency of changes in taxa over time from Table 3. The changes in control plots between years and in response to experimental warming are shown. The taxa are categorized as taxa that did not change (N), changed inconsistently (I), and changed consistently (C) grouped by site
Table III.5: Overall change in species composition expressed as the Euclidean distance of the change of all taxa presented in table 3. Warming responses represent the difference between control and warmed plots at all three samplings (W1, W2, W3). Ambient environmental changes were analyzed as the changes in the control plots between samplings 1 and 2 (A_s) and between samplings 2 and 3 (A_t) . Warming responses were partitioned into changes in warmed plot relative to changes in the control plots between samplings 1 and 2 (*Ws*), and between samplings 2 and 3 (*Wt*). Scaled values were calculated by obtaining a per year change value, extrapolating the change out to 5 years and then calculating Euclidean distance.

Table III.6: Predictions of community indices in later years of the experiment based on the response to warming observed in earlier years. Predictions were made using warming responses measured at the end of the first two years of warming (W1), warming responses between samplings 1 and 2 relative to the changes in the ambient environment (*Ws*), and the warming responses measured at sampling 2 (W2). Statistical significance was determined by analysis of variance with a Tukey's post-hoc test. Sites are the Atqasuk Dry (AD) and Wet (AW), and the Barrow Dry (BD) and Wet (BW).The consistency of response to warming over time from Table 2 is included for comparison.

Index	Response	E3	W1	$W_{\scriptscriptstyle\rm C}$	W2
Species Richness					
AD	N	15.38 A	15.42 A	15.85 A	15.71 A
AW	N	11.29A	8.85B	10.68 A	10.07 AB
BD	C	16.96A	15.71 A	16.82A	16.54A
BW		14.79 A	13.42 A	17.18B	16.11 AB
Shannon Index					
AD	N	2.39A	2.37A	2.41A	2.40A
AW	N	1.84 A	1.89A	1.85A	1.86A
BD	N	2.22A	2.31 AB	2.43C	2.40 BC
BW	N	2.13A	2.22A	2.25A	2.24A

Table III.6 continued*…*

Table III.7: Predictions of canopy heights in later years of the experiment based on the response to warming observed in earlier years. Predictions were made using warming responses measured at the end of the first two years of warming (W1), warming responses between samplings 1 and 2 relative to the changes in the ambient environment (*Ws*), and the warming responses measured at sampling 2 (W2). Statistical significance was determined by analysis of variance with a Tukey's post-hoc test. The consistency of response to warming over time from Table 3 is included for comparison.

¹ *Calamagrostis holmii, Hierochloe pauciflora, Poa arctica*

Table III.8: Predictions of taxa absolute cover in later years of the experiment based on the response to warming observed in earlier years. Predictions were made using initial warming responses measured at the end of the first two years of warming (W1), warming responses between samplings 1 and 2 relative to the changes in the ambient environment (W_s) , and the warming responses measured at sampling 2 (W2).Statistical significance was determined by analysis of variance with a Tukey's post-hoc test. The consistency of response to warming over time from Table 4 is included for comparison.

Table III.8 continued…

Table III.8 continued…

Table III.8 continued…

¹ *Calamagrostis holmii, Hierochloe pauciflora, Poa arctica*

Tab le III.9: Summary of the ability to predict changes in cover of taxa due to warming. Predictions of the cover values observed warmed plots at sampling 3 (E3) were made using warming responses measured at the end of the first two years of warming (W1), warming responses between samplings 1 and 2 relative to the changes in the ambient environment (W_s) , and the warming responses measured at sampling 2 (W2). The number of taxa that the prediction statistically differed from that observed is provided. For the taxa that did not statistically differ, the accuracy of the prediction is categorized as within 1, 1 to 5, and greater than 5 percent difference from the observed.

Chapter IV: Conclusion

Chapter I described the Arctic tundra environment with emphasis on how and why it is so susceptible to climate warming. Warming in high latitude regions has been documented for the past century and has been more pronounced recently. Adaptations to conditions such as cold temperatures and short growing seasons cause plants to be sensitive to fluctuations in climate. The ability to accurately monitor responses of tundra plant communities to warming in the Arctic is important to assessing the potential impacts of climate change.

Chapter II showed that the top and bottom contact only point frame method, as outlined by the ITEX manual, was as effective as the more time and labor intensive all contact method. Despite the top and bottom contact only method omitting intermediate points in sampling the difference between the methods were small and had no effect on the method's ability to detect changes in the community. Both the all contact and the top and bottom contact only methods were similar in their ability to detect responses to warming across all sites. Also, both methods were similar in ability when predicting aboveground biomass in plots using point frame contact data. The major benefit of the top and bottom contact only method is that it is much less time intensive, both in field work and data management and analysis. This ease of use and accuracy in monitoring communities makes it a reasonable choice for use in Arctic tundra systems.

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Chapter III demonstrated that changes in control plots and warming responses were heterogeneous over time and across the landscape. Often times taxa and growth forms within a site respond differently to warming across time and the same taxa and growth forms can have different responses between sites. The changes in control plots were often larger than responses to warming over the duration of the experiment, however often changes in the control plots were in different directions over time. Warming responses were often larger in early years of the experiment and tapered off in later years. Despite the heterogeneity present in both control and warmed plots the responses to warming were more consistent than were changes in control plots. Early responses to warming were poor predictors of communities in later years due to the variability of the response to warming over time.

The heterogeneity of response of tundra plants to warming over time and across the landscape makes extrapolations of community response difficult. Therefore it is important to continue to monitor vegetation changes in the Arctic and to see if more patterns develop. The top and bottom contact only method of point framing measurement continues to be an effective method of measuring tundra communities and for monitoring the effects of environmental changes. This thesis provides the first quantitative validation of the top and bottom only point frame method and is among the few studies that has examined vegetation change over more than 12 years with emphasis on the consistency of the response over time and space.

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Works Cited:

ACIA 2005. Arctic Climate Impact Assessment 2004, Cambridge University Press.

Arft A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jonsdottir, K. Laine, E. Levesque, G. M. Marion, U. Molau, P. Molgaard, U. Nordenhall, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenstrom, M. Stenstrom, O. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. Ecological Monographs, **69:**491-511.

Ayres E., R. Van der Wal, M. Sommerkorn, and R. D. Bardgett. 2006. Direct uptake of soil nitrogen by mosses. Biology Letters, **2:**286-288.

Berghen C. v. d. 1966. Review: [untitled]. Vegetatio, **13:**183.

Billings W. D. and H. A. Mooney. 1968. The Ecology of Arctic and Alpine Plants. Biological Review, **43:**481-529.

Blanken P. D. and W. R. Rouse. 1994. The Role of Willow Birch Forest in the Surface-Energy Balance at Arctic Treeline. Arctic and Alpine Research, **26:**403-411.

Bliss L. C. 1956. A Comparison of Plant Development in Microenvironments of Arctic and Alpine Tundras. Ecological Monographs, **26:**303-337.

Bliss L. C. 1962. Adaptations of Arctic and Alpine Plants to Environmental Conditions. Arctic, **15:**117-144.

Bliss L. C. 1966. Plant Productivity in Alpine Microenvironments on Mt. Washington, New Hampshire. Ecological Monographs, **36:**125-155.

Bliss L. C. 1971. Arctic and Alpine Plant Life Cycles. Annual Review of Ecology and Systematics, **2:**405-438.

Bliss L. C., G. M. Courtin, D. L. Pattie, R. R. Riewe, D. W. A. Whitfield, and P. Widden. 1973. Arctic Tundra Ecosystems. Annual Review of Ecology and Systematics, **4:**359- 399.

Ref Type: Journal

Bokhorst S. F., J. W. Bjerke, H. Tommervik, T. V. Callaghan, and G. K. Phoenix. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. Journal of Ecology, **97:**1408-1415.

Booth D. T., S. E. Cox, T. W. Meikle, and C. Fitzgerald. 2006. The accuracy of groundcover measurements. Rangeland Ecology & Management, **59:**179-188.

Bret-Harte M. S., M. C. Mack, G. R. Goldsmith, D. B. Sloan, J. DeMarco, G. R. Shaver, P. M. Ray, Z. Biesinger, and F. S. Chapin. 2008. Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. Journal of Ecology, **96:**713-726.

Britton M. E. 1957. Vegtation of the arctic tundra. Pages 26-61 *in* HP Hansen, editor. Arctic Biology. Oregon State University, Corvallis, Oregon, USA.

Brochmann C., A. K. Brysting, I. G. Alsos, L. Borgen, H. H. Grundt, A. C. Scheen, and R. Elven. 2004. Polyploidy in arctic plants. Biological Journal of the Linnean Society, **82:**521-536.

Brown J., K. R. Everett, S. F. MacLean, Jr., and D. F. Murray. 1980. The coastal tundra at Barrow. Pages 1-29 *in* J Brown, PC Miller, LL Tieszen, and FL Bunnell, editors. An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania, USA.

Cable J. M., K. Ogle, A. P. Tyler, M. A. Pavao-Zuckerman, and T. E. Huxman. 2009. Woody plant encroachment impacts on soil carbon and microbial processes: results from a hierarchical Bayesian analysis of soil incubation data. Plant and Soil, **320:**153-167.

Campioli M., L. E. Street, A. Michelsen, G. R. Shaver, T. Maere, R. Samson, and R. Lemeur. 2009. Determination of Leaf Area Index, Total Foliar N, and Normalized Difference Vegetation Index for Arctic Ecosystems Dominated by Cassiope tetragona. Arctic Antarctic and Alpine Research, **41:**426-433.

Cattle H. and J. Crossley. 1995. Modeling Arctic Climate-Change. Philosophical Transactions of the Royal Society of London Series A-Mathematical Physical and Engineering Sciences, **352:**201-213.

Chapin F. S.and G. R. Shaver. 1985. Arctic. Pages 16-40 *in* BF Chabot and HA Mooney, editors. Physiological Ecology of North American Plant Communities. Chapman and Hall, New York, NewYork, USA.

Chapin F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. Ecology, **76:**694-711.

Chapin F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, T. S. Rupp, A. H. Lynch, J. P. Schimel, J. Beringer, W. L. Chapman, H. E.

Epstein, E. S. Euskirchen, L. D. Hinzman, G. Jia, C. L. Ping, K. D. Tape, C. D. C. Thompson, D. A. Walker, and J. M. Welker. 2005. Role of land-surface changes in Arctic summer warming. Science, **310:** 657-660.

Cooper E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science, **180:**157-167.

Crawford R. M. M. 2008. Ecological Limits and Climate Change. Pages 199-224 Plants at the Margin. Cambridge University Press, New York, New York, USA.

De Valpine P. and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. Ecology, **82:**637-648.

Dorrepaal E., R. Aerts, J. H. C. Cornelissen, R. S. P. Van Logtestijn, and T. V. Callaghan. 2006. Sphagnum modifies climate-change impacts on subarctic vascular bog plants. Functional Ecology, **20:**31-41.

Edwards K. A. and R. L. Jefferies. 2010. Nitrogen uptake by Carex aquatilis during the winter-spring transition in a low Arctic wet meadow. Journal of Ecology, **98:**737-744.

Engstrom R., A. Hope, H. Kwon, D. Stow, and D. Zamolodchikov. 2005. Spatial distribution of near surface soil moisture and its relationship to microtopography in the Alaskan Arctic coastal plain. Nordic Hydrology, **36:**219-234.

Engstrom R., A. Hope, H. Kwon, and D. Stow. 2008. The relationship between soil moisture and NDVI near Barrow, Alaska. Physical Geography, **29:**38-53.

Epstein H. E., M. P. Calef, M. D. Walker, F. S. Chapin, and A. M. Starfield. 2004. Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. Global Change Biology, **10:**1325-1334.

Gornall J. L., I. S. Jonsdottir, S. J. Woodin, and R. Van der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia, **153:**931-941.

Gough L., G. R. Shaver, J. Carroll, D. L. Royer, and J. A. Laundre. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. Journal of Ecology, **88:**54-66.

Gould W. A. and M. D. Walker. 1999. Plant communities and landscape diversity along a Canadian arctic river. Journal of Vegetation Science, **10:**537-548.

Graglia E., S. Jonasson, A. Michelsen, I. K. Schmidt, M. Havstrom, and L. Gustavsson. 2001. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. Ecography, **24:**5-12.

Hagvar S. and K. Klanderud. 2009. Effect of simulated environmental change on alpine soil arthropods. Global Change Biology, **15:**2972-2980.

Harte J. and R. Shaw. 1995. Shifting Dominance Within A Montane Vegetation Community - Results of A Climate-Warming Experiment. Science, **267:**876-880.

Haugen R. K. and J. Brown. 1980. Coastal-inland distributions of summer air temperature and precipitation in Northern Alaska. Arctic and Alpine Research, **12:**403- 412.

Hinzman L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, G. J. Jia, T. Jorgenson, D. L. Kane, D. R. Klein, G. Kofinas, A. H. Lynch, A. H. Lloyd, A. D. McGuire, F. E. Nelson, W. C. Oechel, T. E. Osterkamp, C. H. Racine, V. E. Romanovsky, R. S. Stone, D. A. Stow, M. Sturm, C. E. Tweedie, G. L. Vourlitis, M. D. Walker, D. A. Walker, P. J. Webber, J. M. Welker, K. Winker, and K. Yoshikawa. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. Climatic Change, **72:**251-298.

Hobbie S. E. and F. S. Chapin. 1998. Response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. Ecology, **79:**1526-1544.

Hollister R. D. and P. J. Webber. 2000. Biotic validation of small open-top chambers in a tundra ecosystem. Global Change Biology, **6:**835-842.

Hollister R. D. 2003. Response of tundra vegetation to temperature: implications for forecasting vegetation change. Michigan State University, East Lansing, MI.

Hollister R. D., P. J. Webber, and C. E. Tweedie. 2005. The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. Global Change Biology, **11:**525-536.

Hollister R. D., P. J. Webber, F. E. Nelson, and C. E. Tweedie. 2006. Soil thaw and temperature response to air warming varies by plant community: Results from an opentop gamber experiment in northern Alaska. Arctic Antarctic and Alpine Research, **38:**206-215.

Hollister R. D. and K. J. Flaherty. 2010. Above- and below-ground plant biomass response to experimental warming in northern Alaska. Applied Vegetation Science, **13:**378-387.

Hudson J. M. G. and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology, **90:**2657-2663.

Hulten E. 1968. Flora of Alaska and Neighboring Territories, Stanford University Press, Stanford, CA, USA.

III F. S. C. and G. R. Shaver. /4. Individualistic Growth Response of Tundra Plant Species to Environmental Manipulations in the Field. Ecology, **66:**564-576.

IPCC 2007. Climate Change 2007: Impacts, Adaptations and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the IPCC, Cambridge University Press, Cambridge, United Kingdon.

IPCC 2007. Climate Change 2007: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report on the IPCC, Cambridge University Press, Cambridge, United Kingdom.

Jagerbrand A. K., K. E. M. Lindblad, R. G. Bjork, J. M. Alatalo, and U. Molau. 2006. Bryophyte and lichen diversity under simulated environmental change compared with observed variation in unmanipulated alpine tundra. Biodiversity and Conservation, **15:**4453-4475.

Jagerbrand A. K., J. M. Alatalo, D. Chrimes, and U. Molau. 2009. Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. Oecologia, **161:**601-610.

Jia G. S. J., H. E. Epstein, and D. A. Walker. 2009. Vegetation greening in the canadian arctic related to decadal warming. Journal of Environmental Monitoring, **11:**2231-2238.

Johnson D. A. and L. L. Tieszen. 1976. Aboveground Biomass Allocation, Leaf Growth, and Photosynthesis Patterns in Tundra Plant Forms in Arctic Alaska. Oecologia, **24:**159- 173.

Joly K., R. R. Jandt, and D. R. Klein. 2009. Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Research, **28:**433-442.

Joly K., F. S. Chapin, and D. R. Klein. 2010. Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. Ecoscience, **17:**321-333.

Kitti H.and B. C. Forbes. 2006. Vegetation: Structure, Cover, and Biomass of Subarctic Tundra Wetlands Used as Summer Pastures. Pages 187-198 *in* BC Forbes, L Bolter, L Muller-Wille, J Hukkinen, F Muller, N Gunslay, and Y Konstantinov, editors. Reindeer Management in Northernmost Europe. Springer-Verlag, Berlin.

Kitti H., B. C. Forbes, and J. Oksanen. 2009. Long- and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biology, **32:**253-261.

Klein J. A., J. Harte, and X. Q. Zhao. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecology Letters, **7:**1170-1179.

Komarkova V. and P. J. Webber. 1980. 2 Low Arctic Vegetation Maps Near Atkasook, Alaska. Arctic and Alpine Research, **12:**447-472.

Kudo G. and S. Suzuki. 2003. Warming effects on growth, production, and vegetation structure of alpine shrubs: a five-year experiment in northern Japan. Oecologia, **135:**280- 287.

Ledrew E. F. and G. Weller. 1978. Comparison of Radiation and Energy-Balance During Growing Season for An Arctic and Alpine Tundra. Arctic and Alpine Research, **10:**665- 678.

Levy E. B. 1927. Grasslands of New Zealand. New Zealand Journal of Agriculture, **34:**143-164.

Mölgaard P. 1982. Temperature Observations in High Arctic Plants in Relation to Microclimate in the Vegetation of Peary Land, North Greenland. Arctic and Alpine Research, **14:**105-115.

McCune B. and M. J. Mefford 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4., MjM Software Design, Gleneden Beach, OR, USA.

McLaren J. R. and R. Turkington. 2010. Ecosystem properties determined by plant functional group identity. Journal of Ecology, **98:**459-469.

Molau U. 1993. International Tundra Experiment (ITEX) Manual, Danish Polar Center, Copenhagen, Denmark.

Molau U. and P. M++lgaard 1996. International Tundra Experiment (ITEX) Manual, 2nd edition. Danish Polar Center, Copenhagen, Denmark.

Oechel W. C., S. J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Grulke. 1993. Recent Change of Arctic Tundra Ecosystems from A Net Carbon-Dioxide Sink to A Source. Nature, **361:**520-523.

Pajunen A. M. 2009. Environmental and Biotic Determinants of Growth and Height of Arctic Willow Shrubs along a Latitudinal Gradient. Arctic Antarctic and Alpine Research, **41:**478-485.

Phoenix G. K. and J. A. Lee. 2004. Predicting impacts of Arctic climate change: Past lessons and future challenges. Ecological Research, **19:**65-74.

Post E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. Van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological Dynamics Across the Arctic Associated with Recent Climate Change. Science, **325:**1355-1358.

Rinnan R., A. Michelsen, E. Baath, and S. Jonasson. 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. Global Change Biology, **13:**28-39.

Russell R. S. and P. S. Wellington. 1940. Physiological and Ecological Studies on an Arctic Vegetation: I. The Vegetation of Jan Mayen Island. Journal of Ecology, **28:**153- 179.

SAS Institute. SAS for Windows Release 9. 2005. Cary, NC, USA, SAS Institute Inc.

Savile D. B. O. 1972. Arctic Adaptations in Plants. Canadian Department of Agriculture Monographs, **6:**1-81.

Schuur E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in alaskan tundra. Ecosystems, **10:**280-292. Ref Type: Journal

Serreze M. C., J. E. Walsh, F. S. Chapin, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change, **46:**159-207.

Shaver G. R. and W. D. Billings. 1976. Carbohydrate Accumulation in Tundra Graminoid Plants As A Function of Season and Tissue Age. Flora, **165:**247-267.

Shaver G. R. and F. S. Chapin. 1991. Production - Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. Ecological Monographs, **61:**1-31.

Shaver G. R. and S. Jonasson. 1999. Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. Polar Research, **18:**245- 252.

Shaver G. R., S. M. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology, **82:**3163-3181.

Sigafoos R. S. 1951. Soil Stability in Tundra Vegetation. Ohio Journal of Science, **51:**281-298.

Sigafoos R. S. 1952. Frost Action as a Primary Physical Factor in Tundra Plant Communities. Ecology, **33:**480-487.

Soppela P., Turunen M., B. C. Forbes et al. 2006. The Chemical Response of Reindeer Summer Pasture Plants in a SubArctic Peatland to Ultraviolet (UV) Radiation. Pages 199-216 *in* BC Forbes, L Bolter, L Muller-Wille, J Hukkinen, F Muller, N Gunslay, and Y Konstantinov, editors. Reindeer Management in Northernmost Europe. Springer-Verlag, Berlin.

Sorensen L. I., J. Mikola, and M. M. Kytoviita. 2008. Defoliation effects on plant and soil properties in an experimental low arctic grassland community - the role of plant community structure. Soil Biology & Biochemistry, **40:**2596-2604.

Sorensen T. 1941. Temperature Relations and Phenology of the Northeast Greenland Flowering Plants, Meddelelser om Gronland.

Stafford J. M., G. Wendler, and J. Curtis. 2000. Temperature and precipitation of Alaska: 50 year trend analysis. Theoretical and Applied Climatology, **67:**33-44.

Stone R. S., E. G. Dutton, J. M. Harris, and D. Longenecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research-Atmospheres, **107**.

Stow D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, K. Tape, L. Hinzman, K. Yoshikawa, C. Tweedie, B. Noyle, C. Silapaswan, D. Douglas, B. Griffith, G. Jia, H. Epstein, D. Walker, S. Daeschner, A.

Petersen, L. M. Zhou, and R. Myneni. 2004. Remote sensing of vegetation and landcover change in Arctic Tundra Ecosystems. Remote Sensing of Environment, **89:**281- 308.

Tape K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology, **12:**686-702.

Tape K. D., R. Lord, H. P. Marshall, and R. W. Ruess. 2010. Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience, **17:**186-193.

Tieszen L. L. 1973. Photosynthesis and Respiration in Arctic Tundra Grasses: Field Light Intensity and Temperature Responses. Arctic and Alpine Research, **5:**239-251.

Uchida M., A. Kishimoto, H. Muraoka, T. Nakatsubo, H. Kanda, and H. Koizumi. 2010. Seasonal shift in factors controlling net ecosystem production in a high Arctic terrestrial ecosystem. Journal of Plant Research, **123:**79-85.

Wager H. G. 1941. On the Respiration and Carbon Assimilation Rates of Some Arctic Plants as Related to Temperature. New Phytologist, **40:**1-19.

Wahren C. H. A., M. D. Walker, and M. S. Bret-Harte. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biology, **11:**537-552.

Walker L. J. 1996. Community baseline measurements for ITEX studies. Pages 39-41 *in* U Molau and P M++lgaard, editors. International Tundra Experiment (ITEX) Manual. Danish Polar Center, Copenhagen, Denmark.

Walker M. D., P. J. Webber, E. H. Arnold, and D. Ebertmay. 1994. Effects of Interannual Climate Variation on Aboveground Phytomass in Alpine Vegetation. Ecology, **75:**393- 408.

Walker M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jonsdottir, J. A. Klein, B. Magnusson, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, O. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America, **103:**1342-1346.

Webber P. J. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. Pages 37-112 *in* LL Tieszen, editor. Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer-Verlag, New York, NY, USA.

Webber P. J. and M. D. Walker. 1991. International Tundra Experiment (ITEX):Resolution. Arctic and Alpine Research, **23:**124.

Wilson J. W. 1959. Observations on the Temperatures of Arctic Plants and Their Environment. Journal of Ecology, **45:**499-531.

Wilson S. D. and C. Nilsson. 2009. Arctic alpine vegetation change over 20 years. Global Change Biology, **15:**1676-1684.

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

Zhao L., J. Li, S. Xu, H. Zhou, Y. Li, S. Gu, and X. Zhao. 2010. Seasonal variations in carbon dioxide exchange in an alpine wetland meadow on the Qinghai-Tibetan Plateau. Biogeosciences, **7:**1207-1221.

Zhou H. K., Y. H. Tang, X. Q. Zhao, and L. Zhou. 2006. Long-term grazing alters species composition and biomass of a shrub meadow on the Qinghai-Tibet Plateau. Pakistan Journal of Botany, **38:**1055-1069.