RESPONSE OF TUNDRA VEGETATION TO TEMPERATURE: IMPLICATIONS FOR FORECASTING VEGETATION CHANGE

By

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ABSTRACT

RESPONSE OF TUNDRA VEGETATION TO TEMPERATURE: IMPLICATIONS FOR FORECASTING VEGETATION CHANGE

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Tundra regions have experienced regional warming and climate models predict continued warming as a result of the greenhouse effect. This study examines the potential effects of future warming by observing the response of tundra vegetation to variation in temperature due to natural temperature gradients, interannual variability, and experimental warming at four sites in northern Alaska. The four sites spanned a temperature gradient from warmer Atqasuk to cooler Barrow and moisture gradients from dry heaths to wet meadows. At each site 24 warmed and 24 control plots were monitored for 5-7 years. The warming treatment (small open-top chambers) increased air temperatures throughout the growing season between 0.6-2.2 ^{o}C depending on the year and site. There was generally a consistent relationship between growing season thawing degree-day totals and plant response irrespective of treatment; thus, it was concluded that experimental differences in plant traits were primarily due to temperature and that the open-top chambers were a reasonable analog of regional climate warming. The plant traits measured were phenological events (leaf emergence, visible buds, and flowering), growth traits (leaf length and change in overall size), and reproductive traits (inflorescence length and number of inflorescences per plot). Plants responded to temperature in 130 of 267 observations (49%). The most common response to warming was earlier phenological development and increased growth and reproductive effort; however, when the response of multiple traits was examined each species response was individualistic and varied among sites. The trajectories of species composition and cover change due to warming were different for each site; nevertheless, the general response to warming was a trend toward lower diversity, an increase in canopy height, an increase in standing dead plant matter, and a decrease in lichens. These findings demonstrate that the response of tundra plant species to warming is complex and varies greatly by species and habitat type. Therefore, it is concluded that forecasts of tundra vegetation change at the regional and species level derived from in situ experimental manipulation will be more accurate than forecasts based on mechanistic or correlational modeling.

“*...the more I learned abut the vegetation of the area as a whole,*
the less I felt inclined to generalize about it.”

Nicholas Polunin (1948)

From the Author

Before the dissertation is read it might be useful to present a few thoughts relating to science and synthesis.

Sir Karl R. Popper (1957) stated,

"Science must begin with myths, and with the criticism of myths."

This dissertation will precariously criticize several of the myths or dogmas current in Polar Ecology while leaning on other myths as support for the presented results. Robert H. MacArthur (1972) has said,

"Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true ... that it is best not to put too much faith in facts until they have been confirmed by theory."

While this dissertation will not propose new theories an attempt is continually made to generalize the results into a synthetic response of tundra vegetation to warming. This effort has been difficult due to the ambitious experimental design that includes many plant species at multiple study sites over many years of observations. Mindful of the statement of Henry A. Gleason (1926),

"it may be said that every species of plant is a law unto itself,"

I am aware of the danger of synthesizing results in order to make generalizations. In fact Fred L. Bunnell (1981) and Sir W. Napier Shaw (1913) have gone so far as to characterize synthesis as a *"fairytale"* due to its inherent simplification of the real complexity associated with natural systems. While fairytale may convey the wrong impression it is fair to conclude that synthesis is a necessary simplification that is invariably somewhat inaccurate in the details. Therefore, a careful examination of the results will reveal exceptions to nearly every generalization presented in this dissertation. However, all presented generalizations have been carefully proposed and it is the opinion of the author that they are valid and a necessary part of the process leading to predictions about arctic vegetation change.

ACKNOWLEDGEMENTS

I would first like to thank my advisor Patrick J. Webber for the many wonderful opportunities and wealth of insight he has provided. I am indebted to Christian Bay for introducing me to Arctic research and the species of the North Slope and Frederick E. Nelson for providing every opportunity he could for me to do research in Barrow. I could not have completed this undertaking without the long hours and hard work provided by the people I worked with and I thank them all including Steve Rewa, Stephanie Grimes, Lisa Walker, Brian Noyle, William Chu, Ian Ramjohn, Lisa Koch, Mark Peterson, Laura Stack, Sharon Osborn, Anna Noson, David Conlin, Bennett Weinstein, Matthew Guisbert, MaryGrace Villanueva, Christie Klimas, Theresa Thomas, Kathryn Wilkinson, Elise Poole, Brandon Baker, Frank Lepera, Christine Jimenez, Meghan Yurenka, Christin Kolarchick, Josh Picotte, Devan Berry, Amy Wren, Dustin Bronson, Shawn Serbin, and Andy Johnson. I especially thank Craig Tweedie for all his assistance particularly running field operations and allowing me time to write this dissertation.

I am grateful to all the researchers who shared their experience and friendship. Dave Norton, Kenneth Hinkel, Jerry Brown, Nikolay Shiklomanov, Jerry Mueller, Anna Klene, Ronald Paetzold, Jim Bockheim, Wendy Eisner, Samuel Outcalt, and Lynn Everett all were especially generous. I thank the Barrow and Atqasuk communities particularly Dario Leiba, Jimmy Nayukok and the people at the Barrow Arctic Science Consortium (BASC), most notably Glenn Sheehan and Richard Glenn. I am indebted to Malcolm Gaylord and Dan Enders at the National Oceanic and Atmospheric

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Chapter I

THE STUDY SYSTEM

I.1 RATIONALE, STRUCTURE, AND OBJECTIVES OF THE DISSERTATION

I.1.1 Rationale for the Study

In recent years there has been interest in species response to elevated temperature due to concern regarding the impact of anthropogenically enhanced climate change. In nearly all climate change scenarios the polar latitudes are projected to warm more than lower latitudes (Cattle and Crossley 1995, Rowntree 1997, McCarthy *et al*. 2001). Since polar organisms are adapted to cold climates, it is of great interest to understand how they might adapt to a warmer climate (Stonehouse 1989, McGraw and Fetcher 1992, Crawford and Abbott 1994, Callaghan and Jonasson 1995, Huntley and Cramer 1997). Such questions are particularly important for plants and vegetation because they form the basis of food chains and give structure to ecosystems. Various research agendas and predicted scenarios of vegetation response to warming have been presented (*e*. *g*. Ford 1982, Cohn 1989, Mooney 1991, Ojima *et al*. 1991, Woodward and Diament 1991, Schlesinger 1993, Root and Schneider 1995) and this has led to a large effort to model vegetation change due to climate warming (*e*. *g*. Bonan *et al.* 1990, Woodward 1993, Shugart and Smith 1996, Kirilenko and Solomon 1998, Cramer *et al*. 2001, Bakkenes *et al*. 2002).

This study examines the response of tundra plants to temperature so that findings can be used in vegetation models attempting to forecast change due to regional warming. Specifically, this dissertation documents the response of plants to variation in temperature due to natural temperature gradients, interannual variability, and experimental warming in wet meadow and dry heath communities at Barrow and Atqasuk, Alaska.

I.1.2 The Structure of the Dissertation

This dissertation is composed of several chapters that were written to become stand alone papers. The status of each chapter is listed in Table I-1. The author of this dissertation is the lead author and principal analyst for each paper.

To streamline chapters for later publication and to set each in context this introductory chapter, "The Study System," comprehensively reviews issues that need only brevity in a paper. Later chapters may provide a more in-depth review of aspects pertaining directly to that chapter. Chapters not already submitted for publication include information that will be scaled down and re-worked with co-authors before submission. This format has led to some repetition between chapters. Where appropriate, references are made to other parts of the dissertation with complementary information.

Table I-1. Status of the chapters presented in this dissertation.

I	The Study System[†] R.D. Hollister No submission intended
II	The Microenvironment of Four Experimentally Warmed Arctic Tundra Communities R.D. Hollister, P.J. Webber, F.E. Nelson, C.E. Tweedie To be submitted for publication
III	Biotic Validation of Open-Top Chambers in a Tundra System[†] R.D. Hollister and P.J. Webber *Global Change Biology* 6, 835-842
IV	Plant Response to Temperature in Northernmost Alaska: Implications for Predicting Vegetation Change R.D. Hollister, P.J. Webber, and C. Bay To be submitted for publication
V	Detection of Community Change due to Moderate Warming of Tundra Vegetation: Separation of Initial and Secondary Response R.D. Hollister, P.J. Webber, C.E. Tweedie To be submitted for publication
VI	Concluding Remarks R.D. Hollister No submission intended

[†] Some of the content included in these chapters overlaps with material presented in Hollister's Master of Science Thesis, Department of Botany and Plant Pathology, 1998 from MSU.

I.1.3 Objectives

The overarching goal of the dissertation is to describe the response of tundra vegetation to temperature to the improve vegetation change forecasts for the Arctic and to address the feasibility of accurately forecasting tundra vegetation change due to warming. The three main objectives are listed below.

1. Evaluate the validity of using the open-top chambers to simulate anthropogenically enhanced climate change (Chapters II, III, and IV).
    - Document the performance of the open-top chambers in relation to the natural environment (Chapter II).
    - Evaluate the response of plant species to similar degree-day totals in the control plots of a warm year with the warmed plots of a cool year (Chapter III).
    - Integrate results from experimental warming, interannual variability, and natural temperature gradients to validate the results obtained from each method (Chapter IV).
2. Describe the response of plant phenological and morphological traits to temperature (Chapter IV).
    - Determine if the response of a species is constant across the range of observed sites.
    - Determine if species have common groupable responses to temperature.
    - Compare plant responses to temperature with the responses to other naturally fluctuating factors.

3. Describe the community changes due to warming that have occurred in each study site (Chapter V).
    - Document changes that have occurred in the warmed plots in relation to changes in the control plots.
    - Separate the warming response into a short-term initial response and a longer-term secondary response.
    - Compare and contrast changes that have occurred due to warming at the four study sites.

I.2 RESEARCH FRAMEWORK

The results presented in this dissertation are a subset of two distinct yet interacting research programs, Arctic System Science (ARCSS) and the International Tundra Experiment (ITEX). All research reported in this dissertation was completed as a part of the Arctic Ecology Laboratory (AEL) at Michigan State University. Each of theses three distinct research entities are described below and their logos are shown in Figure I-1.

I.2.1 The Arctic Ecology Laboratory

The Arctic Ecology Laboratory (AEL) is part of Michigan State University (MSU). MSU is a large, well-equipped research university. The AEL conducts research on aspects of regional change in the Arctic and Alpine ecosystems. Current interests include the potential responses of arctic tundra vegetation to climate change and various human induced impacts. Research efforts focus on the arctic tundra of the North Slope of Alaska, although the AEL has strong circumpolar and international collaborative relationships. The AEL is an active collaborator with the Computational Ecology and Visualization Laboratory (CEVL). CEVL is designed to provide computational facility to conduct spatial analysis research and use intensive mathematical models to address global and complex systems analysis. The AEL library contains volumes and reprints with emphases in Cold Regions, Ecology, Global Change, and Botany; it also houses an extensive map and aerial photograph collection of Northern Alaska, particularly the Barrow region and the National Petroleum Reserve.

I.2.2 The Arctic System Science Program

The Arctic System Science (ARCSS) Program is a subprogram of the office of Polar Programs within the National Science Foundation (ARCUS 1993). ARCSS takes a whole-system approach to understanding the response of the Arctic System to global change and is particularly concerned with the mechanisms and consequences of the amplified response of the high latitudes to greenhouse warming. A principal goal of ARCSS is to enable the prediction of the future state of the Arctic System, on seasonal to century time scales, by integrating observations, process research, modeling, and assessment. The research reported in this dissertation is most closely connected to the Land / Atmosphere / Ice Interactions (LAII) component of ARCSS. The response of tundra vegetation to warming documented in this dissertation will ultimately be incorporated into models that attempt to predict vegetation response to global change.

I.2.3 The International Tundra Experiment

The International Tundra Experiment (ITEX) is a collaborative effort involving scientists from over 11 countries including all the Arctic Nations (Figure I-2). ITEX seeks to examine the response of circumpolar cold adapted plant species to environmental change, specifically to an increase in summer temperature (Webber and Walker 1991). Empirical knowledge based on experiments coupled with available evolutionary history, ecology, and genetics was chosen as the best way to predict species response to climate change. The ITEX research model combines long-term and short-term experimentation with monitoring and has the elegance and simplicity called for to understand ecosystem response and vulnerability to change (Tilman 1987, Rastetter 1996). The experiment is designed to examine the effects of temperature change; maximize geographic representation by minimizing technical and equipment requirements; be long-term; focus primarily on species; and, if resources permit, allow for genetic and system level studies (Molau and Mølgaard 1996). Participation may be at several levels of complexity and sophistication depending on interests and available funding support. Each ITEX site operates some form of warming experiment. Most sites use open-top chambers to warm the tundra. These passive chambers affect plant growth and phenological development in a variety of ways (Marion *et al.* 1997, Henry and Molau 1997). Each ITEX study site is expected to collect similar data following established protocols provided in the ITEX Manual (Molau 1993a, Molau and Mølgaard 1996). Collectively the ITEX network is able to pool its data sets to examine vegetation response at varying levels, for example genetics (from ecotype to functional type), across space (from habitats to ecosystems) and over time (Walker and Jones 1996).

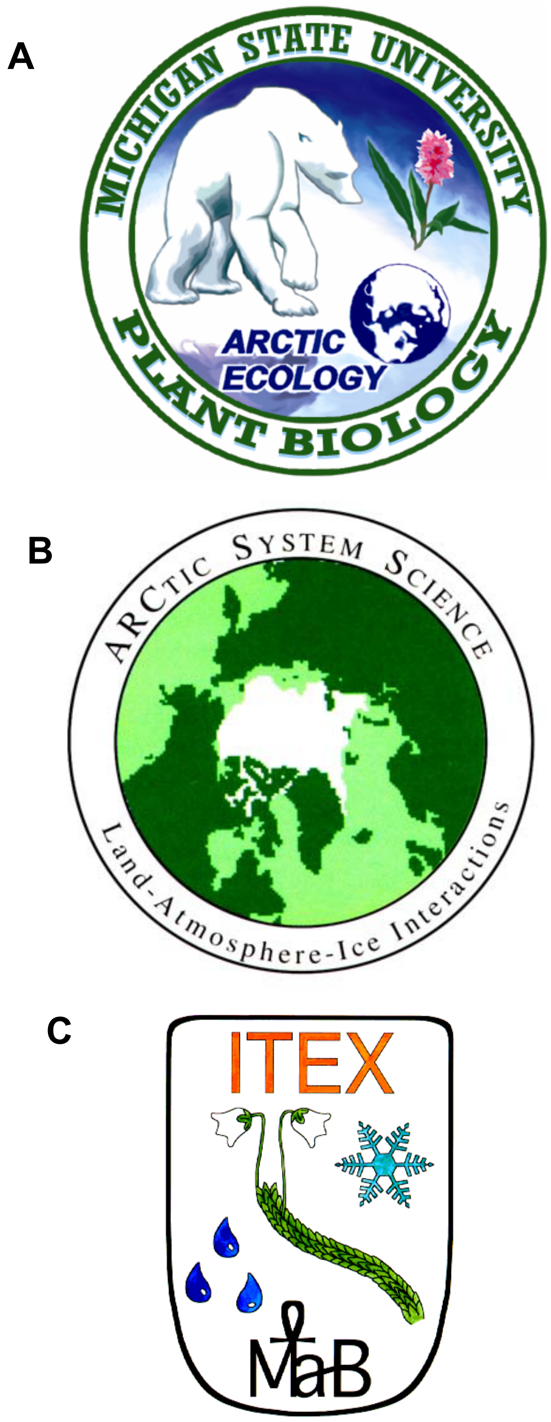

Figure I-1. The logos of the research efforts associated with the research reported in this dissertation: (***A***) the Arctic Ecology Laboratory, (***B***) the National Science Foundation Land-Atmosphere-Ice Interactions component of the Arctic System Science program, and (***C***) the International Tundra Experiment.

Figure I-2. Map of the original International Tundra Experiment (ITEX) study sites. Site 13 is Barrow, Alaska (Molau & Mølgaard 1996).

I.3 VEGETATION AND TEMPERATURE RELATIONS

There is a long rich history of research in the relationship between plants and temperature, which has many of its roots in tundra plants because tundra systems lie on the cold end of the plant-temperature response envelope. The two major historical foci were species compositional changes along natural temperature gradients (climate and vegetation: *e. g.* von Humboldt and Bonpland 1807, de Candolle 1855, Clements 1916, Holdridge 1947, Whittaker 1975, Box 1981, Woodward and Williams 1987) and the role of temperature on plant physiological processes (microclimate and plants: *e. g.* Mooney and Billings 1961, Levitt 1972, Jones 1992, Larcher 1995). These topics are briefly reviewed and an attempt has been made to provide examples from tundra systems. A final section on vegetation change in changing environments is provided in order to review the current state of knowledge with regard to future vegetation response to climate change.

I.3.1 Microclimate and Plants

The microclimate of a plant is the climate in its immediate vicinity. Plants in the same geographic region may experience very different microclimates due to differences in slope, aspect, wind, and vegetation structure (Geiger 1965). Plant–microenvironment interactions are the core of plant physiological ecology. Most chemical reactions, and consequently organismic processes, are temperature dependent; therefore, the rates of physiological processes in plants are related to the external environment. On a daily basis plants may modify tissue temperatures by opening or closing their stomata or by altering the angle of their organs to incident solar radiation. Plants may also modify their morphology and physiology to optimize success in their local environment through acclimatization and adaptation. These adaptive traits become more extensive and elaborate in more extreme environments such as the Arctic (Billings 1974a, also see Section I.4.2). For example, it has been proposed that the high respiration rates at low temperatures in high arctic plants may actually raise tissue temperatures (Mølgaard 1982).

In order to understand the physiological response of a species it is important to first describe its microclimate. For example, the vertical temperature distribution at Barrow, Alaska is shown in Figure I-3. The figure demonstrates how the microclimate near the ground differs from the macroclimate measured at 2 m height and the seasonal dynamics of the difference. Minor differences in micro-topography may also have significant impacts on the microclimate as seen in Figure I-4. More importantly, the temperatures of plant tissues may vary considerably from the immediate surroundings particularly in sunny environments with little wind (Figure I-5). Plant tissue temperatures may also vary by organ and species (Table I-2). Therefore, where an individual lives and its morphology may have a profound affect on the temperature the individual experiences. Morphological changes in size and shape allow plants to optimize the energy balance between themselves and the environment in order to gain heat or dissipate heat; this phenomenon is well described in tundra plants (Bliss 1962, also see Section I.4.2).

Each species has its own unique suite of adaptations to cope with temperature; therefore, each species has its own ecological temperature optimum and tolerance range (Larcher 1995). Plants have evolved to maintain similar rates of physiological processes

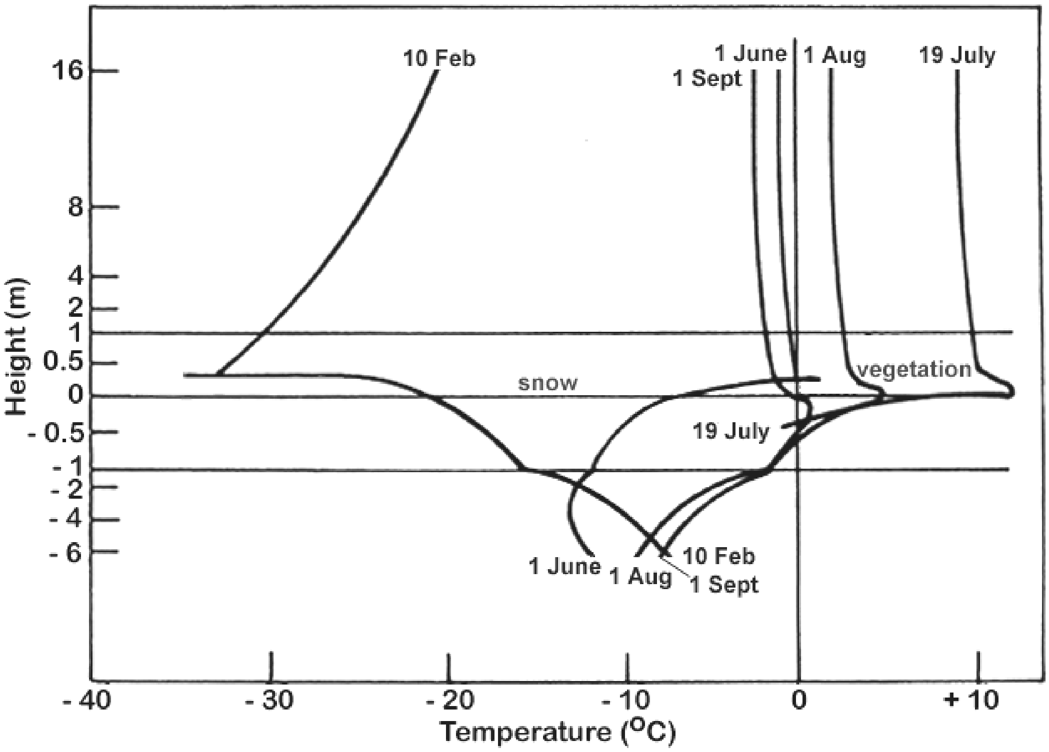

Figure I-3. Vertical temperature gradients in air, snow, vegetation, and soil on five typical days of the year over sedge-moss communities at Barrow, Alaska. Note the effects of snow (10 February and 1 June) and vegetation (1 August and 19 July) on the expanded ±1 m vertical profile (Weller and Holmgren 1974).

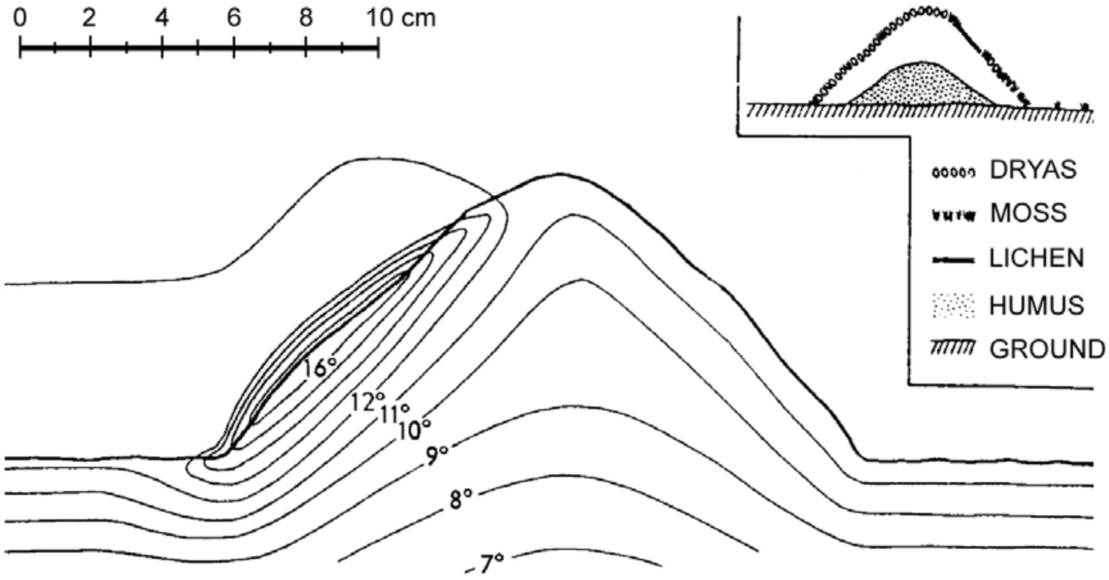

Figure I-4. Temperature distribution (isotherms °C) of a *Dryas octopetala* mound facing south during a moderately windy and sunny mid day in late July in the Canadian Arctic (75°N 95°W). The inset shows the distribution of plants, and humus of the mound (Warren Wilson 1957).

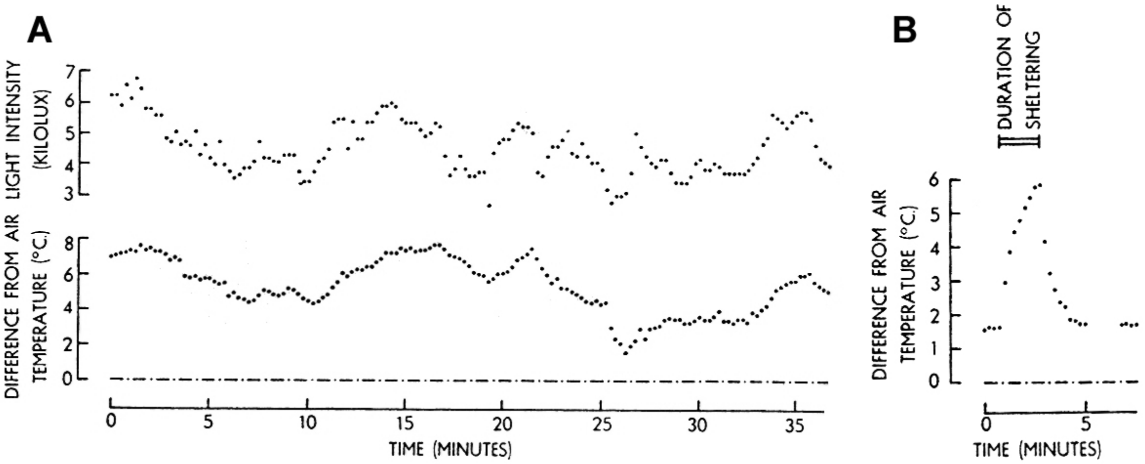

Figure I-5. Records at 15-second intervals of the temperature of a *Salix* leaf, showing changes associated with variation in light intensity (***A***) and artificial sheltering (***B***) (Warren Wilson 1957).

Table I-2. Surface temperatures (°C) relative to air temperature recorded during sunshine and overcast conditions. Temperatures were recorded during the early afternoon of late June in Northern Greenland at air temperatures between 3.5 and 5.0 °C (82°N, 22°W) (reconfigured from Mølgaard 1982).

	Sunshine	Overcast
Open soil	13.5	3.5
Saxifraga oppositifolia[1]		
apex	15.0	3.5
flower	17.5	3.5
Dryas integrifolia[2]		
apex	20.0	4.5
flower	23.5	3.0
Salix arctica[3]		
leaf, upper side	13.5	0.5
leaf, lower side	14.0	0.5
male catkin	10.0	1.5
Cetraria nivalis[4]	13.5	3.5
Moss	15.0	4.0

[1] cushion forb

[2] rosette forb

[3] deciduous shrub

[4] fruticose lichen

across temperature gradients. The temperature relationships of the plant physiological processes photosynthesis, respiration, nutrient absorption, and growth have been the focus of many studies and are described for a number of species. A classic example of photosynthesis and respiration temperature relations is the work of Billings *et al*. (1978) on the tundra plant *Oxyria digyna* shown in Figure I-6; the figure also demonstrates the ability of individuals to acclimate and ecotypes to adapt to local environments. Generally, arctic plants have higher photosynthesis and respiration rates at low temperatures than temperate and tropical plants. One likely mechanism for this difference is higher concentrations of ribulose bisphosphate carboxylase/oxygenase (RuBP or ribisco) in arctic plants (Chapin and Shaver 1985a). The relationship between nutrient absorption and temperature has been described in *Carex aquatilis* for phosphorus (Figure I-7). The mechanisms for acclimatization and adaptation in nutrient absorption of phosphorus in *Carex aquatilis* to local soil temperature are not fully understood but likely involve differences in cell plasma membrane composition in the root tips (Chapin and Shaver 1985a, Clarkson *et al*. 1988, BassiriRad 2000). The relationship between growth and temperature has been described for many plant species. Growth slows non-linearly as temperatures approach a minimum threshold for the species (Figure I-8). The exact temperature is variable between species but the rule of thumb is that 0, 10, 15 ^{o}C are the cardinal minimum temperatures for species of the Arctic, Temperate, and Tropical regions respectively (*cf*. Larcher 1995). A metric called degree-days that incorporates time and temperature is often used. The degree-day is calculated as the area under the curve of daily temperature range above a defined minimum cardinal value – generally 0 ^{o}C for thawing degree-days (TDD) and 5-10 ^{o}C for growing degree-days (GDD).

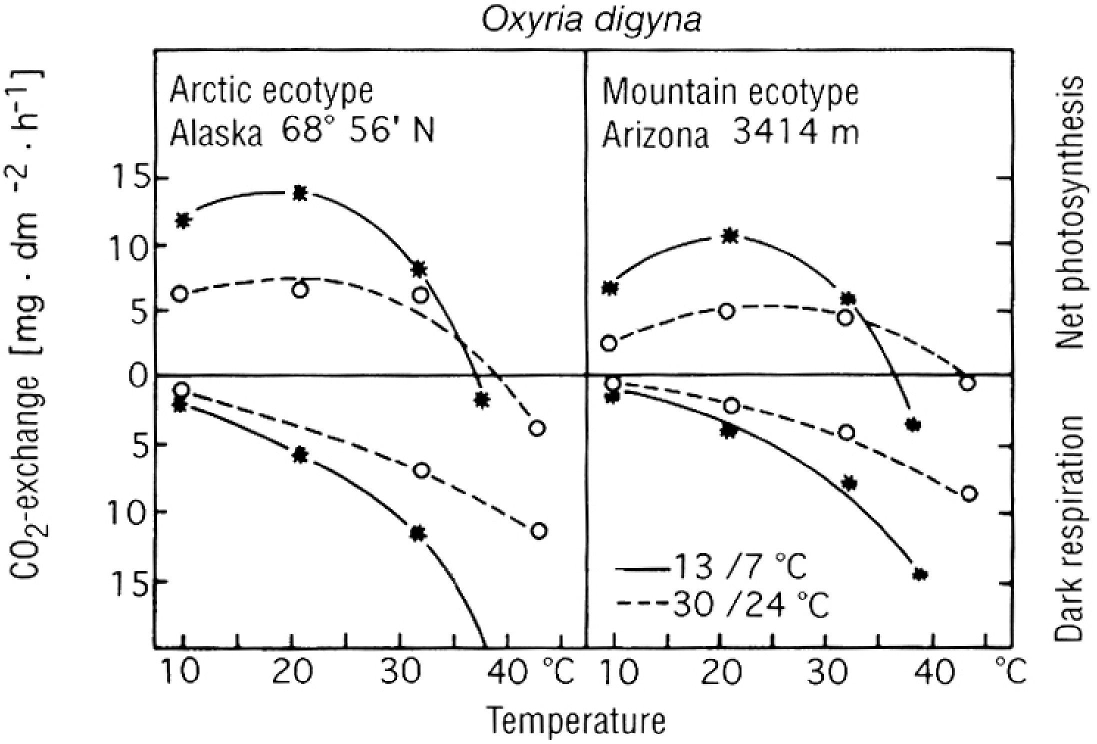

Figure I-6. Temperature response of net photosynthesis and dark respiration in arctic and mountain ecotypes of *Oxyria digyna* grown at low (day/night: 13/7°C) and high (30/24°C) temperatures (Billings *et al*. 1971 as drawn in Larcher 1995).

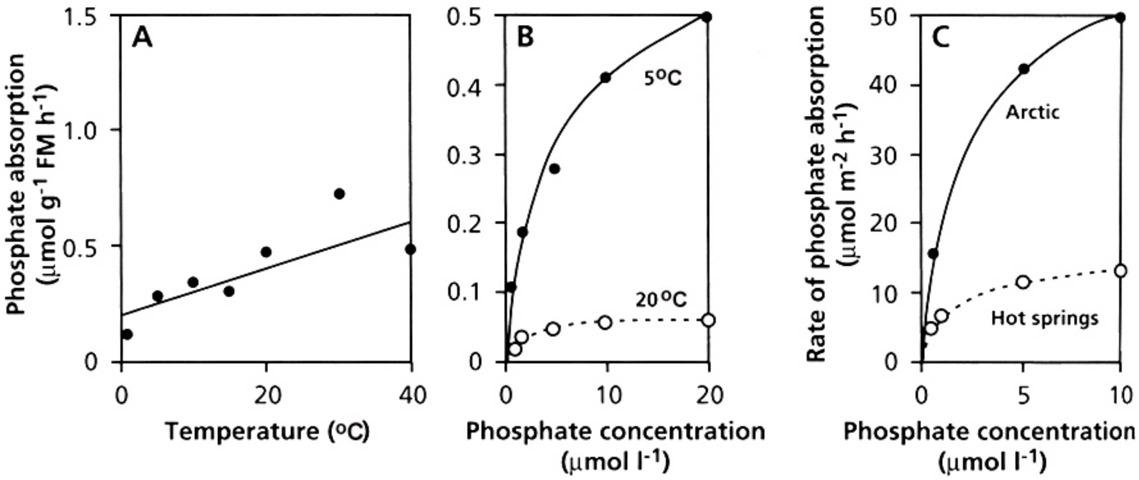

Figure I-7. Response of phosphate uptake by *Carex aquatilis* to temperature at the time scales: (***A***) immediate, (***B***) acclimation, and (***C***) adaptation measured at 5 °C (Lambers *et al*. 1998).

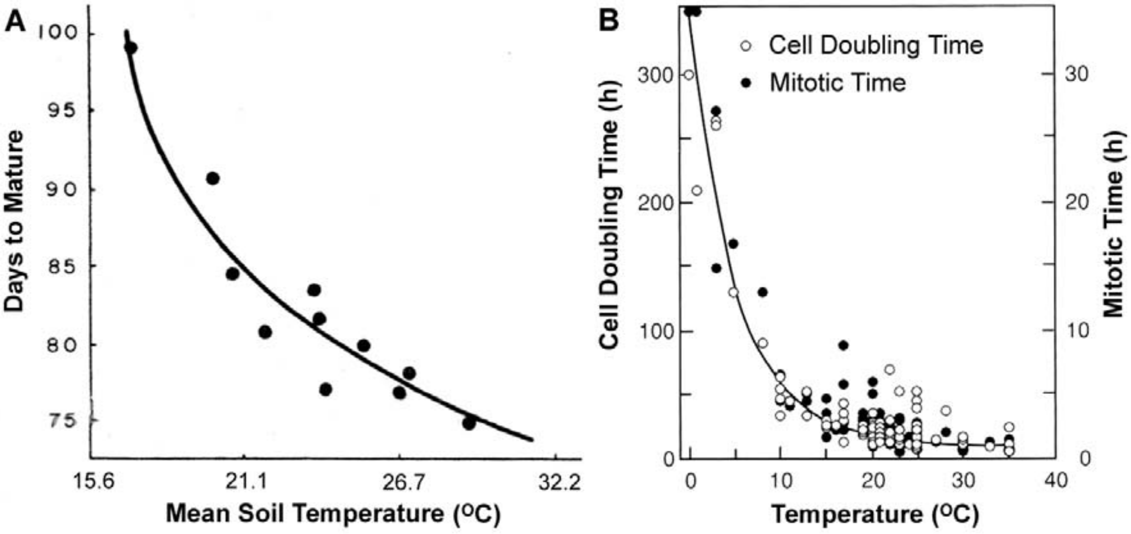

Figure I-8. Temperature dependence of growth. ***A***) The duration of the growing season for sweet corn at Ames, Iowa relative to the mean soil temperature at 2.6 cm depth from year 1939-1950 (Wang 1960). ***B***) Cell doubling time and the length of the mitotic phase in root tip meristems of herbaceous plants grown in controlled environment (Körner 1999).

Degree-days or similar measures have been used to predict the phenological development of crops and natural populations for over 200 years (Lindsey and Newman 1956, Wang 1960, Yang *et al*. 1995, Wielgolaski 1999, Cesaraccio *et al*. 2001).

Often extreme events (for example, drought and high or low temperature) have a critical effect on the survival of an individual and may limit the distribution of a species. For this reason the temperature stress is often examined at the hot and cold ends of the spectrum. Heat may cause biomembranes to become more fluid, while cold may cause biomembranes to become more rigid (Quinn1988, Larcher 1995). Heat stress is generally associated with rapid production of a group of proteins known as heat shock proteins, which presumably act to maintain cellular integrity and function at high temperatures (Ougham and Howarth 1988, Jones 1992). Damage due to cold temperatures can be categorized as chilling injury, presumably due to biomembrane changes, or frost damage due to the formation of ice crystals in the plant tissue. Chilling tolerance is common in most non-tropical plants and is associated with a higher amount of unsaturated fatty acids than saturated fatty acids in the biomembranes (Lambers *et al*. 1998). Frost tolerance is associated with an accumulation of soluble carbohydrates and a wide array of proteins in the cellular fluids (Lambers *et al*. 1998). Frost tolerance changes throughout the year; plants harden (become more frost tolerant) in the fall and winter as seen in Table I-3. Plants are often vulnerable to frost during the spring or fall when unusually cold temperatures are encountered and the individual is not fully hardened. Tundra plants experiencing unusually warm environments or plants exposed to increased CO_2 and UV-B radiation have been found to be more susceptible to harsh frosts presumably due to significant dehardening (Molau 1996a, Beerling *et al*. 2001).

Table I-3. Organ specific freezing tolerance in dehardened and fully hardened (in brackets) temperate zone alpine plants. Numbers are temperatures (^{o}C) at which 50% of the samples were damaged (reconfigured from Körner 1999).

Species	Leaf	Stem	Root
Dwarf shrubs			
Empetrum nigrum	-8(-70)	*nd*(-30)	*nd*(-30)
Vaccinium vitis-idea	-5(-80)	-8(-30)	*nd*(-20)
Calluna vulgaris	-5(-35)	-5(-30)	*nd*(-20)
Cushion forming herbs			
Saxifraga oppositifolia	-10(-196)	-19(-196)	-25(-196)
Silene acaulis	-7(-196)	-8(*nd*)	-11(-196)
Carex firma	-7(-70)	-6(*nd*)	-8(-70)

nd - no data

I.3.2 Climate and Vegetation

It is apparent when viewing vegetation from around the world that certain broad physiognomic patterns are common and that they are generally correlated with climate. The association between climate and vegetation has long been recognized and was formalized in the 1800's by the works of geographers such as von Humbolt and Bonpland (1807) and de Candolle (1855). Since that time the association between climate and vegetation has continued to be refined. One of the simplest representations of the climate vegetation association was done by Whitaker (1975) and shows the distribution of the major biomes along scales of temperature and precipitation (Figure I-9).

Researchers have used various approaches to determine vegetation based on climate; the most often used are the Holdridge (1947) life zone system, the Box (1981) model, and the BIOME model (Prentice *et al*. 1992). These approaches predict vegetation on the basis of various measures of precipitation and temperature. The redistribution of the world's biomes due to CO_2 driven climate warming have been projected based on the above models (Emanuel *et al*. 1985, Cramer and Leemans 1993, Sykes *et al*. 1999); therefore it is worth commenting on each. These three approaches also represent three major types of vegetation models currently being used to predict future vegetation changes. The Holdridge life zone system and the Box model are strictly correlations of vegetation with climate based on observations (Woodward and Williams 1987). The Holdridge life zone systems predicts broad vegetation assemblages such as tropical rain forest or subpolar dry tundra (Figure I-10), because it is a correlation between present climates and present community types it can not predict new community

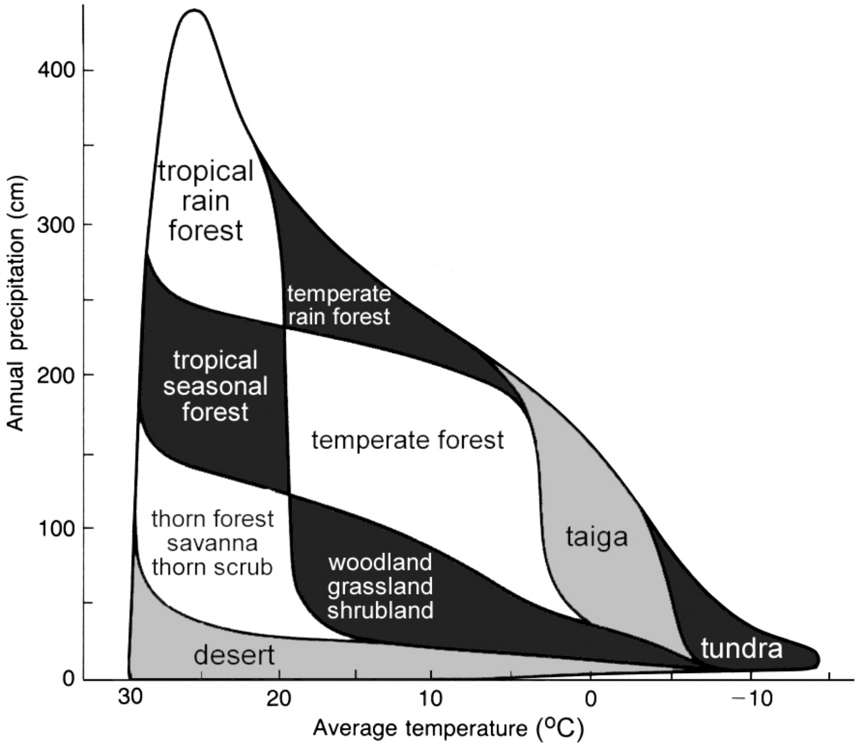

Figure I-9. Whittaker's classification of vegetation types relative to average temperature and annual precipitation (Whittaker 1975).

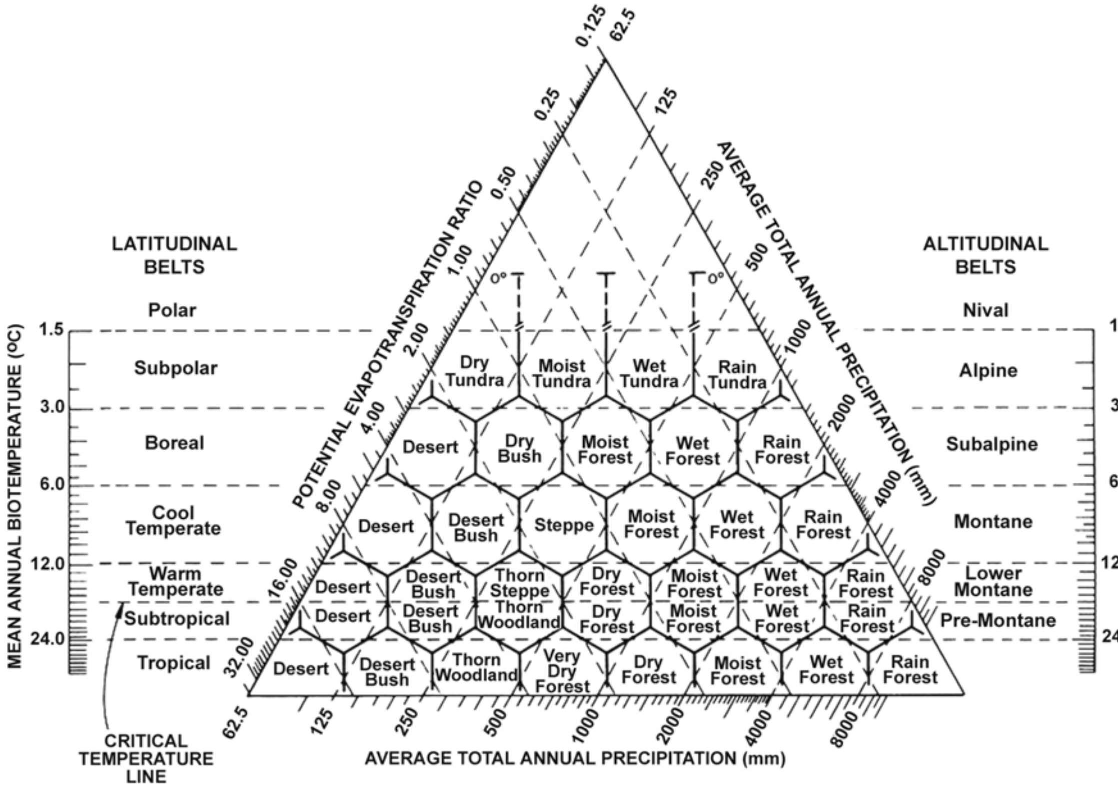

Figure I-10. The Holdridge scheme for the classification of the world's life zones (Holdridge 1947 as drawn in Shugart 1998).

types under changed climates. The Box model predicts the assemblages of nearly 100 life forms differing in structural type, overall size, leaf type, leaf size, leaf structure, and photosynthetic habit. Although the Box model is based on correlation of current vegetation with current climate it does allow for new unique communities under changed climate because the correlation is at the life form level and new combinations of life forms can be created (Shugart 1998). The BIOME model predicts assemblages of thirteen plant functional types. The BIOME model is different from the Holdridge life zone scheme and the Box model because the BIOME model is based on physiological tolerances rather than correlation (Shugart 1998). Recent preference has been towards physiological based models similar to the BIOME model because of their ability to predict unique community assemblages and the influence of their proponents. However, all three types of models are currently being used.

Researchers are also attempting to add vegetation parameters to climate models because of the potential changes in biogeochemical cycles and energy balance related to vegetation feedbacks to the atmosphere (Henderson-Sellers 1993, Beerling *et al*. 1998, Foley *et al*.1998, Levis *et al*. 1999, Eugster *et al*. 2000, Cramer *et al*. 2001, Foley *et al*. 2003). There is also an emphasis on making dynamic vegetation change models that accurately portray rates of vegetation change by incorporating realistic lags due to factors such as migration rates and the resistance of native vegetation to change (Starfield and Chapin 1996, Kirilenko *et al*. 2000, Foley *et al*. 2000). These modeling efforts have received much attention and are often considered high research priorities, yet they are still empirical and there is a continuing need to validate these models with experimental manipulations, paleo-ecological research, and historical information.

I.3.3 Vegetation Change in Changing Environments

Species have the potential to acclimate to changing environments and it is likely that in the short-term many species will cope with new climate regimes as they cope with interannual variability, although this is dependent on the plasticity of a species. Fundamentally, a population has three ultimate responses when presented with a change in the environment beyond its tolerance range or ability to acclimate: adapt, migrate, or go extinct (Stonehouse 1989, Holt 1990). Presumably species respond in the above order. In the long-term some species will likely be replaced by other species that are already adapted to new climatic conditions (from lower latitudes) before they can adapt to the new environment, thus the species' best option for survival may be migration. However, there is a possibility that analogous high alpine and arctic habitats may no longer exist leaving a species with no place to migrate. Species that cannot acclimate or adapt to new conditions or migrate to favorable habitats will become extinct, therefore much recent research has focused on changes in biodiversity associated with climate change (Peters and Lovejoy 1992, Hansell *et al*. 1998, Sala *et al*. 2000, Bakkenes *et al*. 2002).

The proximate response of a species to changing climate may be measured in three ways: change in material balance involving physiology (immediate); change in size involving growth or allocation (short-term); and change in numbers involving reproduction (mid-term). The ultimate response will most likely be measured as changes in species distribution. Of course, there are many non-climatic factors to which species respond and which can modify a species response to climate. These include nutrient availability, succession, competition, herbivory, and disease to name only a few. Species also have a migration rate, climatic sensitivity, homeostatic mechanisms, and internal resistance, which are predetermined and often restricted by prior adaptations and evolutionary history (Löve and Löve 1974, Chapin 1987, Ozenda and Borel 1989, Bradshaw and McNeilly 1991, Huntley 1991, Billings 1992, Hoffmann and Parsons 1997, Etterson and Shaw 2001). These factors in combination cause species to respond uniquely to climate change. The differential response of each species could alter food webs (Petchey *et al*. 1999), disrupt the timing of species interactions (Inouye *et al*. 2000, Stenseth and Mysterud 2002, Watt and McFarlane 2002), modify the risk of disease (Harvell *et al*. 2002), and change herbivore plant interactions (Bale *et al*. 2002, Veteli *et al*. 2002) in addition to traditional changes in species distribution and community assemblages.

Many researchers cite examples of migration during the ice ages as evidence that species respond to climate, and it was believed that intact vegetation zones followed the glacial advances and retreats (Oosting 1953). This reasoning reflects a Clementsian view of a climax community where the climate ultimately dictates the community in an orderly way (Clements 1916). Recent, more detailed studies show that communities did not move *en bloc*; rather, species responded individually, creating new communities as the distribution of individual plant species changed in a Gleasonian way (Gleason 1926, Delcourt and Delcourt 1981, Davis 1989). Paleo-ecological studies have repeatedly shown that the composition of future communities is not easily predicted from current or past communities (Hengeveld 1989, Delcourt and Delcourt 1991, Culver and Rawson 2000) and emphasize that the rates of community change are greatly affected by the dispersal potential of the constituent species (Huntley 1991, Davis and Shaw 2001) and that decadal scale changes may be influenced by the inertia of the current communities and edaphic factors (Delcourt and Delcourt 1991, Camill and Clark 2000, Hoek 2001). Ecological studies have shown that changes in species composition occur through succession and are limited by the biological diversity of the surrounding areas (Peters and Lovejoy 1992, Bazzaz 1996). These factors and the complexity of interactions and feedbacks between populations and the environment make prediction of future community changes due to changing climate difficult (Körner 1994, Billings 1997, Callaghan and Carlsson 1997, Huntley and Cramer 1997, Shugart 1998). In an attempt to address this complexity researchers are currently integrating results from historical/paleo records, experimental manipulations, and modeling to make reasonable forecasts of potential community change. It is the goal of this dissertation to contribute to the improvement of these forecasts by experimentally warming arctic tundra systems and observing plant and community responses to the warming.

I.4 TUNDRA ECOSYSTEMS

Tundra ecosystems are found in both arctic and alpine environments. While the focus of the research presented in this dissertation is arctic tundra, many generalities about arctic ecosystems may be derived from the alpine tundra literature. This review focuses on issues most relevant to tundra at Barrow and Atqasuk, Alaska, but uses examples from many tundra regions. Figure I-11 graphically depicts the important components of the Barrow environment: the climate is cold, even during the summer average daily temperatures fall below zero; the snow free period is short, snowmelt occurs around the time of maximum solar radiation; the depth of seasonally thawed soil is shallow; and the radiation absorbed by the plants is small. The life form spectrum (*sensu* Raunkiaer 1934) for the tundra is termed chamaephytic. The spectrum is generally composed of 0% phanerophytes (trees), 23% chamaephytes (shrubs), 61% hemicryptophytes (*e. g*., graminoids), 15% cryptophytes (*e. g*., bulb forming plants), and less than 1% therophytes (annuals) (Oosting 1953). Tundra species are often found widely throughout the Arctic and have been grouped into four distributional patterns: hyperarctic (inhabit the high Arctic), eurarctic (inhabit the entire Arctic), hemiarctic (inhabit the mid Arctic, not the extremes of high or low), and hyparctic (inhabit the low Arctic and Taiga) (Chernov 1985). These groupings overlap considerably with other groupings based on climate or the composition of characteristic species such as Young's zones (Young 1971).

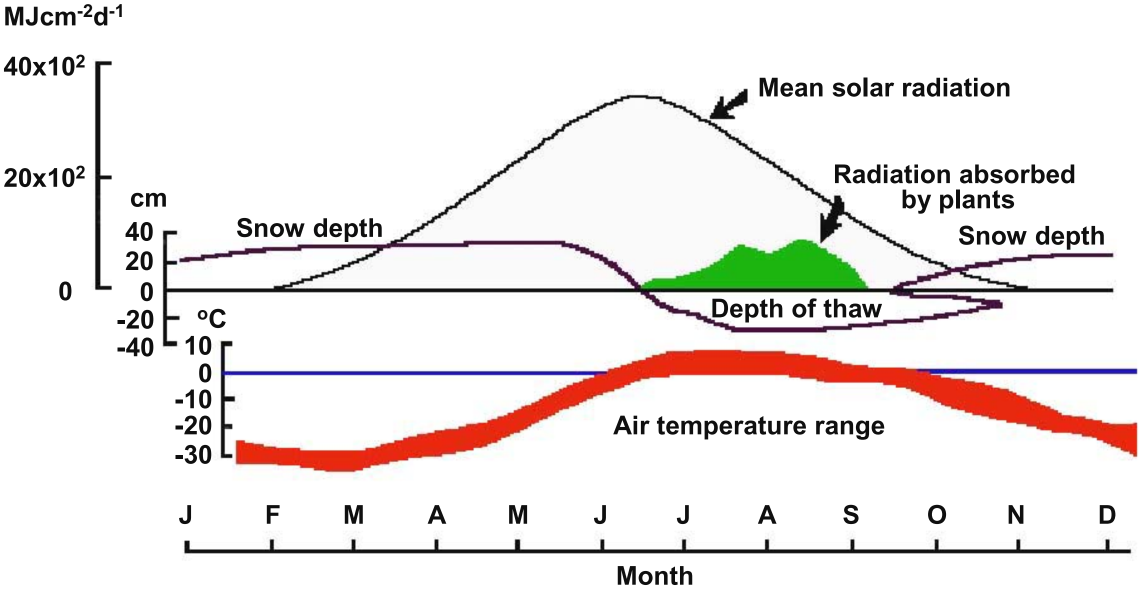

Figure I-11. Diagram of mean, maximum and minimum temperatures, snow depth, active layer thickness, and solar radiation at Barrow, Alaska (Chapin and Shaver 1985a).

The flora of the Arctic is young and is derived from diverse origins and includes 1000-1500 taxa of which ~500 are represented in the Alaskan Arctic (Murray 1995, Bliss 2000). These taxa include many families and numerous genera of which monocotyledons, particularly grasses and sedges, predominate (Löve and Löve 1974). Communities analogous to modern tundra have most likely only existed since the Pleistocene in the lowland regions of the Arctic (Savile 1972, Billings 1974b). Although the communities of the Arctic are young the species are derived from earlier alpine, marsh, and bog floras (Savile 1972, Billings 1974b, Sonesson and Callaghan 1991). The alpine flora most likely originated from temperate forest understory, grassland, and cold desert communities of the Miocene and Pliocene (Billings 1974b). During the Pleistocene the arctic flora was continually changing as species followed the glacial advances and retreats or remained as relic populations in unglaciated areas (Savile 1972, Löve and Löve 1974, Billings 1974b, Murray 1995). During the last 5000-6000 years the vegetation of the Alaskan Coastal Tundra has probably changed little due to the relative consistency of the environment during that period, however the region has changed greatly in the past and is capable of future change (Billings 1992).

I.4.1 Tundra System Controllers

The vegetation of the Arctic is primarily controlled by allogenic processes (Webber *et al*. 1980, Svoboda and Henry 1987, Bliss and Peterson 1992). The most defining factor of the arctic environment is its cold climate. The low amount of solar radiation reaching the Arctic creates a negative heat balance for most of the year. The average annual temperature is below zero degrees Celsius, and consequently much of the system is underlain by permafrost. The typical soils of the tundra are cool and seasonally thaw at most only a few meters. These soils are generally nutrient poor due to slow decomposition and turnover (Swift *et al*. 1979, Hobbie 1996).

Gemorphological processes, driven primarily by the seasonal thawing and freezing of the soils, shape the landscape of arctic tundra. As the soils freeze they expand due to the water content in them. This freeze thaw cycle alters the surface topography and creates many unique features in the landscape (*e. g.* Hussey and Michelson 1966, Bird 1974, Tedrow 1977, Brown *et al*. 1980a, Pielou 1994, Kessler and Werner 2003). The most prominent of these in the Alaskan Arctic is the formation of ice wedges (Figure I-12). The coalescence of these ice wedges on the landscape often form polygonal shapes and may result in "polygonized" tundra (Figure I-12). The presence of permafrost greatly restricts the flow of water through the landscape, and minor differences in elevation can create habitats with substantially different soil moisture (Edlund and Alt 1989). The vegetation type is primarily determined by hydrology in arctic tundra regions (Webber 1978, French 1981, Walker *et al*. 1994a, Henry 1998, Hodkinson et al. 1999). Thus, tundra landscapes generally have high small-scale heterogeneity in vegetation type due to small difference in topography (Figure I-13).

The distribution of snow and ice also influences the distribution of plants (Polunin 1948, Billings and Bliss 1959, Evans *et al*. 1989, Sonesson and Callaghan 1991, Walker *et al*. 1993, Walker *et al*. 2001). Late lying snow beds can shorten the already brief growing season and these areas generally are habitat for a unique assemblage of plant species (Billings and Bliss 1959, Walker *et al*. 2001). The depth of the snow and height of vegetation are often correlated (Bliss 1962). If an individual plant grows taller than

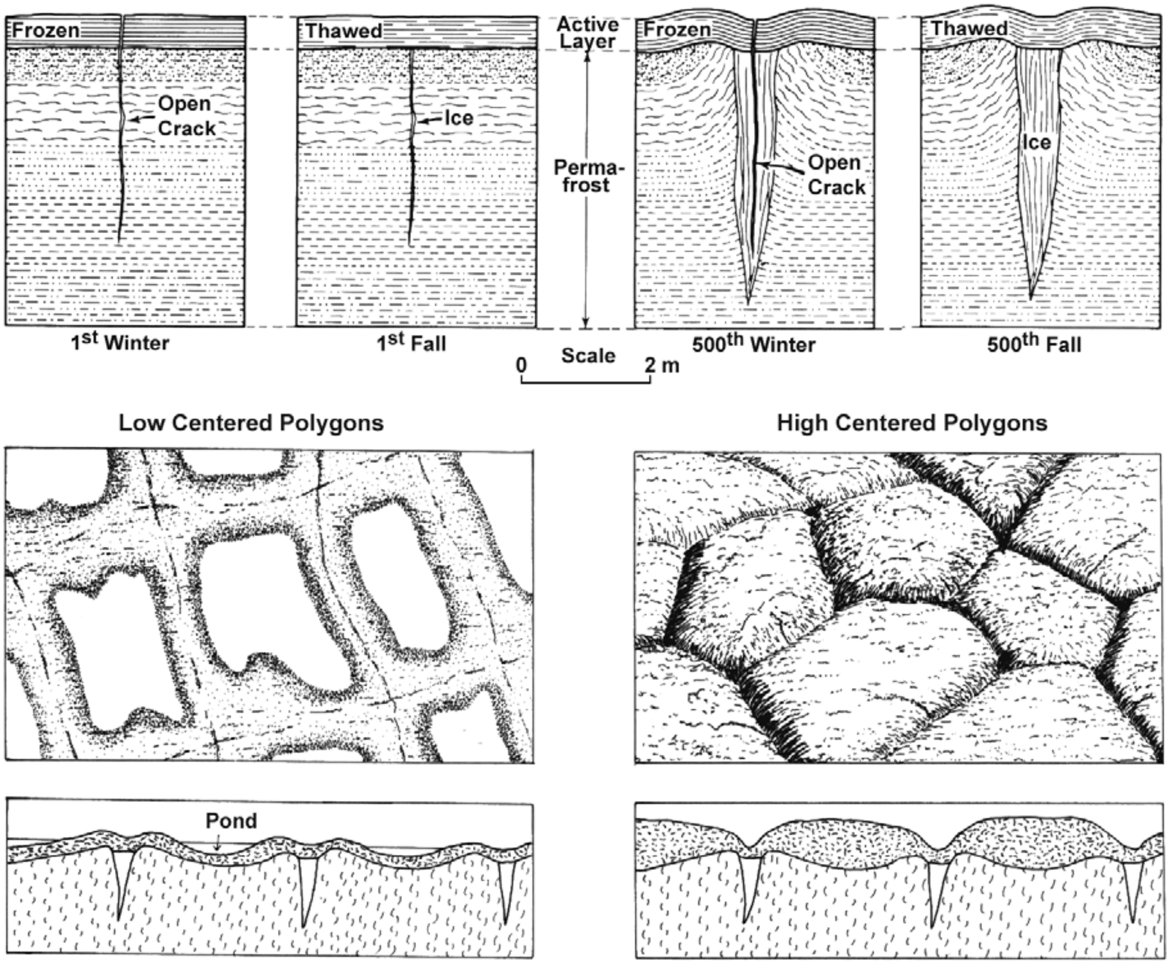

Figure I-12. Diagram of ice wedge formation (***top***) and polygons (***bottom***). The high and low centered polygons are not drawn to scale (redrawn from Tedrow 1977 and Pielou 1994).

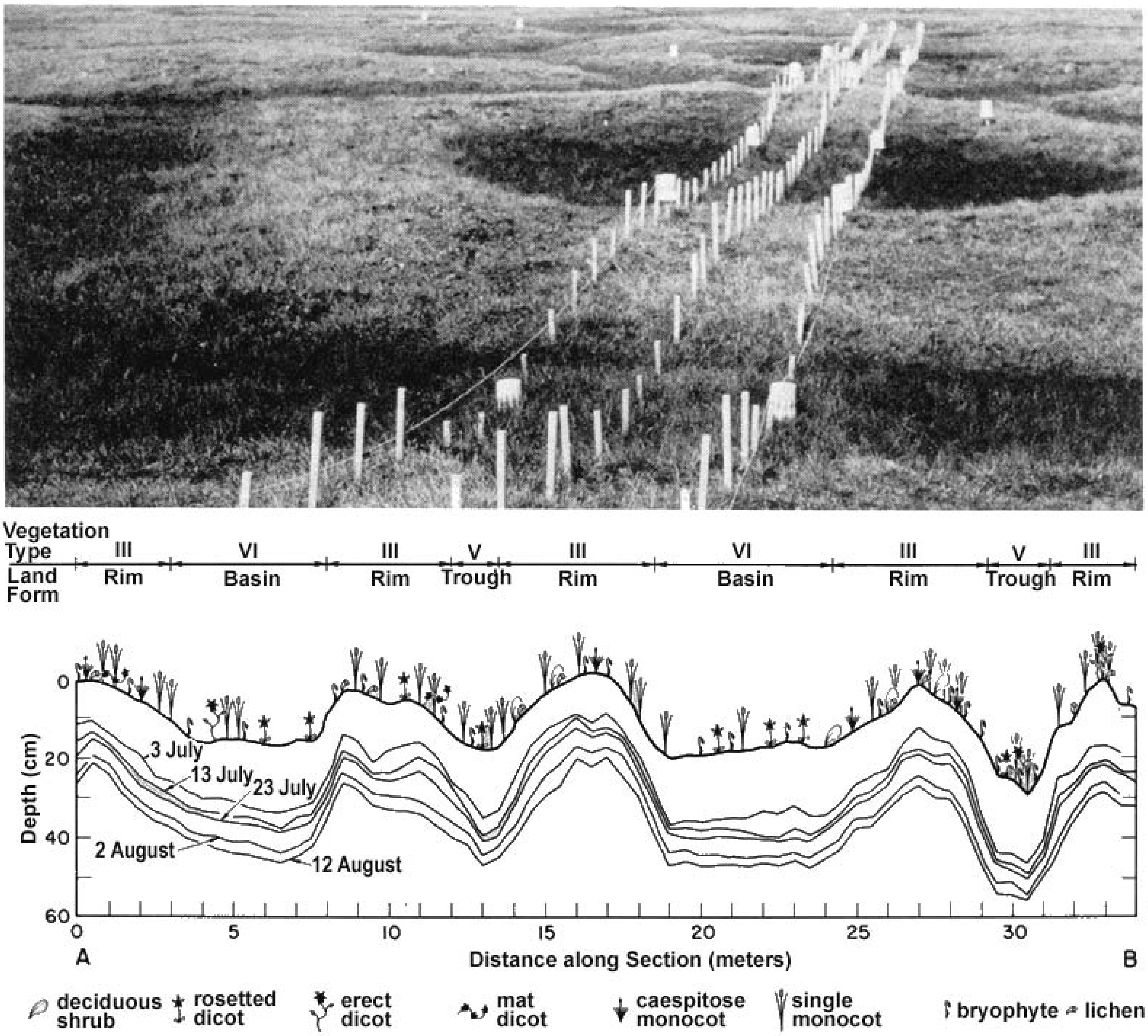

Figure I-13. Ground oblique photograph of a series of low-centered polygons near Barrow, Alaska; the vegetation type and landform classification along the transect; and the microtopographic profile and thaw depths of the transect (Brown *et al*. 1980a). The vegetation types are III - *Carex-Poa* meadow, V - *Dupontia* meadow, and VI - *Carex-Eriophorum* meadow.

the following winter's snow depth, then the emergent branches will be desiccated and abraded by strong winds and blowing snow and ice during the following winter and may die, yet emergent branches tend to trap the snow causing a locally deeper snow patch (Savile 1972); therefore, the causal relationship is not always clear. A positive feedback loop has been proposed for shrub snow interactions where deeper snow insulates soils during the winter causing higher temperatures and increased microbial activity which may increase nutrient availability and further promote shrub growth (Sturm *et al*. 2001a). The distribution of snow on the landscape may also indirectly influence the distribution of plants through changes on the hydrology of the system.

The low temperature, strong winds, low light intensity, low nutrient availability, seasonal water stress, and short growing seasons of the Arctic are believed to limit plant growth (Savile 1972, Bliss *et al*. 1973, Billings 1987). This is one rationale, among many proposed, for the simple community structure (few species, growth forms, and trophic interactions) of the tundra system (Warren Wilson 1957, Billings and Mooney 1968, Walker 1995). Yet, an equally plausible reason for simple community structure is the relative youth of the tundra biome (discussed above), which also explains why the flora is of diverse origin and has no endemic genera and relatively few strictly arctic species compared to other biomes (Dunbar 1968).

Most herbivory in arctic tundra is done by mammalian grazers (Batzli 1975). Herbivory can have large direct (*via* defoliation or destruction) and indirect (*via* soil trampling, grubbing, or nutrient cycling) effects on tundra vegetation, yet the abundances, and therefore impact, of herbivory are site and time specific making it difficult to draw broad generalizations applicable to tundra as a whole (Batzli 1975). It has been assumed that the effect of herbivory on community composition in tundra is relatively minor compared with the influence of the abiotic environment (Archer and Tieszen 1980). In Barrow the primary herbivore is the brown lemming (*Lemmus sibericus*). Lemmings in Barrow undergo large population fluctuations that are still not entirely understood but undoubtedly involve climate (particularly during the winter), predator populations, and plant cover and nutrient status (Bunnell *et al*. 1975, Batzli *et al*. 1980). Periodic intense grazing episodes generally favor graminoid species with below ground meristems, high regrowth capabilities, and leaves that require low carbon and nitrogen investment and greatly hinder shrubby species (Batzli 1975, Tieszen 1978a, Chapin 1980). Table I-4 generalizes the important attributes related to herbivory of the major growth forms in Atqasuk. In Atqasuk herbivory is more diverse and is due primarily to caribou, lemmings, ground squirrels, ptarmigan, and lepidoptera; changes in plant species composition due to herbivory are rare except at sites with concentrated nitrogen and phosphorus loads such as manured sites, large carcasses, and intense burrowing (McKendrick *et al*. 1980).

Table I-4. Attributes of growth forms related to herbivory in Atqasuk, Alaska (Archer and Tieszen 1980).

Growth Form	Photosynthetic rate	Leaf longevity	Herbivore preference	Principal herbivores	Ability to recover from defoliation	Amount of secondary compounds
Graminoid						
single-shooted	high	medium	high	Rodents, & ungulates	high	low
tussock-forming	medium	medium	high		high	low
Forb	medium	medium?	medium	Rodents, & insects	medium?	medium
Deciduous shrub	high	short	medium	Ungulates, insects, & rodents	medium	medium
Evergreen shrub	low	long	low	None	low	high

Competition is generally believed to be less important (Savile 1960, Grime 1977) and facilitation is believed to be more important in extreme environments such as tundra systems (Bertness and Callaway 1994, Brooker and Callaghan 1998, Callaway *et al.* 2002). However some (Newman 1973, Chapin and Shaver 1985b, Tilman 1988) argue that competition is still important in extreme environments but changes from above ground competition for light to below ground competition for nutrients. Experimental evidence primarily from species removal studies has found little evidence for direct effects of competition in tundra (Fetcher 1985, Jonasson 1992, Shevtsova *et al.* 1995, Hobbie *et al.* 1999) and several studies have found evidence for facilitation (Carlsson and Callaghan 1991, Jonasson 1992, Shevtsova *et al.* 1995, Shevtsova *et al.* 1997, Choler *et al.* 2001). Most of these studies are relatively short-term and long-term manipulative studies generally find significant changes in species composition presumably due to altered competition (Graglia *et al.* 2001, Shaver *et al.* 2001) and a few recent studies have found evidence for competition (Dormann and Brooker 2002, Totland and Esaete 2002). Therefore, there is still debate on the importance of competition. The best generalization is that competition is less pronounced in tundra systems and is usually not important until late in the successional process (Billings 1987).

I.4.2 Tundra Plant Adaptations

Tundra plant species often have wide geographic distributions, wide tolerances, and many ecotypes (Billings 1997). Tundra plants are generally long-lived perennials, use asexual and vegetative propagation, allocate large quantities of carbon to reproduction, have large long-lived seed banks, and are polyploid (Bliss 1962, Savile 1972, Billings 1974a, Molau 1993b).

In order to grow during cool arctic summers many arctic plants have evolved ways to absorb heat and maintain considerably higher tissue temperatures than their local environment. Some of these morphological adaptations are short stature, maintaining dead parts to reduce wind, dark pigmentation, and flower heliotropism (Sørensen 1941, Warren Wilson 1957, Bliss 1962, Corbet 1972, Savile 1972, Billings 1974a, Kevan 1975, Mølgaard 1982, Fischer and Kuhn 1984). Arctic plants have been shown to compensate for low rates of metabolic and physiological processes due to low temperatures with high enzyme concentrations and other physiological adaptations that enable them to maximize metabolic and physiological processes including photosynthesis, nutrient absorption, and grow at temperatures lower than related temperate species (Larcher 1995, Heide 1983, Chapin and Shaver 1985a). However, the physiological optima of tundra plants are generally similar to temperate species and when grown in the absence of competition tundra plants often do well in environments much warmer than commonly experienced in the center of their range of distribution.

Due to morphological and physiological adaptations, arctic species are generally believed to be more limited by indirect effects of temperature on other abiotic factors namely nutrient availability and length of growing season, than by direct temperature effects on plant physiology (Ulrich and Gersper 1978, Chapin 1983, Chapin and Shaver 1985a, Shaver *et al.* 1992). The effect of low nutrient availability of tundra soils is compounded by the fact that tundra plants have higher than average nutrient demands due to their high enzyme and lipid concentrations (Chapin and Shaver 1985a).

Tundra communities are dominated by species with high root to shoot ratios and community productivity responds to nutrient additions with increased productivity (Babb and Whitfield 1977, Shaver and Chapin 1986, Henry *et al*. 1986, Jonasson 1992). In situations where nutrients and water are not limiting, the largest constraint on productivity is the length of the growing season. In fact, the vegetation of the tundra can be as productive on a daily basis as the vegetation of temperate regions (Webber 1978, Bliss 2000). On a daily basis, the relative growth rate of *Eriophorum angustifolium* can be as high as 128 mg g-1 d-1; this is greater than the typical range of growth rates in temperate plants of 16 to 60 mg g-1 d-1 (Chapin and Shaver 1985a).

In order to carry out life's necessary functions in a short growing season tundra plants often: are long-lived perennials, are evergreen or semi-evergreen (also referred to as wintergreen) (Sørensen 1941), preform vegetative and flowering buds up to several years in advance (Sørensen 1941, Diggle 1997), and lack protective scales or hard parts over buds so that they can readily expand at the onset of snowmelt (Savile 1972). Tundra plants often begin to grow when the soil is still frozen (Shaver and Kummerow 1992, Wielgolaski 1997) and maintain a negative carbon balance for the beginning of the season while relying on stored carbon and nutrients from the previous year (Berendse and Jonasson 1992). Generally tundra plants allocate more of their resources to above ground growth at the beginning of the summer and more to below ground growth in fine roots and storage organs later in the summer (Shaver and Kummerow 1992).

In tundra systems asexual plant reproduction is common. The short growing season of most arctic environments restricts the development of seeds. Generally sexual reproduction is highly episodic and only successful during the exceptionally warm year

(Billings and Mooney 1968, Philipp *et al*. 1990). Nevertheless, tundra plants devote a proportionally large allocation of resources to sexual reproduction relative to temperate relatives (Chapin and Shaver 1985a, Philipp *et al*. 1990). Seeds are often dispersed long distances (Savile 1972), and may remain viable for long periods of time (Porsild *et al*. 1967). Tundra soils generally have large seed banks (Billings 1974a, McGraw 1980, Molau 1993b).

Two often distinctly different growth strategies have been recognized in the Arctic. These are known as periodic and aperiodic growth (Sørensen 1941). Species that show periodic growth are considered to be less receptive to changes in heat accumulation and generally grow to a predetermined size regardless of a current season's climate. Species that show aperiodic growth (*e. g*., *Cardamine pratensis*, *Cochlearia officinalis*, *Luzula arctica*, *Trisetum spicatum*) commonly respond directly to climate and may take advantage of warmer seasonal temperatures – particularly in the late season. Aperiodic growth may allow a species to fully utilize the growth potential of a season; however, the individual could be more susceptible to harsh summer or early fall conditions (Sørensen 1941, Savile 1972). The periodic growth strategy may be considered to be more conservative and to reduce the risk of damage due to harsh weather. Periodic growth (*e. g*., *Cassiope tetragona*, *Draba lactea*, *Dupontia fisheri*, *Luzula confusa*) is more common in the high Arctic (Savile 1972). Although not reported in the literature it appears plausible that the genomic size of arctic plants could be related to their periodic / aperiodic nature. Grime suggest that genome size is a good indicator of plant response to warming and that small genome sized plants have the ability to respond more quickly to warming because they can under go mitosis faster (Macgillivray and Grime 1995, Grime

1997). It has been suggested that probably the most limiting factor for tundra plant growth in cold environments is the time for mitotic division during cell division (Körner 1999, also see Figure I-8). Implications are that cell elongation is much less temperature dependent (Körner 1999). Because the time needed for mitotic division increases with genome sizes, large genome sized plants are more likely to preform tissues for rapid cell elongation the following year. Therefore, these plants would only be able to grow a predetermined amount the following year and would be termed periodic according to Sørensen. While small genome sized plants are able to perform cell division faster and are less likely to preform tissue and more likely to continue cell division throughout the growing season.

Many adaptations have multiple functions and it is difficult to clearly identify a specific role (Billings 1992). For example the short stature of tundra plants not only allows plants to maximize tissue temperatures by growing within the warmer boundary layer, it also reduces winter desiccation and abrasion by staying under the snow in the winter. Therefore, the prediction of future response based on current operational-adaptations is complex and likely to be difficult.

I.4.3 Response of Tundra Systems to Warming: A Review

The Arctic is predicted to warm more than other regions of the world and the Arctic is believed to be one of the most vulnerable biomes to changes in temperature. Therefore, the Arctic is believed to be the system where some of the first observable regional changes will occur due to anthropocentrically enhanced climate change (Webber and Walker 1991, Callaghan and Jonasson 1995, Everett and Fitzharris 1998, Sala *et al.*

2000, Houghton *et al*. 2001). From an examination of Figure I-11 the potential for the Arctic System to respond to warming can be identified. With modest warming the average daily range of temperatures exceed the biological threshold of 0 °C during the summer; the growing season could lengthen as snowmelt occurs earlier or begins to accumulate later; and the active layer (region of annually thawing soil) may warm and deepen allowing increased biological activity and nutrient cycling. The combination of these factors could create a longer and warmer growing season and increase the availability of nutrients (Anderson 1991, Nadelhoffer *et al*. 1992, Hobbie 1996, Anisimov *et al*. 1997). Each of these factors alone could affect the system, and there is also the potential for synergism between these factors (Chapin 1984, Parsons *et al*. 1994).

Climate models predict that the Arctic will warm significantly more than other geographic regions under a CO_2 driven warming scenario. The reasons for this polar amplification are: 1) a reduced sea ice extent will lower the surface albedo and lead to greater solar heating; 2) thinner sea ice cover will allow a greater flux of heat through the ice to the atmosphere in winter; 3) reduced extent of snow and longer snow free periods will reduce surface albedo and increase solar heating; 4) the density stratification of the polar atmosphere confines solar warming near the surface; 5) a stronger influx of moisture from lower latitudes will increase latent heat; 6) changes in the global circulation will likely increase the influx of lower latitude air masses; and 7) a shift in vegetation towards higher stature will reduce surface albedo and increase solar warming (Kutzbach *et al*. 1996).

I.4.3-1 Observed Recent Changes

Most of the recent documented changes in the Arctic have been changes in the abiotic environment. Serreze *et al*. (2000) reviews the recent literature and finds: annual air temperatures have increased by as much as 1.5 ^{o}C from 1966 to 1995 in most regions of the Arctic, and that this magnitude of warming is unprecedented over the past 400 years; atmospheric circulation has increased activity and intensity; precipitation has generally increased particularly during the autumn and winter; precipitation minus evaporation shows no trend; snow covered areas have decreased by 10% since 1972 and snow depths have decreased particularly in spring; sea ice extent has decreased; ocean waters have warmed in some layers; permafrost temperatures have increased; glaciers have decreased in mass; plant growth has increased and treeline has moved northward and shrubs have expanded in tundra regions; and the tundra has changed from a net sink of carbon to a net source. Serreze *et al*. (2000) state that the poor spatial and temporal coverage of the available data sets make most of their conclusions tenuous but that the consistency of their finds suggest that the Arctic is experiencing and responding to climate change. Morison *et al*. (2000) attributes most of the observed warming trends in the Arctic to the Arctic Oscillation (AO). The AO is a circulation pattern over the Arctic; when the AO is higher in intensity it has the propensity to draw warmer air from lower latitudes and warms the Arctic as a whole. The intensity of the AO has increased over recent years and can be considered a form of climate change in itself.

There is a growing body of research documenting biotic changes that are consistent with anticipated changes associated with climate change. Several recent reviews on the topic find evidence for change from nearly all regions of the world and many different types of organisms (Watson *et al*. 1998, Kappelle *et al*. 1999, Hughes 2000, McCarthy *et al*. 2001, McCarty 2001, Walther 2001, Menzel and Estrella 2001, Walther et al. 2002, Parmesan and Yohe 2003, Root *et al*. 2003). Some of the most striking evidence for climate related change in vegetative communities comes from studies based in cold adapted systems (Hinzman *et al*. submitted) and include increasing growth and phenological development in northern vegetation (Keeling *et al*. 1996, Myneni *et al*. 1997, Tuker *et al*. 2001, Lucht *et al*. 2002), increasing vegetation cover in the Antarctic (Smith 1994, Kennedy 1995a, Convey 2001), treeline advances (Wardle *et al*. 1992, Suarez *et al*. 1999, Meshinev *et al*. 2000, Kullman 2002), species diversity in European mountains (Grabherr *et al*. 1994, Keller *et al*. 2000, Pauli *et al*. 2001), and shrub expansion in the low Arctic (Chapin *et al*. 1995, Sturm *et al*. 2001b). While these do provide examples of anticipated changes associated with changing climates several other studies have found unexpected changes. For example, Barber *et al*. (2000) and Lloyd and Fastie (2002) found declines in tree growth near treeline in regions experiencing warming trends and attribute the decline to increased water stress. Some studies have found little vegetation change despite documented warming trends (Theurillat and Guisan 2001, Diemer 2002) and this phenomenon is probably more common, yet less likely to be published (Jensen 2003).

In Barrow, Alaska snowmelt is on average about 8 days earlier than it was 50 years ago and the average annual temperature is about 1.6 ^{o}C warmer with most of the increase occurring in the winter and early spring (Stafford *et al*. 2000, Stone 2001, Stone *et al*. 2002) and there has also been a decrease in precipitation (Curtis *et al*. 1998). There have been no published studies on vegetation change in the Barrow region, but ongoing research by the author of this dissertation and colleagues at Michigan State University suggests that certain community types have been changing in the region but that all the observed changes can be attributed to natural successional processes and changes in local hydrology.

I.4.3-2 *In Situ* Warming Experiments

Most of the recent research on the relationship between plants and temperature in arctic tundra communities has been with the use of experimental warming. Primarily this research has focused on physiological or plant allocation/growth studies of vascular plants. Many of the warming experiments are factorial manipulations that include fertilizers, shading, CO_2 enrichment, or watering. Generally the statistics presented are main effects, which may be biased by interactions with the other manipulations. For example, the warming response of *Betula nana* in a study presented by Chapin *et al*. 1995 are based purely on the interaction between warming and nutrient addition which is large enough to cause a main effect of warming. However, when the data are viewed as warmed versus control only there is no biomass increase in *Betula*, in fact there is a small decline in the warmed plots relative to the controls. Several of the other studies had similar issues; therefore, an attempt was made in this review to compare only warmed with control plots. This may cause the results summarized here to be contradictory to results presented in the abstracts of several of the papers and a general reading of the review literature.

The results of many warming studies conducted in tundra or near tundra environments are summarized in Table I-5. The table includes results from 18 geographic regions, 34 communities, 50 sites, and 69 papers. This review also incorporates generalizations presented in mini-review papers (Jonasson *et al*. 1996, Henry and Molau 1997, Press *et al*. 1998, Shaver and Jonasson 1999, Callaghan *et al*. 1999) and recent synthesis papers based on analysis of data from published and unpublished studies (Arft *et al*. 1999, Cornelissen *et al*. 2001, Rustad *et al*. 2001, Dormann and Woodin 2002). Overall the response of tundra plants to warming has been smaller than was expected based on known plant physiology-temperature relations and latitudinal trends. When a change has been detectable the trend was toward increased photosynthesis, CO_2 efflux, growth, reproductive effort, and cover and decreased tissue nitrogen. In general, mesic sites respond more than dry or wet sites (Walker *et al*. in prep), and high arctic sites respond more than low arctic sites (Wookey *et al*. 1993, Henry and Molau 1997, Jonasson *et al*. 1999a). Short summaries of the responses of each character provided in Table I-5 (photosynthesis, growth, reproduction, cover, and tissue nitrogen) are provided below.

The relationship between photosynthesis and temperature has long been studied particularly on tundra plants. Photosynthesis shows strong temperature dependence, and tundra plants generally experience temperatures below their photosynthetic optima (Tieszen 1973, also see Section I.4.1). Shading and CO_2 enhancement experiments have documented initial readjustments in photosynthetic output but little to no long-term changes (Tissue and Oechel 1987, Oechel *et al*. 1994a, Chapin and Shaver 1996, Shaver *et al*. 1998). This and other evidence suggest that tundra plants in general are probably not carbon limited (Körner 1999). *In situ* photosynthesis has been studied in only a few of the warming experiments. These studies found a trend of increased photosynthesis and respiration at the species and ecosystem level. Generally the increase in respiration was larger than the increase in photosynthesis causing a small efflux of CO_2 from the system. Thus, warmed plots do not sequester significantly more carbon. Few of the studies have clearly separated plant respiration from soil respiration, but it has been assumed that most of the increase in CO_2 efflux is due to increased soil respiration. These studies have been relatively short-term and the increased efflux of CO_2 is likely labile carbon resulting in a one-time pulse that probably will not be sustained in the long-term. Several researchers have stated that these trends and recent measurements of unaltered tundra indicate that with modest warming the arctic tundra will likely or has already switched from a net sink of carbon to a net source (Oechel *et al*. 1993, Welker *et al*. 2000), yet this conclusion is tenuous due to short-term and often incomplete data.

The growth response to warming has been measured in a variety of ways ranging from shoot lengths to number of leaves to biomass. Biomass can also be used to estimate productivity, but most of the warming experiments are long-term manipulations, which prevent the destructive clipping of biomass for yearly measures. In fact, many of the studies that provide biomass data are actually estimates based on allometric equations using lengths, widths, and numbers of leaves or correlations with cover data. In general if a species responded to temperature it increased its growth in the warmed environment, but most of the reported results were no change and occasionally growth decreased. This generalization supports the assumption that cool temperatures limit production in tundra systems. Contrary to this assumption a meta-analysis of the 13 warming studies showed that the low arctic sites actually responded to warming more than the high arctic sites in growth (Arft *et al*. 1999). Growth measures can be skewed towards a positive response because they are based on preexisting healthy individuals; furthermore, if an individual plant dies it is generally removed from the analysis. Thus, an increase in growth does not necessarily translate to increases in cover. For example, *Ranunculus nivalis* consistently increased in growth during 1 to 5 years of warming when individual plants were measured in Scandinavian alpine tundra, yet the plant decreased a small amount in absolute cover and greatly declined in relative cover (Molau 1997, Molau 2001).

The amount of energy allocated to reproduction, termed reproductive effort, was measured in a variety of ways ranging from the length of the inflorescence to the number of fruiting bodies to the weight of seeds. The response varied greatly depending on the metric examined. Generally the size of inflorescences and seeds and the number of flowers increased in the warmer environments, yet in several studies the number of fertilized flowers and seeds decreased. When the numbers of seeds declined in the warmed plots the authors suggest that the method of warming, a form of chamber, reduced pollination and was an unwanted artifact of the experimental design and was not a direct effect of warming (Jones *et al*. 1997, Totland and Eide 1999, Richardson *et al*. 2000, Molau 2001). The ratio of flowers in the warmed plots relative to the control plots often varied by year and generally became more pronounced with time. These changes were attributed to the long preformation times of tundra plant flowers (see Section I.4.2). Overall the reproductive effort increased in the warmed environment; generally seeds were heavier and inflorescences were longer. There is an underlining assumption that increased effort leads to increased success in these studies, yet reproductive success is difficult to quantify and was rarely measured.

Plant cover and plot level biomass response to warming varied by species and location. The gross generalization is that vascular plants, particularly graminoids and shrubs, increased while non-vascular plants decreased in biomass and cover. Non-vascular plants generally declined in closed communities and this decline is attributed to competition for light. Lichens as a whole declined in most warming experiments and are predicted to continue to decline further (Cornelissen *et al*. 2001), yet bryophytes increased in several warmed communities (Potter *et al*. 1995, Shaver *et al*. 1998, Jonasson *et al*. 1999a).

Tissue nitrogen was only measured in a few of the warming experiments. These studies show a clear trend of lower tissue nitrogen concentrations in warmed plants. Tolvanen and Henry (2001) used this finding to suggest that plants are able to increase their photosynthetic rate without a comparable increase in nutrient acquisition, therefore, tissue nitrogen concentrations become dilute. This finding supports and is based on the notion that tundra plants are more limited by indirect effects of temperature on nutrient acquisition rates than direct effects on physiological processes. Tundra plants have high nitrogen levels in their tissues. This is assumed to be an adaptation that compensates for low enzyme activity at low temperatures with high enzyme concentrations (Chapin and Shaver 1985a). Thus, an alternative explanation for the low tissue nitrogen concentrations in the warmed plots is the reduced need for higher enzyme concentrations.

Most of the data in the published literature are from two study locations: Toolik Lake, Alaska and Abisko, Sweden. The experimental design and methods of the work at Toolik and Abisko are similar and focus on the interactions of warming and fertilization. The similarity of findings at Toolik and Abisko has caused wide acceptance of the findings and proposed mechanisms involved in tundra warming and these mechanisms have often been generalized to the whole Arctic (Shaver and Jonasson 1999). Therefore, it is important to briefly describe the two sites. Toolik and Abisko are both located at 68^{o}N latitude and they both represent low arctic tundra, yet the two sites experience quite different abiotic environments. At Abisko the climate is heavily influenced by the North Atlantic currents making the winters and summers relatively mild given the high latitude. At Toolik the climate is mostly Continental with some influence from the Arctic Ocean; therefore, the winters are harsh and the summers can be very warm. The Abisko region is essentially at treeline and the study sites achieve tundra status through elevation. The Toolik sites are at the southern end of the North Slope on the Foothills of the Brooks Range and the depth of thaw is generally less than 50 cm; therefore, the soils are very cold throughout the summer relative to air temperatures and the thaw season is short. The Abisko sites are not underlain by permafrost and soils are warmer and soil processes are active longer due to a longer thaw season and accelerated activity due to higher temperatures.

Most of the recent below ground studies on arctic tundra have been done at these two sites. The theory that tundra systems are less limited by direct effects of temperature on plant physiological processes and more limited by the indirect effects of low temperature on other processes, namely nutrient cycling, was developed at Barrow (Ulrich and Gersper 1978), and now its largest proponents are based at Toolik (Chapin 1983, Chapin and Shaver 1985a). At Toolik plants generally respond little to warming experiments and respond greatly to nutrient additions; therefore, it has been theorized that the mechanism causing the response to warming is increased nutrient availability resulting from soil warming. Due to the magnitude of studies published and the internal consistency of the findings based at Toolik and to some extent Abisko, the dogma has become that the warming of the tundra will result in changes in the below ground dynamics which will ultimately drive vegetation change. These researchers have proposed that observed changes associated with fertilizer experiments might be used to predict the ultimate vegetation response to warming. There is no disagreement that below ground change are important components of climate warming on all tundra systems, yet the importance is likely to be greatest in the low Arctic, while the direct effect of warming has been shown to be greater in the high Arctic. The utility of fertilization studies to simulate future climate induced changes in vegetation is questionable because these studies generally supply nutrients at levels much greater than the increases in nutrient cycling observed in warming studies and fertilization additions circumvent microbial cycling (Jonasson *et al*. 1993, Robinson *et al*. 1995, Jonasson *et al*. 1999b, Hartley *et al*. 1999). Furthermore, soil temperatures are greatly affected by the vegetation type and the underlying permafrost, which may both vary spatially and temporally under warming, thus it is not likely that an increase in air temperatures will result in a corresponding increase in soil temperatures (Ng and Miller 1977, Kane *et al*. 1992, Jonasson *et al*. 1993, Coulson *et al*. 1993). Ulrich and Gersper (1978) proposed a negative feedback where as nutrients were added biomass and standing dead plant matter accumulated and insulated the soil surface causing lower soil temperatures and reduced nutrient availability. Therefore, the theory that warming induced vegetation change in the Arctic will be driven by changes in below ground processes is probably true in many tundra environments but is likely to be a less important mechanism than is commonly believed.

Table I-5. Summary of results from all warming studies conducted in tundra environments published before January of 2003. Several of the studies report significance based on the main effect of multiple treatments in combination with warming; therefore, the significance given in this table is based on a subjective, common sense interpretation of a likely response to an exclusively warming manipulation. For many of the papers several variables were measured that could be categorized in a single column, in those cases the overall response is presented. When biomass of individual plants was reported the significance is reported as a merged column of growth length (Ln) and number (No). The sites are presented in order of High Arctic, Low Arctic, and Alpine zones. Within a zone the studies are presented by geographic region, moisture level, study site, and year of reporting.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
High Arctic																
1 **Ellesmere Island, Canada (78^{O}N 75^{O}W)**																
1 Dry	30 m a.s.l.	1 1992	T	Jones et al. 1997	2	*Salix arctica*	–	–	·	–	·	↓	·	·	·	·
				Jones et al. 1999	1-3	*Salix arctica* male	·	↑	·	·	↗	·	·	·	↘	·
					1-3	*Salix arctica* female	·	↑	·	·	↗	·	·	·	↗	·
2 Mesic	30 m a.s.l.	2 1992	T	Tolvanen & Henry 2001	5	*Cassiope tetragona*	·	·	·	·	·	·	·	↓	·	·
					5	*Dryas integrifolia*	·	·	·	·	·	·	·	↓	·	·
					5	*Salix arctica*	·	·	·	·	·	·	·	↓	·	·
					5	*Oxyria digyna*	·	·	·	·	·	·	·	–	·	·
					5	*Carex stans*	·	·	·	·	·	·	·	–	·	·
3 Wet	30 m a.s.l.	3 1992	T	Jones et al. 1999	1-3	*Salix arctica* male	·	–	·	·	↗	·	·	·	–	·
					1-3	*Salix arctica* female	·	–	·	·	–	·	·	·	↘	·
4 Polar desert	500 m a.s.l.	4 1993	T	Stenström et al. 1997	1-3	*Saxifraga oppositifolia*	·	·	·	↑	–	↓	·	·	·	·
2 **Disko Island, Greenland (69^{O}N 53^{O}W)**																
5 Dry	20 m a.s.l.	5 1992	T	Mølgaard & Christensen 1997	1-5	*Papaver radicatum*	·	↑		↑	·	↑	·	·	·	·
3 **Zackenburg, Greenland (74^{O}N 20^{O}W)**																
6 Wet	25 m a.s.l.	6 1998	T	Mertens et al. 2001	1	Total vegetation	·	·	·	·	·	·	·	·	–	↑

Note:

Treatments
T warming
F fertilizer addition
W watering
L shading
C carbon dioxide enhancement
R species removal
A acid rain
S snow manipulation

Variables
Ph phenology
Ln length or size
No number
Co plot cover or biomass
N nitrogen concentration
Pn gross photosynthesis
Ge gross carbon dioxide exchange

Responses
↑ significant increase
↗ increasing trend
– no consistent trend
↓ significant decrease
↘ decreasing trend
· no data

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
High Arctic																
4 **Svalbard, Norway (78°N 11°E)**																
7 Dry heath	10 m a.s.l.	7 1990	T x F x L	Havström et al. 1993	1	*Cassiope tetragona*	·	↑	↑	·	·	·	·	·	·	·
	22 m a.s.l.	8 1991	T x F x W	Wookey et al. 1993	1	*Dryas octopetala*	·	·	·	↑	·	↑	·	·	·	·
				Welker et al. 1993	1	*Dryas octopetala*	·	↘	↘	·	·	·	·	↓	·	·
				Wookey et al. 1994	2	*Polygonum viviparum*	·	–	–	·	↗	↗	·	·	↗	·
				Wookey et al. 1995	3	*Dryas octopetala*	·	·	·	↑	↗	↘	↗	↘	↗	·
				Robinson et al. 1998	3	*Dryas octopetala*	·	·	·	·	·	·	–	·	·	·
					3	*Saxifraga oppositifolia*	·	·	·	·	·	·	–	·	·	·
					3	*Salix polaris*	·	·	·	·	·	·	↘	·	·	·
					3	*Polygonum viviparum*	·	·	·	·	·	·	↓	·	·	·
					3	Lichens	·	·	·	·	·	·	–	·	·	·
					3	Bryophytes	·	·	·	·	·	·	↘	·	·	·
					3	Total bare ground	·	·	·	·	·	·	↗	·	·	·
					3	Total dead	·	·	·	·	·	·	–	·	·	·
					3	Total vegetation	·	·	·	·	·	·	↘	·	·	·
					5	*Dryas octopetala*	·	·	·	·	·	·	↗	·	·	·
					5	*Saxifraga oppositifolia*	·	·	·	·	·	·	↘	·	·	·
					5	*Salix polaris*	·	·	·	·	·	·	↘	·	·	·
					5	*Polygonum viviparum*	·	·	·	·	·	·	↓	·	·	·
					5	Lichens	·	·	·	·	·	·	↗	·	·	·
					5	Bryophytes	·	·	·	·	·	·	↓	·	·	·
					5	Total bare ground	·	·	·	·	·	·	↗	·	·	·
					5	Total dead	·	·	·	·	·	·	↘	·	·	·
					5	Total	·	·	·	·	·	·	↑	·	·	·
	Unreported	9 1997	T	Wada & Kanda 2000	1	*Dryas octopetala*	·	·	·	·	↗	·	·	·	·	·
5 **Barrow, USA (71°N 156°W)**																
8 Dry heath	5 m a.s.l.	10 1994	T	Jones et al. 1997	2	*Salix rotundifolia* male	–	↑	·	↑	·	↘	·	·	·	·
					2	*Salix rotundifolia* female	–	↑	·	↑	·	·	·	·	·	·

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth Ph	Growth Ln	Growth No	Reproduction Ph	Reproduction Ln	Reproduction No	Co	N	Pn	Ge
High Arctic																
5 **Barrow, USA (71°N 156°W)**																
9 Wet meadow	5 m a.s.l.	11 1995	T	Hollister & Webber 2000	1-2	*Cardamine pratensis*	·	↑	·	·	·	–	·	·	·	·
					1-2	*Carex stans*	·	–	·	–	↑	↑	·	·	·	·
					1-2	*Draba lactea*	·	–	·	–	↑	·	·	·	·	·
					1-2	*Dupontia fisheri*	·	–	·	↑	↑	–	·	·	·	·
					1-2	*Eriophorum triste*	·	–	·	–	–	·	·	·	·	·
					1-2	*Hierochloe pauciflora*	·	·	·	↑	↑	↑	·	·	·	·
					1-2	*Juncus biglumis*	·	·	·	–	↑	·	·	·	·	·
					1-2	*Luzula arctica*	·	–	·	↑	↑	·	·	·	·	·
					1-2	*Luzula confusa*	·	–	·	↑	↑	·	·	·	·	·
					1-2	*Saxifraga cernua*	·	–	·	·	↑	–	·	·	·	·
					1-2	*Saxifraga foliolosa*	·	–	·	·	↑	–	·	·	·	·
					1-2	*Saxifraga hieracifolia*	·	–	·	–	↑	·	·	·	·	·
					1-2	*Saxifraga hirculus*	·	·	·	↑	–	–	·	·	·	·
Low Arctic																
6 **Prudhoe Bay, USA (70°N 148°W)**																
10 Wet meadow	Unreported	12 1993	T x W	Oechel et al. 1998	1-2	Total	·	·	·	·	·	·	·	·	·	↗
7 **Toolik Lake, USA (68°N 149°W)**																
11 Tussock	760 m a.s.l.	13 1979	T x F x L	Chapin & Shaver 1985	2	*Aulacomnium turgidum*	·	↘		·	·	·	·	·	·	·
					2	*Betula nana*	·	↑		·	·	·	·	·	·	·
					2	*Carex bigelowii*	·	↘		·	·	·	·	·	·	·
					2	*Empetrum nigrum*	·	↑		·	·	·	·	·	·	·
					2	*Eriophorum vaginatum*	·	↘		·	·	·	·	·	·	·
					2	*Ledum palustre*	·	↑		·	·	·	·	·	·	·
					2	*Polygonum bistorta*	·	↓		·	·	·	·	·	·	·
					2	*Rubus chamaemorus*	·	↗		·	·	·	·	·	·	·
					2	*Salix pulchra*	·	–		·	·	·	·	·	·	·
					2	*Vaccinium vitis-idaea*	·	–		·	·	·	·	·	·	·
				Shaver et al. 1986	1-3	*Eriophorum vaginatum*	·	·	·	·	·	·	·	↓	·	·
				Chapin et al. 1986	1-3	*Eriophorum vaginatum*	·	·	·	·	·	·	·	↓	·	·

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
Low Arctic																
7 **Toolik Lake, USA (68^{O}N 149^{O}W)**																
11 Tussock	760 m a.s.l.	14 1981	T x F x L	Chapin et al. 1995	3	*Aulacomnium* spp.	·	·	·	·	·	·	–	·	·	·
					3	*Betula nana*	·	·	·	·	·	·	↘	·	·	·
					3	*Carex bigelowii*	·	·	·	·	·	·	–	·	·	·
					3	*Eriophorum vaginatum*	·	·	·	·	·	·	↗	·	·	·
					3	*Hylocomium splendens*	·	·	·	·	·	·	↘	·	·	·
					3	*Ledum palustre*	·	·	·	·	·	·	↘	·	·	·
					3	*Rubus chamaemorus*	·	·	·	·	·	·	–	·	·	·
					3	*Sphagnum* spp.	·	·	·	·	·	·	↗	·	·	·
					3	*Vaccinium vitis-idaea*	·	·	·	·	·	·	↗	·	·	·
					9	*Betula nana*	·	·	·	·	·	·	–	·	·	·
					9	*Carex bigelowii*	·	·	·	·	·	·	↘	·	·	·
					9	*Eriophorum vaginatum*	·	·	·	·	·	·	↗	·	·	·
					9	*Ledum palustre*	·	·	·	·	·	·	↗	·	·	·
					9	*Rubus chamaemorus*	·	·	·	·	·	·	↗	·	·	·
					9	*Vaccinium vitis-idaea*	·	·	·	·	·	·	↑	·	·	·
					3,9	Total vegetation	·	·	·	·	·	·	↘	·	·	·
					3,9	Nonvascular plants	·	·	·	·	·	·	↘	·	·	·
					3,9	Vascular plants	·	·	·	·	·	·	–	·	·	·
					3,9	Deciduous shrubs	·	·	·	·	·	·	–	·	·	·
					3,9	Graminoids	·	·	·	·	·	·	–	·	·	·
					3,9	Evergreen shrubs	·	·	·	·	·	·	–	·	·	·
				Chapin & Shaver 1996	3,9	*Eriophorum vaginatum*	↗	↗		·	·	·	↗	–	↗	·
					3,9	*Betula nana*	↗	↗		·	·	·	–	–	↗	·
					3,9	*Ledum palustre*	↗	↑		·	·	·	–	↘	–	·
					3,9	*Vaccinium vitis-idaea*	↗	↑		·	·	·	↗	–	–	·
		15 1983	T x C	Tissue & Oechel 1987	1	*Eriophorum vaginatum*	·	–	·	·	·	·	·	·	–	·
		16 1987	T x F	Molau & Shaver 1997	9	*Eriophorum vaginatum*	·	·	·	·	·	↘	·	·	·	·

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
Low Arctic																
7 **Toolik Lake, USA (68°N 149°W)**																
11 Tussock	760 m a.s.l.	17 1988	T x F	Bret-Harte et al. 2001 / Bret-Harte et al. 2002	7-9	*Betula nana*	·	–		·	·	↗	↗	·	↗	·
					7-9	*Salix pulchra*	·	↗		·	·	·	↘	·	↗	·
					7-9	*Ledum palustre*	·	–		·	·	↗	↗	·	↗	·
					7-9	*Eriophorum vaginatum*	·	·	·	·	·	·	–	·	·	·
					7-9	*Rubus chamaemorus*	·	·	·	·	·	·	↘	·	·	·
					7-9	*Cassiope tetragona*	·	·	·	·	·	·	↘	·	·	·
					7-9	*Vaccinium uliginosum*	·	·	·	·	·	·	↘	·	·	·
					7-9	*Carex bigelowii*	·	·	·	·	·	·	↘	·	·	·
					7-9	Vascular plants	·	·	·	·	·	·	↗	·	·	·
		18 1990	T	Hobbie & Chapin 1998	4	*Eriophorum vaginatum*	·	·	·	·	·	·	↘	↘	·	·
					4	*Carex bigelowii*	·	·	·	·	·	·	↗	↗	·	·
					4	*Betula nana*	·	·	·	·	·	·	↗	↗	·	·
					4	*Salix pulchra*	·	·	·	·	·	·	–	–	·	·
					4	*Rubus chamaemorus*	·	·	·	·	·	·	–	–	·	·
					4	*Arctostaphylos alpina*	·	·	·	·	·	·	–	–	·	·
					4	*Vaccinium uliginosum*	·	·	·	·	·	·	↘	↘	·	·
					4	*Vaccinium vitis-idaea*	·	·	·	·	·	·	↘	↘	·	·
					4	*Ledum palustre*	·	·	·	·	·	·	–	–	·	·
					4	*Cassiope tetragona*	·	·	·	·	·	·	–	–	·	·
					4	*Empetrum nigrum*	·	·	·	·	·	·	–	–	·	·
					4	*Andromeda polifolia*	·	·	·	·	·	·	–	–	·	·
					4	*Pedicularis* spp.	·	·	·	·	·	·	–	–	·	·
					4	*Polygonum bistorta*	·	·	·	·	·	·	–	–	·	·
					4	*Sphagnum* spp.	·	·	·	·	·	·	↗	↗	·	·
					4	*Aulocomnium turgidum*	·	·	·	·	·	·	–	–	·	·
					4	*Dicranum* spp.	·	·	·	·	·	·	↘	↘	·	·
					4	*Pleurozium schreberi*	·	·	·	·	·	·	↘	↘	·	·
					4	*Polytrichum* spp.	·	·	·	·	·	·	↗	↗	·	·
					4	*Tomenthypnum nitens*	·	·	·	·	·	·	–	–	·	·
					4	*Ptilium crista-castrensis*	·	·	·	·	·	·	–	–	·	·
					4	Lichens	·	·	·	·	·	·	↘	↘	·	·
					4	Vascular plants	·	·	·	·	·	·	–	·	·	·
					4	Nonvascular plants	·	·	·	·	·	·	–	·	·	·
					4	Total vegetation	·	·	·	·	·	·	·	·	↑	–

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth Ph	Growth Ln	Growth No	Reproduction Ph	Reproduction Ln	Reproduction No	Co	N	Pn	Ge
Low Arctic																
7 **Toolik Lake, USA (68°N 149°W)**																
11 Tussock	760 m a.s.l.	19 1990	T x R	Hobbie et al. 1999	2-4	*Carex bigelowii*	·	↑	·	·	·	–	↗	·	·	·
					2-4	*Eriophorum vaginatum*	·	↑	·	·	·	·	↘	·	·	·
					2-4	*Betula nana*	·	↑	·	·	·	·	↑	·	·	·
					2-4	*Ledum palustre*	·	↑	·	·	·	↘	↗	·	·	·
					2-4	*Vaccinium vitis-idaea*	·	↑	·	·	·	↓	–	·	·	·
					4	*Rubus chamaemorus*	·	·	·	·	·	·	–	·	·	·
					4	*Vaccinium uliginosum*	·	·	·	·	·	·	↘	·	·	·
					4	*Andromeda polifolia*	·	·	·	·	·	·	–	·	·	·
					4	*Cassiope tetragona*	·	·	·	·	·	·	↓	·	·	·
					4	*Empetrum nigrum*	·	·	·	·	·	·	–	·	·	·
					4	*Pedicularis spp.*	·	·	·	·	·	·	–	·	·	·
					4	*Polygonum bistorta*	·	·	·	·	·	·	↘	·	·	·
					2-4	*Hylocomium splendens*	·	↓	·	·	·	·	–	·	·	·
					2-4	*Sphagnum* spp.	·	↓	·	·	·	·	↘	·	·	·
					4	*Aulacomnium turgidum*	·	·	·	·	·	·	↘	·	·	·
					4	*Dicranum spp.*	·	·	·	·	·	·	↓	·	·	·
					4	Lichens	·	·	·	·	·	·	↓	·	·	·
					4	Nonvascular plants	·	·	·	·	·	·	↓	·	·	·
					4	Vascular plants	·	·	·	·	·	·	↗	·	·	·
		20 1995	T x S	Oberbauer et al. 1998	1-2	*Salix pulchra*	·	·	·	↑	·	·	·	·	·	·
					1-2	*Betula nana*	·	·	·	↑	·	·	·	·	·	·
					1-2	Total vegetation	·	·	·	·	·	·	↗	·	·	–
				Starr et al. 2000	1-2	*Polygonum bistorta*	↑	–	·	↑	·	·	·	–	–	·
				Pop et al. 2000	1-3	*Salix pulchra*	·	·	·	↗	·	·	·	·	·	·
					1-3	*Betula nana*	·	·	·	↗	·	·	·	·	·	·
		21 1997	T	Grogan & Chapin 2000	1	Total vegetation	·	·	·	·	·	·	·	·	·	↑
		22 1995	T x S	Jones et al. 1998	2	Total vegetation	·	·	·	·	·	·	·	·	·	↑
				Welker et al. 1999	1-3	Total vegetation	·	·	·	·	·	·	·	·	·	↑
12 Wet meadow	850 m a.s.l.	23 1979	T x F x L	Chapin & Shaver 1985	2	*Carex aquatilis*	·	–		·	·	·	·	·	·	·
					2	*Eriophorum angustifolium*	·	↓		·	·	·	·	·	·	·

Table I-5. Continued.

Location Community type	Elevation		Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth Ph	Growth Ln	Growth No	Reproduction Ph	Reproduction Ln	Reproduction No	Co	N	Pn	Ge
Low Arctic																	
7 **Toolik Lake, USA (68°N 149°W)**																	
Inlet	760 m a.s.l.	24	1989	T x F x L	Shaver et al. 1998	5-6	*Carex cordorrhiza*	·	·	·	·	·	·	–	↘	·	·
						5-6	*Carex rotundata*	·	·	·	·	·	·	↘	↘	·	·
						5-6	*Eriophorum angustifolium*	·	·	·	·	·	·	–	–	·	·
						5-6	*Trichophorum caespitosum*	·	·	·	·	·	·	↑	–	·	·
						5-6	Other sedges	·	·	·	·	·	·	↘	↘	·	·
						5-6	Graminoids	·	·	·	·	·	·	↗	·	·	·
						5-6	Deciduous shrubs	·	·	·	·	·	·	–	·	·	·
						5-6	Evergreen shrubs	·	·	·	·	·	·	↗	·	·	·
						5-6	Forbs	·	·	·	·	·	·	–	·	·	·
						5-6	Mosses	·	·	·	·	·	·	↑	↘	·	·
						5-6	Lichens	·	·	·	·	·	·	–	·	·	·
						5-6	Total vegetation	·	·	·	·	·	·	↑	↘	↗	↗
Outlet	760 m a.s.l.	25	1989	T x F x L	Shaver et al. 1998	5-6	*Carex cordorrhiza*	·	·	·	·	·	·	↘	↘	·	·
						5-6	*Carex rotundata*	·	·	·	·	·	·	–	↘	·	·
						5-6	*Eriophorum angustifolium*	·	·	·	·	·	·	↗	↗	·	·
						5-6	Other sedges	·	·	·	·	·	·	↘	–	·	·
						5-6	Graminoids	·	·	·	·	·	·	↑	·	·	·
						5-6	Deciduous shrubs	·	·	·	·	·	·	–	·	·	·
						5-6	Evergreen shrubs	·	·	·	·	·	·	–	·	·	·
						5-6	Forbs	·	·	·	·	·	·	–	·	·	·
						5-6	Mosses	·	·	·	·	·	·	–	·	·	·
						5-6	Lichens	·	·	·	·	·	·	–	·	·	·
						5-6	Total vegetation	·	·	·	·	·	·	↑	↘	↗	–
13 Dry	760 m a.s.l.	26	1995	T x S	Welker et al. 1997	1	*Dryas octopetala*	·	↓	–	·	–	·	·	·	·	·
					Jones et al. 1998	2	Total vegetation	·	·	·	·	·	·	·	·	·	↑
					Welker et al. 1999	3	Total vegetation	·	·	·	·	·	·	·	·	·	↑
					Walker et al. 1999	1	*Dryas octopetala*	↑	·	·	↑	·	·	·	·	·	·
					Welker et al. 2000	1-3	Total vegetation	·	·	·	·	·	·	·	·	·	↑

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
Low Arctic																
8 **Abisko, Sweden (68^{O}N 18^{O}E)**																
14 Understory	380 m a.s.l.	27 1993	T	Hartley et al. 1999	1-5	*Empetrum hermaphroditum*	·	–	–	↗	·	·	–	–	·	·
					1-5	*Vaccinium myrtillus*	↗	–	–	·	·	·	–	–	·	·
					1-5	*Vaccinium vitis-idaea*	↗	–	–	↗	·	·	–	–	·	·
					1-5	*Vaccinium uliginosum*	–	–	–	·	·	·	–	–	·	·
					1-5	Mosses	·	·	·	·	·	·	–	·	·	·
					1-5	Lichens	·	·	·	·	·	·	–	·	·	·
					1-5	Grasses	·	·	·	·	·	·	–	·	·	·
					1	Total vegetation	·	·	·	·	·	·	·	–	·	·
15 Heath	400 m a.s.l.	28 1991	T x F x W	Wookey et al. 1993	1	*Empetrum hermaphroditum*	·	·	·	·	·	↘	·	·	·	·
				Parsons et al. 1994	1	*Empetrum hermaphroditum*	·	↘	·	·	·	·	–	·	·	·
					1	*Vaccinium vitis-idaea*	·	–	–	·	·	·	–	·	·	·
					1	*Vaccinium uliginosum*	·	–	–	·	·	·	↑	·	·	·
					1	*Vaccinium myrtillus*	·	·	·	·	·	·	↓	·	·	·
					2	*Empetrum hermaphroditum*	·	↗	·	·	·	·	–	·	·	·
					2	*Vaccinium vitis-idaea*	·	↑	↑	·	·	·	–	·	·	·
					2	*Vaccinium uliginosum*	·	↘	↘	·	·	·	↑	·	·	·
					2	*Vaccinium myrtillus*	·	↗	↑	·	·	·	↓	·	·	·
				Parsons et al. 1995	2-3	*Calamagrostis lapponica*	·	↑	·	·	·	–	–	·	·	·
				Potter et al. 1995	4	*Hylocomium splendens*	·	·	·	·	·	·	↗	·	·	·
					4	*Polytrichum commune*	·	–	–	·	·	·	↘	·	·	·
					4	Mosses	·	·	·	·	·	·	↗	·	·	·
				Press et al. 1998	5	Dwarf shrubs	·	·	·	·	·	·	↘	·	·	·
					5	*Andromeda polifolia*	·	·	·	·	·	·	–	·	·	·
					5	*Arctostaphylos uva-ursi*	·	·	·	·	·	·	–	·	·	·
					5	*Empetrum hermaphroditum*	·	·	·	·	·	·	↘	·	·	·
					5	*Salix phylicifolia*	·	·	·	·	·	·	–	·	·	·
					5	*Vaccinium myrtillus*	·	·	·	·	·	·	–	·	·	·
					5	*Vaccinium uliginosum*	·	·	·	·	·	·	↗	·	·	·
					5	*Vaccinium vitis-idaea*	·	·	·	·	·	·	↗	·	·	·
					5	Herbs	·	·	·	·	·	·	–	·	·	·
					5	*Linnaea borealis*	·	·	·	·	·	·	–	·	·	·
					5	*Pedicularis lapponica*	·	·	·	·	·	·	–	·	·	·
					5	*Rubus chamaemorus*	·	·	·	·	·	·	–	·	·	·
					5	Grasses	·	·	·	·	·	·	↗	·	·	·

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
							Ph	Ln	No	Ph	Ln	No				
Low Arctic																
8 **Abisko, Sweden (68^{O}N 18^{O}E)**																
15 Heath	400 m a.s.l.	28 1991	T x F x W	Press et al. 1998 continued	5	*Calamagrostis lapponica*	·	·	·	·	·	·	↗	·	·	·
					5	*Deschampsia flexuosa*	·	·	·	·	·	·	↗	·	·	·
					5	*Festuca ovina*	·	·	·	·	·	·	↗	·	·	·
					5	*Poa pratensis*	·	·	·	·	·	·	↘	·	·	·
					5	Vascular cryptogams	·	·	·	·	·	·	–	·	·	·
					5	*Equisetum arvense*	·	·	·	·	·	·	–	·	·	·
					5	*Equisetum pratemse*	·	·	·	·	·	·	↘	·	·	·
					5	*Equisetum sylvaticum*	·	·	·	·	·	·	–	·	·	·
					5	*Equisetum variegatum*	·	·	·	·	·	·	–	·	·	·
					5	*Lycopodium annotinum*	·	·	·	·	·	·	–	·	·	·
					5	Bryophytes	·	·	·	·	·	·	↘	·	·	·
					5	*Barbilophozia hatcheri*	·	·	·	·	·	·	–	·	·	·
					5	*Ptilidium ciliare*	·	·	·	·	·	·	↘	·	·	·
					5	Other liverworts	·	·	·	·	·	·	↓	·	·	·
					5	*Brachythecium* spp.	·	·	·	·	·	·	–	·	·	·
					5	*Dicranum scoparium*	·	·	·	·	·	·	–	·	·	·
					5	*Hylocomium splendens*	·	·	·	·	·	·	–	·	·	·
					5	*Pleurozium schreberi*	·	·	·	·	·	·	↘	·	·	·
					5	*Pohlia nutans*	·	·	·	·	·	·	↓	·	·	·
					5	*Polytricum commune*	·	·	·	·	·	·	↘	·	·	·
					5	*Polytricum juniperinum*	·	·	·	·	·	·	–	·	·	·
					5	Lichens	·	·	·	·	·	·	–	·	·	·
					5	*Cetraria cucculata*	·	·	·	·	·	·	–	·	·	·
					5	*Cladonia arbuscula*	·	·	·	·	·	·	–	·	·	·
					5	*Cladonia coccifera*	·	·	·	·	·	·	–	·	·	·
					5	*Cladonia furcata*	·	·	·	·	·	·	–	·	·	·
					5	*Cladonia gracilis*	·	·	·	·	·	·	↘	·	·	·
					5	*Cladonia rangiferina*	·	·	·	·	·	·	↓	·	·	·
					5	Other *Cladonia* spp.	·	·	·	·	·	·	–	·	·	·
					5	*Lobaria linita*	·	·	·	·	·	·	–	·	·	·
					5	*Nephroma arcticum*	·	·	·	·	·	·	–	·	·	·
					5	*Peltigera aphthosa*	·	·	·	·	·	·	↘	·	·	·

Table I-5. Continued.

Location Community type	Elevation	Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth Ph	Growth Ln	Growth No	Reproduction Ph	Reproduction Ln	Reproduction No	Co	N	Pn	Ge
Low Arctic																
8 **Abisko, Sweden (68°N 18°E)**																
15 Heath	400 m a.s.l. 28	1991	T x F x W	Press et al. 1998 continued	5	*Peltigera malacea*	·	·	·	·	·	·	–	·	·	·
					5	*Peltigera scabrosa*	·	·	·	·	·	·	–	·	·	·
					5	*Stereocaulon paschale*	·	·	·	·	·	·	–	·	·	·
					5	Total vegetation	·	·	·	·	·	·	↗	·	·	·
					5	Angiosperm live	·	·	·	·	·	·	↑	·	·	·
					5	Angiosperm standing dead	·	·	·	·	·	·	↗	·	·	·
				Richardson et al. 2002	9	*Vaccinium myrtillus*	·	·	·	·	·	·	↗	·	·	·
					9	*Vaccinium uliginosum*	·	·	·	·	·	·	–	·	·	·
					9	*Vaccinium vitis-idaea*	·	·	·	·	·	·	↗	·	·	·
					9	Deciduous shrubs	·	·	·	·	·	·	–	·	·	·
					9	Evergreen shrubs	·	·	·	·	·	·	↗	·	·	·
					9	Shrubs	·	·	·	·	·	·	↗	·	·	·
					9	Grasses	·	·	·	·	·	·	–	·	·	·
					9	Lichens	·	·	·	·	·	·	↘	·	·	·
					9	Bryophytes	·	·	·	·	·	·	↓	·	·	·
					9	Total vegetation	·	·	·	·	·	·	↗	·	·	·
16 Heath	450 m a.s.l. 29	1989	T x F x L	Havström et al. 1993	1-3	*Cassiope tetragona*	·	–	–	·	·	·	·	·	·	·
				Michelsen et al. 1996	5	*Cassiope tetragona*	·	·	·	·	·	·	↑	↓	·	·
					5	*Empetrum hermaphroditum*	·	·	·	·	·	·	–	·	·	·
				Jonasson et al. 1999	5	Deciduous shrubs	·	·	·	·	·	·	↗	–	·	·
					5	Evergreen shrubs	·	·	·	·	·	·	↑	↘	·	·
					5	Herbs	·	·	·	·	·	·	–	–	·	·
					5	Mosses	·	·	·	·	·	·	–	–	·	·
				Graglia et al. 1997	6	*Arctostaphylos alpina*	·	↗	·	·	·	·	↗	·	·	·
					6	*Betula nana*	·	↘	·	·	·	·	–	·	·	·
					6	*Empetrum hermaphroditum*	·	–	·	·	·	·	–	·	·	·
					6	*Rhododendrom lapponicum*	·	–	·	·	·	·	–	·	·	·
					6	*Vaccinium uliginosum*	·	–	·	·	·	·	↑	·	·	·
					6	Vascular plants	·	·	·	·	·	·	↗	·	·	·

Table I-5. Continued.

Location Community type	Elevation		Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth Ph	Growth Ln	Growth No	Reproduction Ph	Reproduction Ln	Reproduction No	Co	N	Pn	Ge
Low Arctic																	
8 **Abisko, Sweden (68^{O}N 18^{O}E)**																	
16 Heath	450 m a.s.l.	29	1989	T x F x L	Graglia et al. 2001	3,7,10	*Calamagrostis lapponica*	·	·	·	·	·	·	↑	·	·	·
						3,7,10	*Calamagrostis vaginata*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Poa alpigena*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Equisetum scrpoides*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Polygonum viviparum*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Tofieldia pusilla*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Asctostaphylos alpina*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Vaccinium uliginosum*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Salix reticulata*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Cassiope tetragona*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Andromeda polifolia*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Empetrum hermaphroditum*	·	·	·	·	·	·	–	·	·	·
						3,7,10	Graminoids	·	·	·	·	·	·	–	·	·	·
						3,7,10	Forbs	·	·	·	·	·	·	–	·	·	·
						3,7,10	Shrubs	·	·	·	·	·	·	–	·	·	·
						3,7,10	Deciduous shrubs	·	·	·	·	·	·	–	·	·	·
						3,7,10	Evergreen shrubs	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Aulacomnium*	·	·	·	·	·	·	–	·	·	·
						3,7,10	*Hylocomium*	·	·	·	·	·	·	↘	·	·	·
						3,7,10	*Tomenthypnum*	·	·	·	·	·	·	↓	·	·	·
						3,7,10	*Bryophytes sp.*	·	·	·	·	·	·	↓	·	·	·
						3,7,10	Bryophytes	·	·	·	·	·	·	↓	·	·	·
						3,7,10	Lichens	·	·	·	·	·	·	↓	·	·	·
17 Fellfield	1150 m a.s.l.	30	1989	T x L x F	Havström et al. 1993	1-3	*Cassiope tetragona*	·	↑	↑	·	·	·	·	·	·	·
					Michelsen et al. 1996	5	*Cassiope tetragona*	·	·	·	·	·	·	↑	↓	·	·
					Jonasson et al. 1999	5	Deciduous shrubs	·	·	·	·	·	·	–	–	·	·
						5	Evergreen shrubs	·	·	·	·	·	·	↑	–	·	·
						5	Herbs (grasses & forbs)	·	·	·	·	·	·	–	↓	·	·
						5	Mosses	·	·	·	·	·	·	↗	–	·	·

Table I-5. Continued.

Location Community type	Elevation		Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
								Ph	Ln	No	Ph	Ln	No				
Low Arctic																	
8 **Abisko, Sweden (68^{O}N 18^{O}E)**																	
17 Fellfield	1150 m a.s.l.	30	1989	T x L x F	Graglia et al. 1997	6	*Salix polaris x herbacaea*	·	↑	·	·	·	·	–	·	·	·
						6	*Vaccinium uliginosum*	·	↑	·	·	·	·	↑	·	·	·
					Graglia et al. 2001	3,7,10	*Calamagrostis lapponica*	·	·	·	·	·	·	↓	·	·	·
						3,7,10	Graminoids	·	·	·	·	·	·	–	·	·	·
						3,7,10	Forbs	·	·	·	·	·	·	↗	·	·	·
						3,7,10	Shrubs	·	·	·	·	·	·	–	·	·	·
						3,7,10	Deciduous shrubs	·	·	·	·	·	·	↗	·	·	·
						3,7,10	Evergreen shrubs	·	·	·	·	·	·	–	·	·	·
						3,7,10	Bryophytes	·	·	·	·	·	·	–	·	·	·
						3,7,10	Lichens	·	·	·	·	·	·	–	·	·	·
9 **Latnjajaure, Sweden (68^{O}N 18^{O}E)**																	
18 *C. tetragona*	981 m a.s.l.	31	1993	T	Jones et al. 1997	2	*Salix herbacea*	·	·	·	↑	·	↓	·	·	·	·
					Molau 1997	1-3	*Cassiope tetragona*	·	–	·	↗	·	–	·	·	·	·
					Molau 2001	1-5	*Cassiope tetragona*	·	–	·	↑	·	·	·	·	·	·
S. oppositifolia	981 m a.s.l.	32	1993	T	Stenström et al. 1997	1-3	*Saxifraga oppositifolia*	·	·	·	↗	·	–	·	·	·	·
					Alatalo & Totland 1997	2	*Silene acaulis*	·	·	·	↑	·	↑	·	·	·	·
19 E. vaginatum	981 m a.s.l.	33	1993	T	Molau & Shaver 1997	1-3	*Eriophorum vaginatum*	·	·	·	↑	·	–	·	·	·	·
					Molau 2001	1-9	*Eriophorum vaginatum*	·	↑	–	↑	·	↘	·	·	·	·
R. nivalis	981 m a.s.l.	34	1993	T	Molau 1997	1-3	*Ranunculus nivalis*	·	↑	·	–	·	↑	·	·	·	·
					Molau 2001	1-5	*Ranunculus nivalis*	·	↑	·	–	↑	↑	·	·	·	·
D. octopetala	981 m a.s.l.	35	1994	T	Welker et al. 1997	1	*Dryas octopetala*	·	·	·	↑	↑	↗	·	·	·	·
					Molau 2001	1-4	*Dryas octopetala*	·	↑	·	↑	·	–	·	·	·	·
						1-4	*Polygonum viviparum*	·	↑	·	–	↑	↗	·	·	·	·
20 *C. bigelowii*	981 m a.s.l.	36	1994	T	Stenström & Jónsdóttir 1997	1-2	*Carex bigelowii*	·	↑	–	↑	↗	↗	·	·	·	·
					Stenström 1999	2-4	*Carex bigelowii*	·	·	·	·	↗	↗	·	·	·	·
21 Meadow	981 m a.s.l.	37	1996	T x F	Molau & Alatalo 1998	2	Total vegetation	·	·	·	·	·	·	–	·	·	·
22 Heath	981 m a.s.l.	38	1996	T x F	Molau & Alatalo 1998	2	Total vegetation	·	·	·	·	·	·	↑	·	·	·
10 **Kevo, Finland (69^{O}N 27^{O}E)**																	
23 Shruby	85 m a.s.l.	39	1992	T x W x R x A	Shevtsova et al. 1997	2-3	*Empetrum nigrum*	↗	↗	·	·	·	·	·	·	·	·
						2	*Vaccinium vitis-idaea*	↗	↗	·	·	·	·	·	·	·	·

Table I-5. Continued.

Location Community type	Elevation		Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
								Ph	Ln	No	Ph	Ln	No				
Alpine																	
11 **Val Bercla, Switzerland (46^{O}N 09^{O}E)**																	
24 Heath	2490 m a.s.l.	40	1994	T	Stenström et al. 1997	1-2	*Saxifraga oppositifolia*	·	·	·	↗	·	–	·	·	·	·
					Gugerli & Bauert 2001	1-3	*Polygonum viviparum*	·	↗	·	·	↑	↗	·	·	·	·
12 **Niwot Ridge, USA (40^{O}N 105^{O}W)**																	
25 Heath	4085 m a.s.l.	41	1994	T x S	Welker et al. 1997	2	*Dryas octopetala*	↑	–	–	·	↑	·	·	↘	·	·
					Welker et al. 1999	3	Total vegetation	·	·	·	·	·	·	·	·	·	↑
					Walker et al. 1999	1	*Acomastylis rossii*	↑	↑	·	↑	↑	·	·	·	·	·
						1	*Bistorta bistrortoides*	↑	↑	·	↑	–	·	·	·	·	·
13 **Finse, Norway (60^{O}N 07^{O}E)**																	
26 S. acaulis	1500 m a.s.l.	42	1994	T	Alatalo & Totland 1997	1	*Silene acaulis*	·	·	·	↗	·	–	·	·	·	·
					Totland 1997	1-2	*Leontodon autumnalis*	·	·	·	↑	↑	↑	·	·	·	·
					Totland & Nyléhn 1998	4	*Bistorta vivipara*	·	↑		·	·	↗	·	·	·	·
					Nyléhn & Totland 1999	2-4	*Euphrasia frigida*	·	↑		·	↑	↑	↓	·	·	·
					Totland / Totland & Eide 1999	1-4	*Ranunculus acris*	·	·	↗	–	·	↑	·	·	·	·
27 Snowbed	1380 m a.s.l.	43	1995	T x F x S	Sandvik & Totland 2000	1-3	*Saxifraga stellaris*	·	↗	·	↗	·	↗	↗	·	·	·
14 **Taisetsu, Japan (43^{O}N 142^{O}E)**																	
28 Fellfield	1680 m a.s.l.	44	1995	T	Suzuki & Kudo 1997	1	*Arctous alpinus*	↗	·	·	–	·	·	·	↓	·	·
						1	*Vaccinium uliginosum*	↗	·	·	↗	·	·	·	↘	·	·
						1	*Vaccinium vitis-idaea*	·	·	·	·	·	·	·	–	·	·
						1	*Ledum palustre*	–	·	·	↗	·	·	·	↘	·	·
						1	*Empetrum nigrum*	↗	·	·	·	·	·	·	↓	·	·
					Suzuki & Kudo 2000	1-3	*Arctous alpinus*	↗	·	↗	·	–	–	·	↘	·	·
						1-3	*Vaccinium uliginosum*	↑	·	–	↗	–	↗	·	↘	·	·
						1-3	*Vaccinium vitis-idaea*	↗	·	↗	·	↑	–	·	↘	·	·
						1-3	*Ledum palustre*	–	·	↗	·	↑	–	·	↘	·	·
						1-3	*Empetrum nigrum*	↗	·	↗	·	↑	·	·	↘	·	·

Table I-5. Continued.

Location	Elevation		Year of establishment	Treatments	Citation	Years of treatment	Species or Groupings	Growth			Reproduction			Co	N	Pn	Ge
Community type								Ph	Ln	No	Ph	Ln	No				
Alpine																	
15 **Tateyama, Japan (36^{O}N 137^{O}E)**																	
29 Plateau	2800 m a.s.l.	45	1995	T	Kojima et al. 1997	1	*Empetrum nigrum*	·	↑	·	·	·	·	·	·	·	·
						1	*Loiseleuria procumbens*	·	↑	·	·	·	·	·	·	·	·
					Wada et al. 2002	2	*Empetrum nigrum*	·	↑		·	·	·	·	·	·	·
						2	*Loiseleuria procumbens*	·	↑		·	·	·	·	·	·	·
30 East-facing	2800 m a.s.l.	46	1995	T	Kojima et al. 1997	1	*Empetrum nigrum*	·	↑	·	·	·	·	·	·	·	·
						1	*Loiseleuria procumbens*	·	↑	·	·	·	·	·	·	·	·
					Wada et al. 2002	2	*Empetrum nigrum*	·	–		·	·	·	·	·	·	·
						2	*Loiseleuria procumbens*	·	↓		·	·	·	·	·	·	·
31 North-facing	2700 m a.s.l.	47	1996	T	Wada et al. 1998	1	*Geum pentapetalum*	·	–	–	·	–	↑	·	·	·	·
					Wada 2000	1	*Sieversia pentapetala*	·	·	·	·	↑	·	·	·	·	·
16 **Kisokomagatake, Japan (35^{O}N 137^{O}E)**																	
32 Fellfield	2850 m a.s.l.	48	1995	T	Nakashinden et al. 1997	1	*Arctous alpinus*	↑	·	·	↗	·	↗	·	·	·	·
						1	*Diapensia lapponica*	↑	·	·	–	·	·	·	·	·	·
17 **Qilian, Tibet (37^{O}N 101^{O}E)**																	
33 Meadow	3250 m a.s.l.	49	1991	T x S	Zhang & Welker 1996	1	Grasses	·	·	·	·	·	·	↗	·	·	·
						1	Sedges	·	·	·	·	·	·	–	·	·	·
						1	Forbs	·	·	·	·	·	·	↘	·	·	·
18 **Obergurgl, Austria (46^{O}N 11^{O}E)**																	
34 Moraine	2400 m a.s.l.	50	1996	T	Erschbaner 2001	2-4	*Carex curvula*	·	·	↑	·	·	↑	·	·	·	·
						2-4	*Trifolium pallescens*	·	↑		·	·	↑	·	–	·	·
						2-4	*Poa alpina*	·	↓		·	·	↓	·	–	·	·

I.5 DESIGN OF THE RESEARCH PROJECT

Patrick Webber and Christian Bay began the project associated with the research presented in this dissertation in 1994 as an International Tundra Experiment (see Section I.2.3) study site following the standardized data collection methods outlined in the International Tundra Experiment Manual (Molau 1993a, Molau and Mølgaard 1996). At that time the project consisted of one study site in Barrow (Bay 1995). In 1995 two new graduate students, Lisa Walker and Robert Hollister, joined the project. Lisa Walker became primarily responsible for the Barrow dry site and Robert Hollister established a new Barrow wet site and assumed primary responsibility for it. Christian Bay completed his management role in the project at the end of 1995 (Bay 1996). Both students, Lisa Walker and Robert Hollister, completed their Master's degrees on the data collected through 1996 for their respective sites (Walker 1997, Hollister 1998). In 1996 Robert Hollister expanded the project to Atqasuk and in 1997 he became primarily responsible for the data collection for the entire project. During this period the data collection was modified and expanded.

I.5.1 Study Area

I.5.1-1 North Slope

The study sites are located at Barrow and Atqasuk on the Arctic North Slope of Alaska (Figure I-14). The North Slope is the region of Alaska that drains to the Arctic Ocean and includes the northern half of the Brooks Range, the Foothills, and the Coastal Plain. The region is underlain by permafrost reaching depths of up to 600 m (Brown *et al*. 1980a). The East-West orientation of the Brooks Range acts as a biogeographic barrier to treeline and the treeline of Alaska is more abrupt than in many regions of the Arctic due to the complex gradients associated with latitude and altitude. The Foothills consist of rolling hills of tussock tundra dominated by the sedge *Eriophorum vaginatum* and several shrubs including species of *Salix*, *Betula*, *Vaccinium*, and *Ledum*. The Foothills were partially glaciated during the Pleistocene but the northern region of the Foothills was never glaciated (Brown *et al*. 1980a). The Coastal Plain is relatively flat and dominated by a series of oriented elliptical lakes that cover up to 40% of the surface area (Brown *et al*. 1980a). The divide between the Coastal Plain and Foothills is the 75 m topographic contour line (Brown *et al*. 1980a). The shallow thaw of the active layer (seasonally thawed soils) and the low relief of the Costal Plain create an environment where minor differences of sometimes less than a meter in elevation have significantly different soil water content and vegetation. Grasses and sedges dominate the vegetation of the Coastal Plain. For the last 10,000 years meandering streams and processes associated with the thaw lake cycle (Figure I-15) have reworked the surface (Brown *et al*. 1980a, Eisner and Peterson 1998).

The climate of the most northern part of the Coastal Plain is heavily influenced by the Arctic Ocean (Table I-6). On a typical summer day coastal areas experience cloudy, moist, cool, and windy conditions throughout the day, while at inland areas the air is heated in the morning and low clouds and fog dissipate by early afternoon. The gradient in daily temperatures can be steep from the coast inland following the prevailing winds. The 7 ^{o}C July isothermal delineates the coastal zone generally referred to as littoral tundra (Cantlon 1961, Haugen and Brown 1980). The Barrow sites lie within the littoral tundra and the Atqasuk sites lie beyond the extent of the littoral tundra; therefore the summer climate of Atqasuk is warmer than would be expected from its approximately 100 km position south of Barrow (Table I-7).

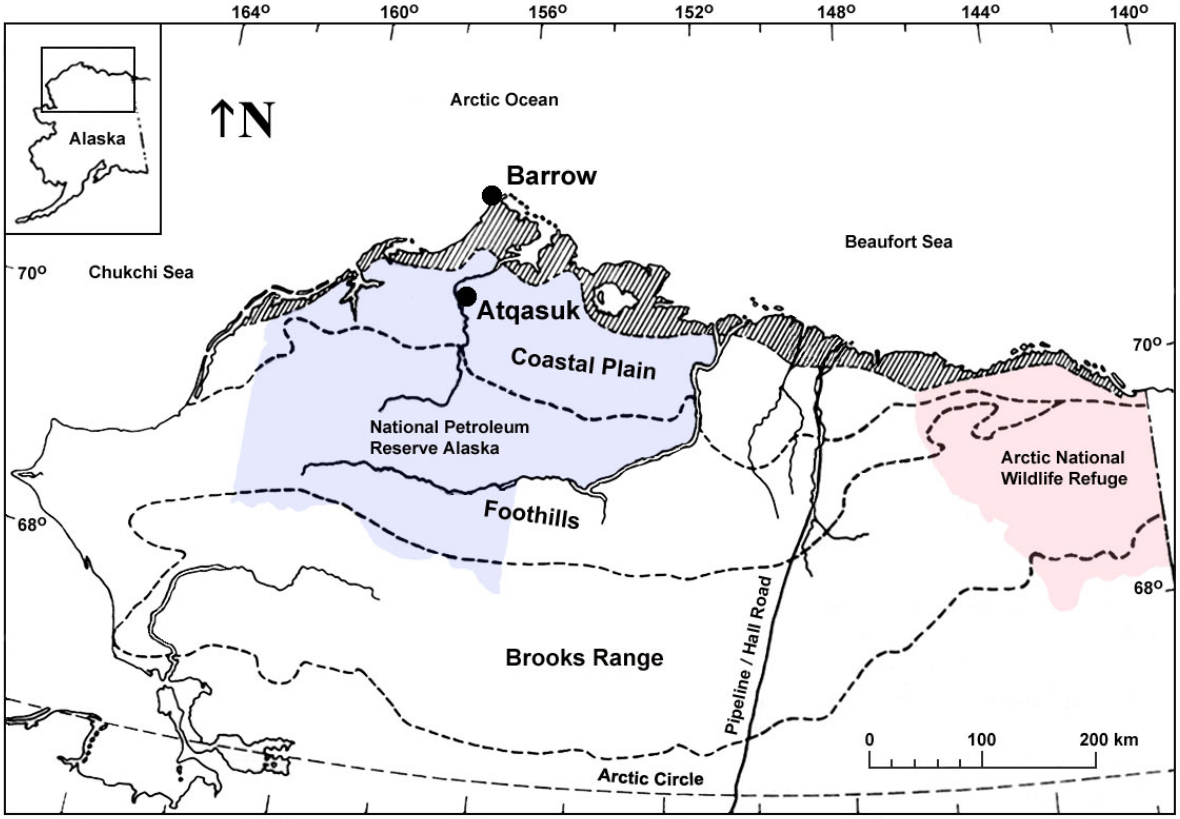

Figure I-14. Map of northern Alaska showing the Arctic North Slope, Barrow, Atqasuk, and other prominent features. The hashed zone represents the littoral tundra, dashed lines represent the borders between regions, and shading represents political zones (redrawn from Haugen and Brown 1980).

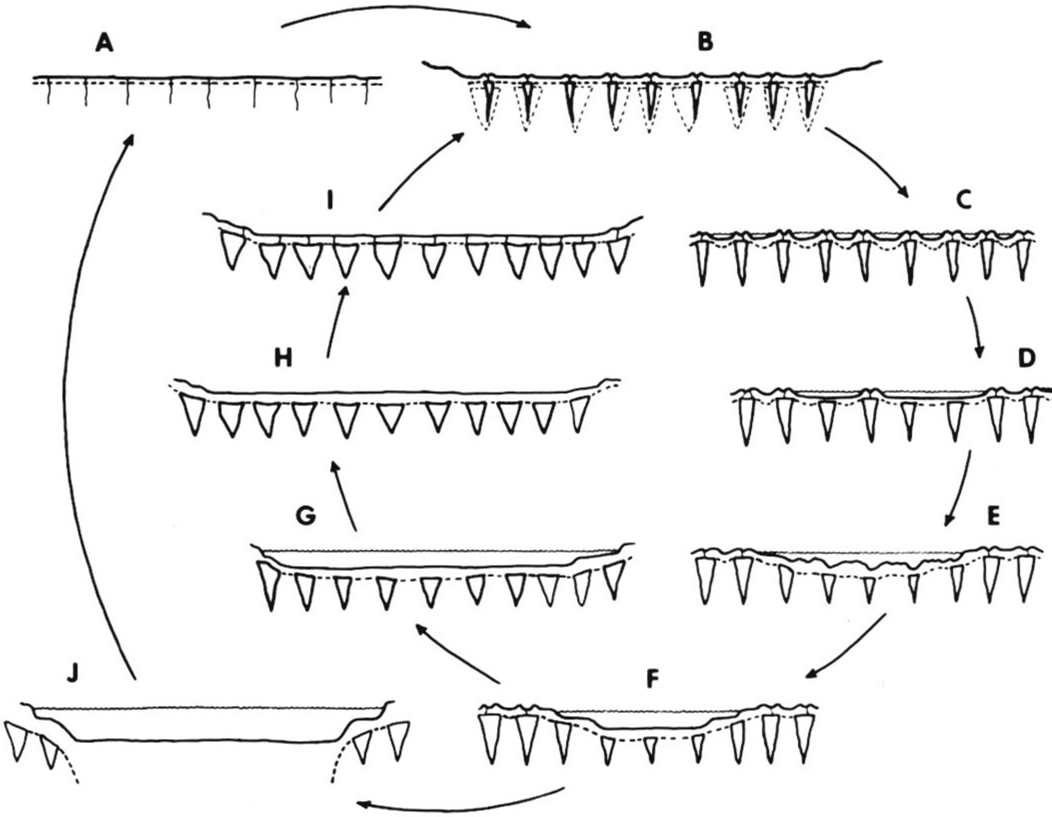

Figure I-15. Side view diagram of the thaw-lake cycle. ***A***) Newly exposed marine sediments with contraction cracks into the permafrost (denoted with dashes). ***B*** & ***C***) The growth of ice wedges and low-centered polygons in the sediments (dashed wedges represent possible previous ice wedges). ***D***) The formation of thaw-ponds by erosion and coalescence of low-center polygons. ***E*** & ***F***) A young thaw-lake. ***G***) A mature shallow thaw-lake. ***H*** & ***I***) A drained shallow thaw-lake. ***J***) A deep thaw-lake with permafrost and ice-wedges melted below it (Billings and Peterson 1980).

Table I-6. Climate data for the Barrow region (Brown *et al.* 1980a).

Month	Temperature (^{o}C)	Precipitation (mm)	Wind speed (m s^{-1})	Solar radiation (MJ m^{-2} day^{-1})	Day length (hrs)
Jan	-25.9	5.8	5.0	0.0	0.7
Feb	-28.1	5.1	4.9	1.6	6.8
Mar	-26.2	4.8	5.0	7.4	11.7
Apr	-18.3	5.3	5.2	15.5	16.7
May	-7.2	4.3	5.2	21.9	23.1
June	0.6	8.9	5.1	23.0	24.0
July	3.7	22.4	5.2	18.5	24.0
Aug	3.1	26.4	5.5	10.8	19.0
Sept	-0.9	14.7	5.9	5.0	13.4
Oct	-9.3	14.0	6.0	1.7	8.6
Nov	-18.1	7.6	5.6	0.2	2.4
Dec	-24.6	4.8	5.0	0.0	0.0
Year	-12.6	124.1	5.3		

Note: Reported values are averages over the years 1941-1970 from the National Weather Service station in Barrow. Solar radiation is based on only 14 years (presumably 1967-1970).

Table I-7. Summer climate of Barrow and Atqasuk, Alaska. Data were collected between 1975 and 1978. Numbers in parentheses represent the long-term mean; Atqasuk long-term means were estimated (Haugen and Brown 1980).

Region	Temperature (^{o}C)			Precipitation (mm)			
	June	July	August	June	July	August	TDD
Atqasuk	3.8(3.2)	7.2(8.7)	4.8(7.8)	23	31	26	618
Barrow	0.8(0.6)	3.0(3.7)	1.5(3.1)	2(9)	25(22)	29(26)	251(369)

TDD – thawing degree-days

I.5.1-2 Barrow

Barrow, Alaska (71°18'N 156°40'W) lies on the most northern point on the Alaskan Arctic Costal Plain. The climate of Barrow consists of long cold winters and short cool summers during which the temperature can fall below zero on any day (Table I-6, Table I-7, Figure I-11). The sun does not rise from November 19 until January 23 and rise is 24 hours a day from May 10 until August 2. The snow free period is variable but generally begins in early June and continues until early September during which time an average of 369 thawing degree-days are accrued (Brown *et al.*1980a). The summer is generally cloudy, foggy, and wet; during this time approximately 37% of the annual precipitation is received and average humidity is over 80% (Brown *et al.* 1980a). However, the climate has been changing and the above values are based on trends ending in the 1970s (Section I.4.3-1).

Britton (1957), Cantlon (1961), Webber (1978), and others have described the vegetation of the region as impoverished in terms of the number of species and community types. The vascular plant flora consists of ~120 species (Murray and Murray 1978). The low diversity of the region is likely due to the harsh climate and low habitat diversity. The distinction between community types is primarily due to difference in abundance rather than species composition as many of the Barrow species can be found in multiple community types (Webber 1978). Above ground biomass most likely peaks at the end of July or early August depending on the year and community type (Tieszen 1972, Dennis *et al*. 1978). The vegetation appears to be primarily controlled by soil moisture, soil anaerobicity, soil phosphate, and snow cover (Webber *et al*. 1980).

The Barrow region has been home to the native Iñupiat people for over a thousand years. Barrow has been the home of the Naval Arctic Research Laboratory (NARL) and its succeeding institutions since 1947 and has one of the longest and richest histories of research of any location in the Arctic making it one of the best-known ecosystems of any in the world (Reed and Ronhovde 1971). Recently the community of Barrow established the Barrow Environmental Observatory (BEO) to preserve a large tract of tundra for future research and major renovations to the Barrow research facilities are being planned. The logistics foundation has made it possible to stage all forms of research from Barrow including atmospheric, oceanic, geological, limnological, and terrestrial. Barrow was the site for the Tundra Biome program of the International Biological Programme (Tieszen 1978b, Brown *et al.* 1980b, Hobbie 1980). A Climate Diagnostic Laboratory run by NOAA provides historical climate data as well as detailed current conditions and is the site of one of the longest CO_2 and greenhouse gas records in the world (Stone *et al.* 1996). Webber and Hollister (2001) recently reviewed the history of vegetation research in Barrow and characterized it as changing from a focus on description and study of plant distributions toward understanding and predicting how the system will respond to pressures of land use, land cover, and climate change.

I.5.1-3 Atqasuk

Atqasuk, Alaska (70^{o}29'N 157^{o}25'W) lies in approximately the middle of the Alaskan Arctic Coastal Plain. The climate of Atqasuk consists of long cold winters and short moderate summers during which the temperature can fall below zero on any day and daily maximums may reach into the 20s ^{o}C (Table I-7). The sun does not rise from November 23 until January 19 and rise is 24 hours a day from May 15 until July 30. The snow free period is variable, but generally begins in late May and continues until early September during which time an average of 618 thawing degree-days are accrued (Haugen and Brown 1980).

Komárková and Webber (1980) and Komárková and McKendrick (1988) described the vegetation of the Atqasuk region as relatively diverse in terms of numbers of species and community assemblages given its climate. The higher diversity relative to Barrow is attributed primarily to a greater diversity of landscapes (Komárková and Webber 1980). The vascular plant flora consists of ~250 species (Komárková and Webber 1977). The community types are more distinct than in Barrow in terms of species composition and abundances. Depending on the year and community type above ground biomass generally peaks at the end of July or early August (Johnson and Tieszen 1976). The vegetation appears to be primarily controlled by moisture and permafrost and is modified locally by disturbance (Komárková and Webber 1980, Komárková and McKendrick 1998)

Atqasuk was traditionally a summer fishing and berry picking location for the native Iñupiat peoples, but historically there has not been a significant year round population until recently. In the 1940's coal was mined in Atqasuk to supply Barrow In the 60's when natural gas was discovered in Barrow the mining ended and the population dwindled. In 1977 the village of Atqasuk was established as part of the North Slope Borough. Atqasuk has a record of ecological research and was the site of the RATE project (Research on Arctic Tundra Environments) (Batzli 1980). The research location changed names several times from Meade River to Atkasook to the current name Atqasuk. Currently there is a good logistics support, courtesy of the National Science

Foundation and the Barrow Arctic Science Consortium (BASC), and a significant amount of terrestrial and atmospheric research is being done.

I.5.2 Research Approach

The approach of this research is to use variation in temperature related to three causes natural temperature gradients (Barrow to Atqasuk), interannual variability (1994-2000), and experimental warming (open-top chambers) to understand plant-temperature relations (Figure I-16).

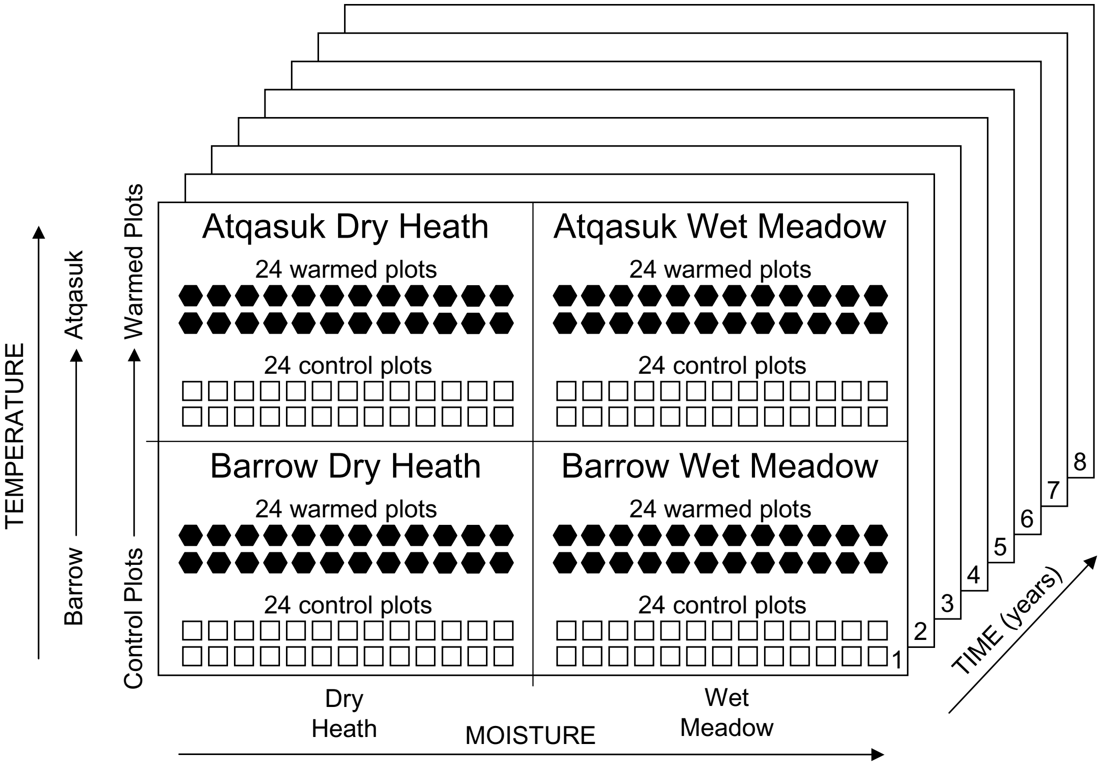

Figure I-16. Illustration of the research approach. The project uses natural variation in temperature between four field sites, interannual variability, and experimental warming to characterize the relationship between plants and temperature. The four study sites span a temperature and moisture gradient and consist of 24 warmed and control plots that are monitored over many years.

I.5.2-1 Natural Temperature Gradients

There is a natural temperature gradient between Barrow and Atqasuk that has been well described (Haugen and Brown 1980, Figure I-17, also see Section I.5.1-1). Atqasuk is approximately 4 ^{o}C warmer during the summer months than Barrow; this makes it possible to compare vegetation attributes between the two regions in relation to their respective climates. In both regions study sites were established in wet and dry communities to avoid site-specific conclusions. The wet site communities melt out later than the more exposed and thinly snow covered dry sites at both Barrow and Atqasuk.

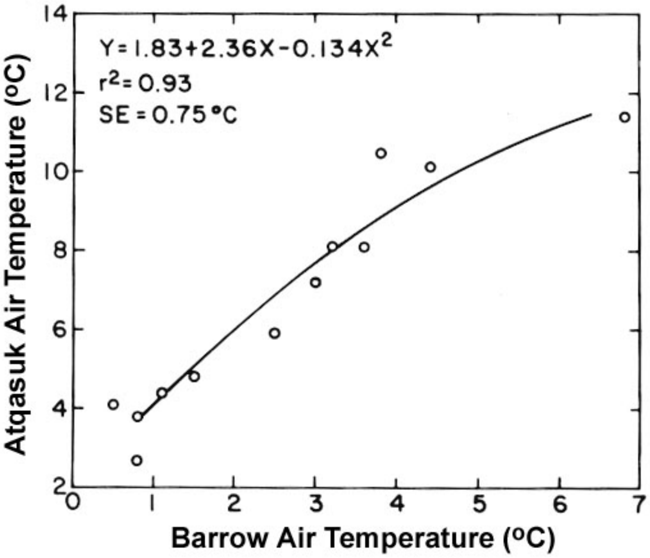

Figure I-17. Regression for estimation of normal monthly temperatures for Atqasuk based on the monthly June, July, and August air temperatures for Barrow and Atqasuk, 1975 through 1978 (Haugen and Brown 1980).

I.5.2-2 Interannual Variability

Data from each site was gathered each year since site establishment (1994-1996) in order to address the vegetative response of natural differences in weather between years. The variability in the permanent un-manipulated plots between years has been used by other tundra studies to address controlling mechanisms (Walker *et al*. 1994b, Walker *et al*. 1995). The effect of experimental warming in different years is also of interest. Molau (2001) has reported a stronger experimental effect during cool years, suggesting that during naturally warmer years the benefits of experimental warming are minimized. Arft *et al*. (1999) suggested that the long-term effect of warming was different from the short-term effect. Therefore, it is important to address each year's response in relation to that year's ambient weather and the potential cumulative effects of warming in previous years.

I.5.2-3 Experimental Warming

The plant canopy was experimentally warmed with the use of passive open-top chambers (Figure I-18). The chambers were hexagonal with sloping sides constructed of Sun-Lite HPTM fiberglass (Solar Components Corporation, Manchester, New Hampshire). The open-top chambers were 35 cm tall and the distance between parallel sides is 103 cm at the base and 60 cm at the top (Figure I-19). Marion *et al*. (1993, 1997) described the general performance of the open-top chambers. The performance of the chambers in Barrow and Atqasuk is addressed in Chapter II and the validity of using the open-top chambers to simulate regional warming is addressed in Chapter III. In general the chambers warm the plant canopy between 0.6 and 2.2 ^{o}C on average during the summer. At any given time the chambers may be as much as 10 °C warmer or 2 °C cooler than the ambient environment depending primarily on wind, and solar intensity (Marion *et al*. 1997, Chapter II).

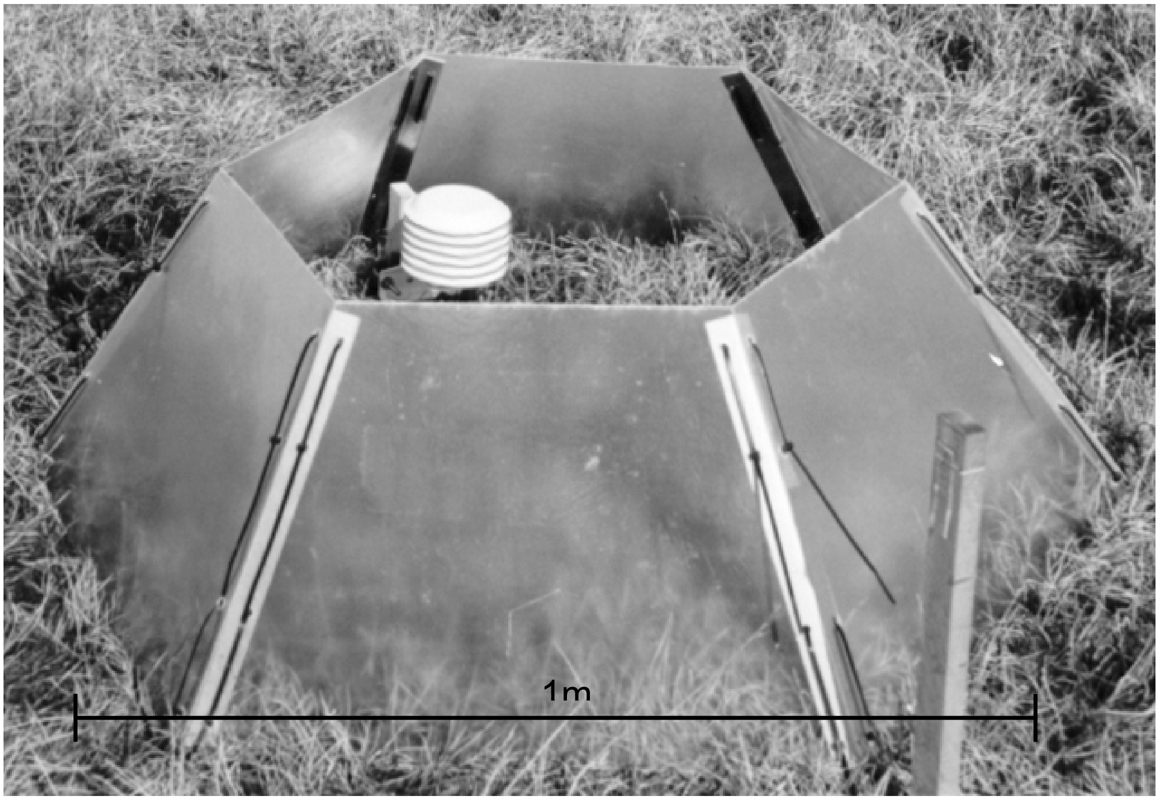

Figure I-18. An open-top chamber (OTC) used to passively warm the plant canopy. The passively ventilated radiation shield housing the temperature and relative humidity sensors can be seen near the north side of the chamber. The scale bar is 1 meter.

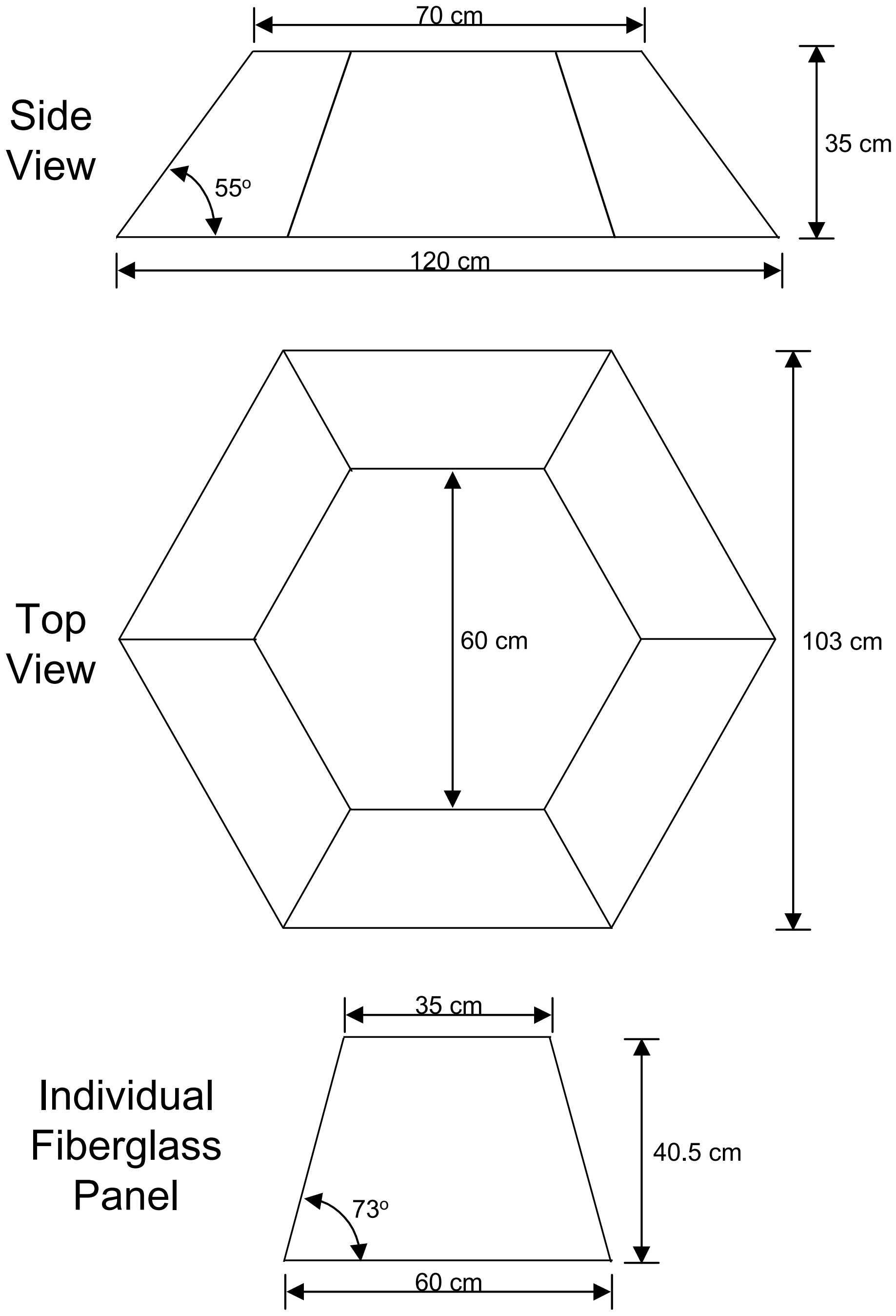

Figure I-19. The design of the open-top chambers.

I.5.3 Site Establishment

At both Barrow and Atqasuk a study site was established in a wet meadow and dry heath community (Figure I-20, Figure I-21). The study sites were chosen to occupy topographically and physiognomically equivalent community types and it was important that they had some species in common. At each study site 24 experimental warmed plots and 24 control plots were established as a completely randomized design with one treatment factor (warming). The designation of control or experimental plot was randomly determined after all plots were located. The 48 plots at each site were chosen to contain preferred species (different for each site) and high diversity within an area of similar vegetation, elevation, hydrology, and soils.

A wooden stake was installed near each open-top chamber for permanent identification. Each year, open-top chambers where installed shortly after snowmelt and removed in mid to late August. Wooden stakes and string were used to delineate a 1x1m square of tundra for each control plot. A path was established through each site to minimize disturbance due to foot traffic. Boardwalks were later built over the paths to further reduce disturbance. The Barrow boardwalks were built in July 1997 and the Atqasuk boardwalks were built in June 1998.

The principal differences between the sites apart from the greater diversity of flora and habitats were the underlying substrates. The dry site at Barrow was located on a raised beach of fine marine silts, sands, and gravels whereas the dry site at Atqasuk was located on a stabilized sand dune. Both wet sites had deep organic layers underlain by fine silts and sands and both were located on the margins of drained thaw lakes. A brief description of the physical and vegetation attributes of the four study sites is provided in

Table I-8. The results of a detailed study of the vegetation through time are provided in Chapter V. A brief description of each site is provided below.

I.5.3-1 Barrow Dry Heath (BD)

The Barrow dry site was established in 1994 within a heath community, which lies on a former raised beach ridge and is subsequently referred to as the Barrow Dry Heath (BD) site (Figure I-20). The species of focus at the time of site establishment were *Cassiope tetragona*, *Salix rotundifolia*, *Potentilla hyparctica*, and *Saxifraga punctata*. A map of the plot layout of the site is provided in Appendix A and a photograph of the site is shown in Chapter II. The soil was a moderately well drained xeric pergelic cryaquept underlain with fine silt, sand, and gravel (Table I-8). The vegetation would be classified between nodum I (dry *Luzula confusa* heath; characteristic species = *Luzula confusa*, *Potentilla hyparctica*, *Alectoria nigricans*, *Pogonatum alpinum*, and *Psilopilum cavifolium*; microrelief = high-centered-polygons) and nodum II (mesic *Salix rotundifolia* heath; characteristic species = *Salix rotundifolia*, *Arctagrostis latifolia*, *Saxifraga punctata*, *Sphaerophorus globosus*, and *Brachythecium salebrosum*; microrelief = low-centered-polygons and sloping creek banks) according to Webber 1978. The study site was located on the same former beach ridge that was described by Wiggins (1951, site No. 5) and Koranda (1954). The soils adjacent to the site were studied by Bockheim *et al*. (2001, pedon reference No. A95-15).

Table I-8. Summary of the physical site descriptions and listing of abundant and characteristic plant species of the four study sites.

	Atqasuk		Barrow	
	Dry Heath (AD)	Wet Meadow (AW)	Dry Heath (BD)	Wet Meadow (BW)
Elevation (m a.s.l.)	15.5	15.0	4.5-5.0	4.0
Slope	0	0	0.5° W	0
Land form	stabilized sand dune	thaw lake basin margin	raised beach ridge	thaw lake basin margin
Substrate	aolian sand	aolian, sand, & silt	silt, sand, & gravel	silt
Soil	Pergelic Cryopsamment	Histic Pergelic Cryaquept	Pergelic Cryaquept	Histic Pergelic Cryaquept
Vascular plants (in order of abundance)	*Ledum palustre* *Cassiope tetragona* *Luzula confusa* *Vaccinium vitis-idaea* *Hierochloe alpina* *Diapensia lapponica* *Carex bigelowii* *Trisetum spicatum* *Polygonum bistorta* *Salix phlebophylla*	*Carex aquatilis* *Eriophorum russeolum* *Salix pulchra* *Eriophorum angustifolium* *Salix polaris* *Pedicularis sudetica* *Betula nana* *Dupontia fisheri/psilosantha* *Juncus biglumis* *Luzula wahlenbergii*	*Salix rotundifolia* *Cassiope tetragona* *Luzula confusa* *Stellaria laeta* *Potentilla hyparctica* *Arctagrostis latifolia* *Poa arctica* *Luzula arctica* *Saxifraga punctata* *Senecio atropurpureus*	*Carex aquatilis/stans* *Eriophorum angustifolium/triste* *Dupontia fisheri* *Hierochloe pauciflora* *Calamagrostis holmii* *Poa arctica* *Saxifraga hirculus* *Stellaria laeta* *Cerastium beeringianum* *Eriophorum russeolum*
Characteristic bryophytes	*Polytrichastrum alpinum* *Pogonatum dentatum*	*Onocphorus wahlenbergii* *Aulacomnium turgidum*	*Dicranum elongatum* *Racomitrium lanuginosum*	*Drepanocladus brevifolius* *Campylium stellatum*
Characteristic lichens	*Alectoria nigricans* *Flavocetraria cucullata*	*Peltigera aphthosa* *Thamnolia vermicularis*	*Alectoria nigricans* *Thamnolia vermicularis*	*Peltigera aphthosa* *Cetraria islandica*

I.5.3-2 Barrow Wet Meadow (BW)

The Barrow wet site was established in 1995 within a meadow community that is in a transition zone between a drained lake basin and the former raised beach ridge (the dry site) and is subsequently referred to as the Barrow Wet Meadow (BW) site (Figure I-20). The species of focus at the time of site establishment were *Carex aquatilis/stans*, *Eriophorum angustifolium/triste*, *Saxifraga hieracifolia*, and *Saxifraga hirculus*. A map of the plot layout of the site is provided in Appendix A and a photograph of the site is shown in Chapter II. The plots were located 1-6 m from a retreating late lying snow bed and formed a near linear pattern due to the nature of the snow bed. The site is on recovered former vehicle tracks. The soil was a poor drained histic pergelic cryaquept underlain with fine silt (Table I-8). The vegetation would be classified between nodum IV (moist *Carex aquatilis-Oncophorus wahlenbergii* meadow; characteristic species = *Carex aquatilis*, *Oncophorus wahlenbergii*, *Dupontia fisheri*, *Peltigera aphthosa*, and *Aulacomnium turgidum*; microrelief = moist, flat sites and drained polygon troughs) and nodum V (wet *Dupontia fisheri-Eriophorum angustifolium* meadow; characteristic species = *Dupontia fisheri*, *Eriophorum angustifolium*, *Saxifraga foliolosa*, *Calliergon sarmentosum*, and *Calliergon giganteum*; microrelief = wet, flat sites and polygon troughs) according to Webber 1978. The soils adjacent to the site were studied by Bockheim *et al*. (2001, pedon reference No. A96-23).

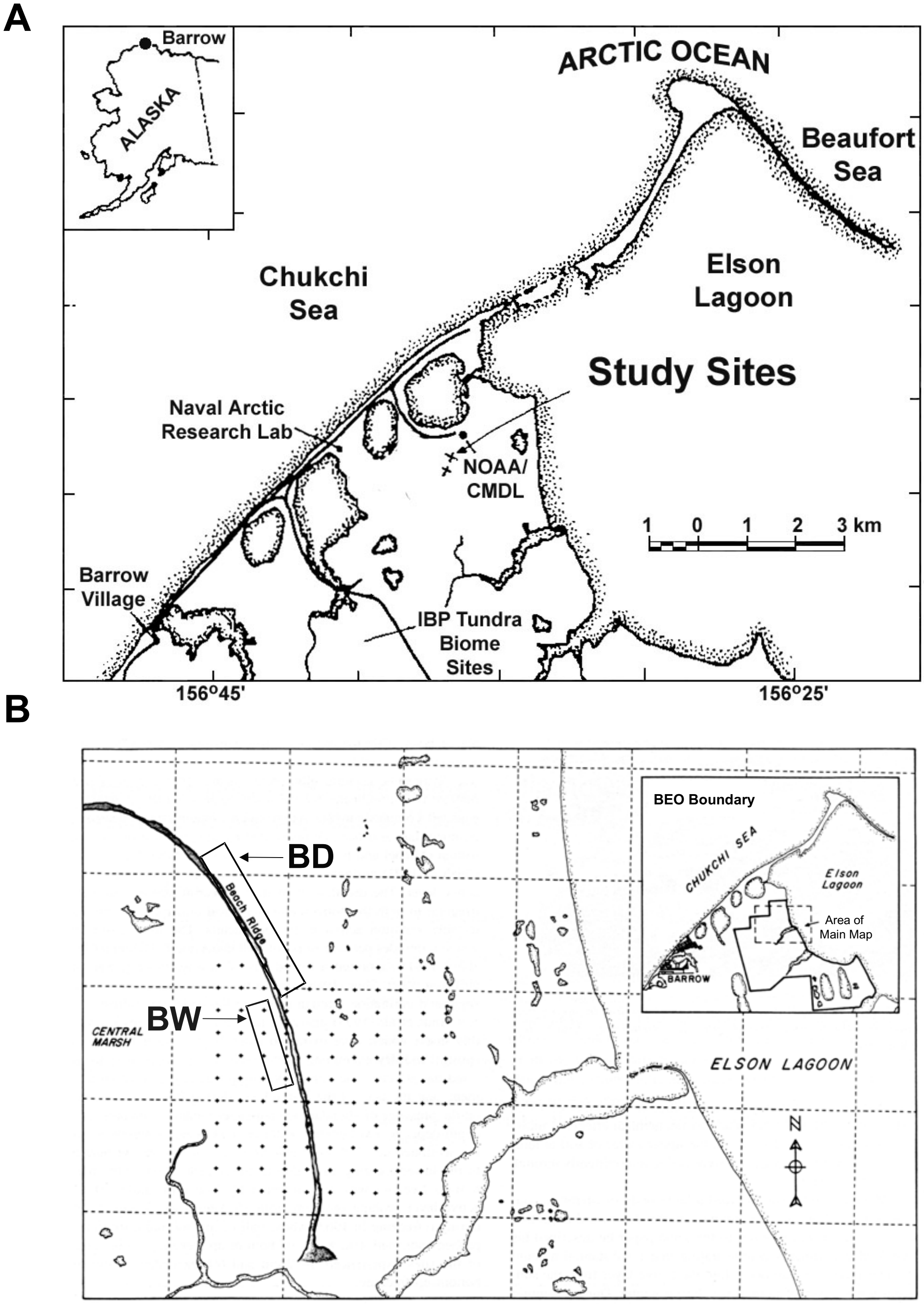

Figure I-20. ***A***) Map of Barrow Peninsula and Alaska (*inset*) showing the study sites and other landmarks (Allessio and Tieszen 1975). ***B***) Map of the research area and Barrow Peninsula (*inset*). The map displays the location of the sites (BD - Barrow Dry Heath; BW - Barrow Wet Meadow), ARCSS 1x1km grid (*crosses*), and other prominent features. The Boundary of the Barrow Environmental Observatory (BEO) is displayed on the inset (Hinkel *et al.* 1996).

I.5.3-3 Atqasuk Dry Heath (AD)

The Atqasuk dry site was established in 1996 within a heath community, which lies on the rim of a partially drained lake margin and is subsequently referred to as the Atqasuk Dry Heath (AD) site (Figure I-21). The species of focus at the time of site establishment were *Cassiope tetragona*, *Salix phlebophylla*, and *Polygonum bistorta*. A map of the plot layout of the site is provided in Appendix A and a photograph of the site is shown in Chapter II. The soil was a well drained pergelic cryopsamment underlain with aolian sand (Table I-8). The vegetation of the site would be mapped as unit # 6 of map 2 (important taxa = *Diapensia lapponica*, *Alectoria* spp.; vegetation unit = evergreen dwarf scrub; landform = ridge) according to Komárková and Webber 1980.

I.5.3-4 Atqasuk Wet Meadow (AW)

The Atqasuk wet site was established in 1996 within a meadow community near a pond margin and is subsequently referred to as the Atqasuk Wet Meadow (AW) site (Figure I-21). The species of focus at the time of site establishment were *Carex aquatilis*, *Salix pulchra*, *Eriophorum angustifolium*, and *Pedicularis sudetica*. A map of the plot layout of the site is provided in Appendix A and a photograph of the site is shown in Chapter II. The soil was a poor drained histic pergelic cryaquept underlain with aolian sand and silt (Table I-8). The vegetation of the site would be mapped as unit # 15 of map 2 (important taxa = *Carex aquatilis*, *Salix pulchra*, *Sphagnum* spp.; vegetation unit = complex [85% flarks and 15% Stränge]; landform = Strangmoor) according to Komárková and Webber 1980.

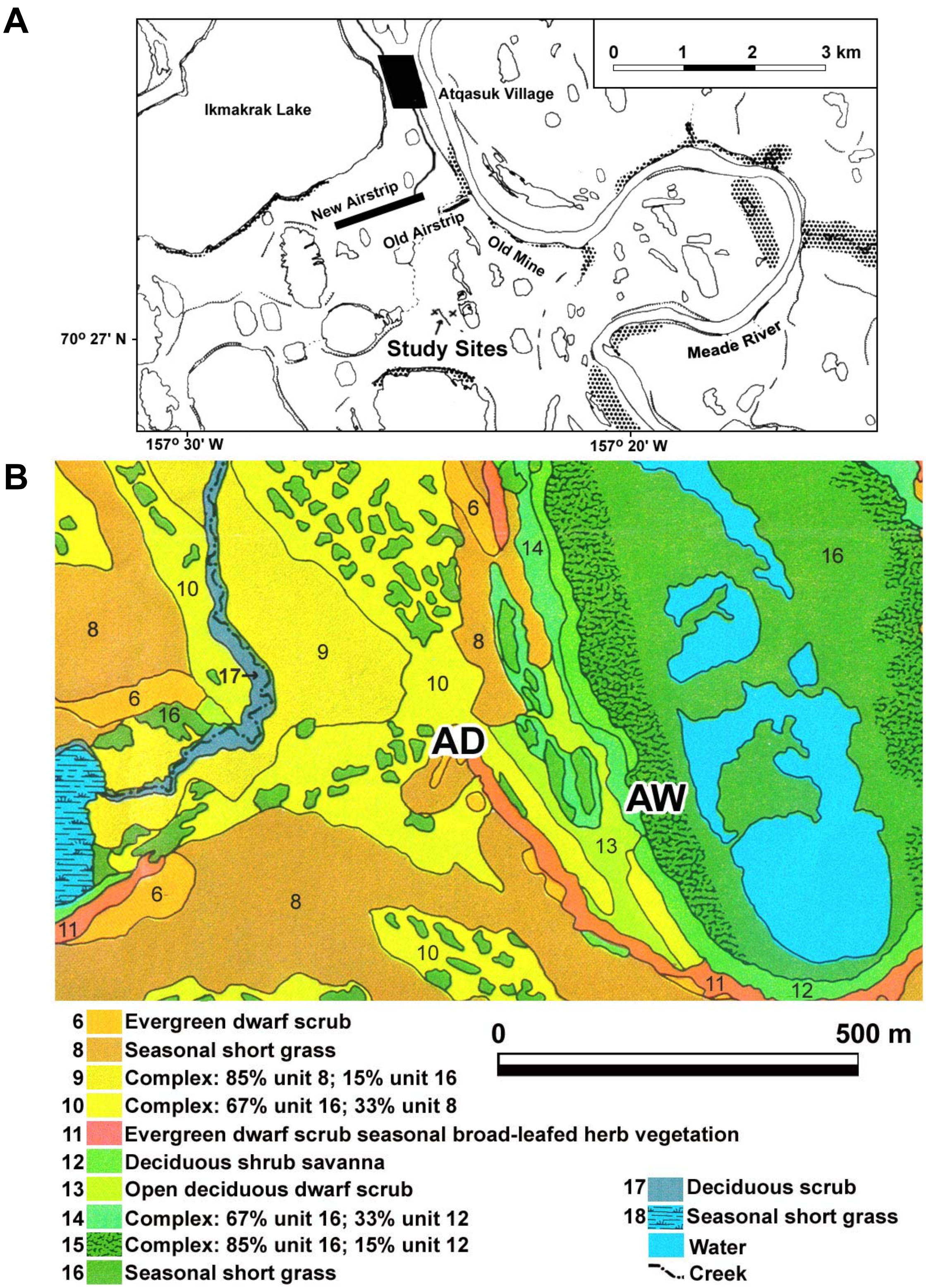

Figure I-21. ***A***) Map of the Atqasuk area showing the study sites and other landmarks (redrawn from Komárková and Webber 1977). ***B***) Map of the vegetation surrounding the sites (AD - Atqasuk Dry Heath, AW - Atqasuk Wet Meadow)(Komárková and Webber 1980).

I.5.4 Data Collection and Archival

The project expanded in scope from 1994 to 1998, it reached a plateau at a high level of activity from 1998 to 2000, and from 2001 onward it has been scaled back. There were also differences in personnel responsible for the data collection (Table I-9). The amount of data collected has varied by year and site, however the same protocols were used at all sites. All the data have been managed in a relational database run in Microsoft ® Access (Table I-10). The data collected have been archived at the National Snow and Ice Data Center (449 UCB, University of Colorado Boulder, CO 80309-0449). Summary metadata files for each data sets submitted are provided in Appendix B. A brief discussion of each data type is provided below.

Table I-9. Persons responsible for collecting the plant measurements at the four study sites during the first 7 years of the project. Patrick Webber and Christian Bay initiated the project in 1994. Robert Hollister has and overseen data collection since 1997.

	Atqasuk		Barrow	
Year	Dry Heath (AD)	Wet Meadow (AW)	Dry Heath (BD)	Wet Meadow (BW)
1994	---	---	Christian Bay	---
1995	---	---	Lisa Walker	Robert Hollister
1996	Robert Hollister	Robert Hollister	Lisa Walker	Robert Hollister
1997	David Conlin	David Conlin	Bennett Weinstein	Anna Noson
1998	Steven Rewa	MaryGrace Villanueva	Theresa Thomas	Christie Klimas
1999	Steven Rewa	Frank Lepera	Brandon Baker	Kathryn Wilkinson
2000	Steven Rewa	Christin Kolarchick	Meghan Yurenka	Josh Picotte

Table I-10. Number of records in the database of each data type by site (AD - Atqasuk Dry Heath, AW - Atqasuk Wet Meadow, BD - Barrow Dry Heath, BW - Barrow Wet Meadow).

Data Set		AD	AW	BD	BW	Total
Macroclimate		26,448	---	26,064	---	52,512
Microclimate	*whole site*	108,984	97,296	203,496	148,224	558,000
	detailed plots	105,792	105,792	104,256	104,256	420,096
Thaw Depth		624	624	2,208	2,400	5,856
Vascular Plants		161,480	117,383	255,933	348,632	883,428
Community Composition		19,200	19,200	19,200	19,200	76,800
	Total	422,528	340,295	611,157	622,712	1,996,692

I.5.4-1 Macroclimate

At both Barrow and Atqasuk an automated weather station was established in 1998. Hourly screen height temperature, precipitation, wind speed near the ground, and light intensity were recorded (Appendix B.1). During times that the weather stations were not operational data from the National Ocean and Atmospheric Association (NOAA) Climate Monitoring and Diagnostics Laboratory (CMDL) in Barrow was used. The station is staffed year round and collects data on climate and trace gas concentrations (Stone et al. 1996, also see Section I.5.1-2). More details are provided in Chapter II.

I.5.4-2 Plot Microclimate

Temperature and relative humidity was recorded at each site each year within open-top chambers and over control plots during the snow free season at the four study sites (Appendix B.2). Measurements were recorded every 10 to 80 minutes (depending on the sensor type) from shortly after snowmelt until August 15. This date was the minimum last day the data were collected each year of the experiment at all sites due to logistic constrains and the need to finish the field season in time for the academic year. The placement of temperature recording loggers was determined randomly each year; the recording of relative humidity was systematically determined from the plots already recording temperature. Generally the number of plots per site and treatment for which temperature data were collected was between 5 and 10. Sensors were housed in 6-plate radiation shields at approximately 13 cm above the ground (Figure I-18). At all four study sites an additional two experimental open-top chamber plots and two control plots were established in 1998 to provide information on the effect of open-top chambers on the underlying soils. These plots were monitored hourly throughout the growing seasons of 1999 and 2000 for plant canopy temperature, soil temperature, soil moisture, and soil salinity (Appendix B.3). More details are provided in Chapter II.

I.5.4-3 Thaw Depth

The depth of thaw was measured daily to seasonally for each plot at all four sites (Appendix B.4). Thaw depths were measured to the nearest cm by inserting a slender graduated metal rod into the ground until the frozen surface was reached. For control plots 2-4 of the corners of each plot were measured and averaged. For warmed plots the center was measured. Previous holes were avoided in subsequent probing because of the potential for unrepresentative thaw depths caused by differential heat transfer from water and air in former holes (Hinkel *et al*. 1997).

I.5.4-4 Vascular Plants

Plant measures were determined based on species morphology and ease of collection. All species within each site were monitored (Table I-11). Within each plot three permanently marked individuals of each species were monitored if possible and their location within the plot was mapped (Figure I-22). For species that do not form distinct individuals, such as clonal graminoids, unit areas were established to monitor change over years. Due to the low percentage of flowering, data on reproductive effort required the measurement of non-marked plants. Four different types of data were collected: 1) permanently marked individual plants of each species within a plot; 2) total plot measures of a species, such as the number of flowers per plot or the first occurrence of a phenophase; 3) the largest flowering individual plants of a species within a plot; and 4) the largest non-flowering individual plants of a species within a plot. The data collected included: phenological development (date of first - leaf bud burst, inflorescence emergence, flower bud, flower opening, flower withering, seed development, seed dispersal, and senescence); seasonal growth (length of leaf and length of inflorescence on a given day); seasonal flowering (number of inflorescences in flower within a plot on a given day); occurrence of events (did the plant produce a - leaf, inflorescence, bud, flower, or seed), and annual growth and reproductive effort (number of leaves, diameter of rosette, number of branches, maximum leaf length, number of inflorescences, maximum inflorescence length, number of buds, number of flowers, and number of seeds). Measurements were collected daily, weekly, or yearly for all plant species during the summers of 1994-2000 for all plots at the four sites.

The list of potential measures recorded is provided for each species in Appendix C. The actual measures recorded varied among years, sites, and species due to changing personnel and associated differences in interpretation and recording efficiency. Minor adjustments in data collection were made each year based on previous experience with a general tendency to increase data collection each year. Data collection was also streamlined or expanded depending on the capabilities of the recorder. All data have been carefully and methodically scrutinized and corrected, annotated, and purged as appropriate. The data set is considered to be of high quality and virtually error free (Appendix B.5).

Table I-11. List of all the vascular plant species in each study site. Species with reasonable replication are in bold.

Atqasuk		Barrow	
Dry Heath (AD)	Wet Meadow (AW)	Dry Heath (BD)	Wet Meadow (BW)
Antennaria friesiana	*Betula nana*	***Alopecurus alpinus***	*Alopecurus alpinus*
Arctagrostis latifolia	*Calamagrostis sp.*	***Arctagrostis latifolia***	*Arctophila fulva*
Artemisia borealis	***Carex aquatilis***	***Carex aquatilis/stans***	***Calamagrostis holmii***
Carex bigelowii	*Carex rariflora*	***Cassiope tetragona***	***Cardamine pratensis***
Cassiope tetragona	*Carex rotundata*	***Draba lactea***	***Carex aquatilis/stans***
Diapensia lapponica	***Dupontia fisheri/psilosantha***	***Draba micropetala***	***Carex subspathacea***
Hierochloe alpina	***Eriophorum angustifolium***	*Festuca brachyphylla*	***Cerastium beeringianum***
Ledum palustre	***Eriophorum russeolum***	*Juncus biglumis*	*Chrysosplenium tetrandrum*
Luzula arctica	*Juncus biglumis*	***Luzula arctica***	***Cochlearia officinalis***
Luzula confusa	***Luzula wahlenbergii***	***Luzula confusa***	***Draba lactea***
Minuartia obtusiloba	***Pedicularis sudetica***	*Oxyria digyna*	*Draba micropetala*
Pedicularis lapponica	***Polygonum viviparum***	***Papaver hultenii***	***Dupontia fisheri***
Polygonum bistorta	***Salix polaris***	*Papaver lapponicum*	***Eriophorum angustifolium/triste***
Salix phlebophylla	*Salix pulchra*	***Pedicularis kanei***	***Eriophorum russeolum***
Trisetum spicatum	*Saxifraga foliolosa*	***Poa arctica***	*Eriophorum scheuchzeri*
Vaccinium vitis-idaea	***Eriophorum russeolum***	*Poa malacantha*	***Hierochloe pauciflora***
	Juncus biglumis	***Potentilla hyparctica***	***Juncus biglumis***
	Luzula wahlenbergii	*Ranunculus nivalis*	***Luzula arctica***
		Ranunculus pygmaeus	***Luzula confusa***
		Salix rotundifolia	*Melandrium apetalum*
		Saxifraga caespitosa	*Pedicularis kanei*
		Saxifraga cernua	*Petasites frigidus*
		Saxifraga flagellaris	***Poa arctica***
		Saxifraga foliolosa	*Ranunculus nivalis*
		Saxifraga nivalis	*Ranunculus pygmaeus*
		Saxifraga punctata	*Salix pulchra*
		Senecio atropurpureus	*Salix rotundifolia*
		Stellaria laeta	*Saxifraga caespitosa*
		Vaccinium vitis-idaea	***Saxifraga cernua***
			Saxifraga foliolosa
			Saxifraga hieracifolia
			Saxifraga hirculus
			Stellaria humifusa
			Stellaria laeta

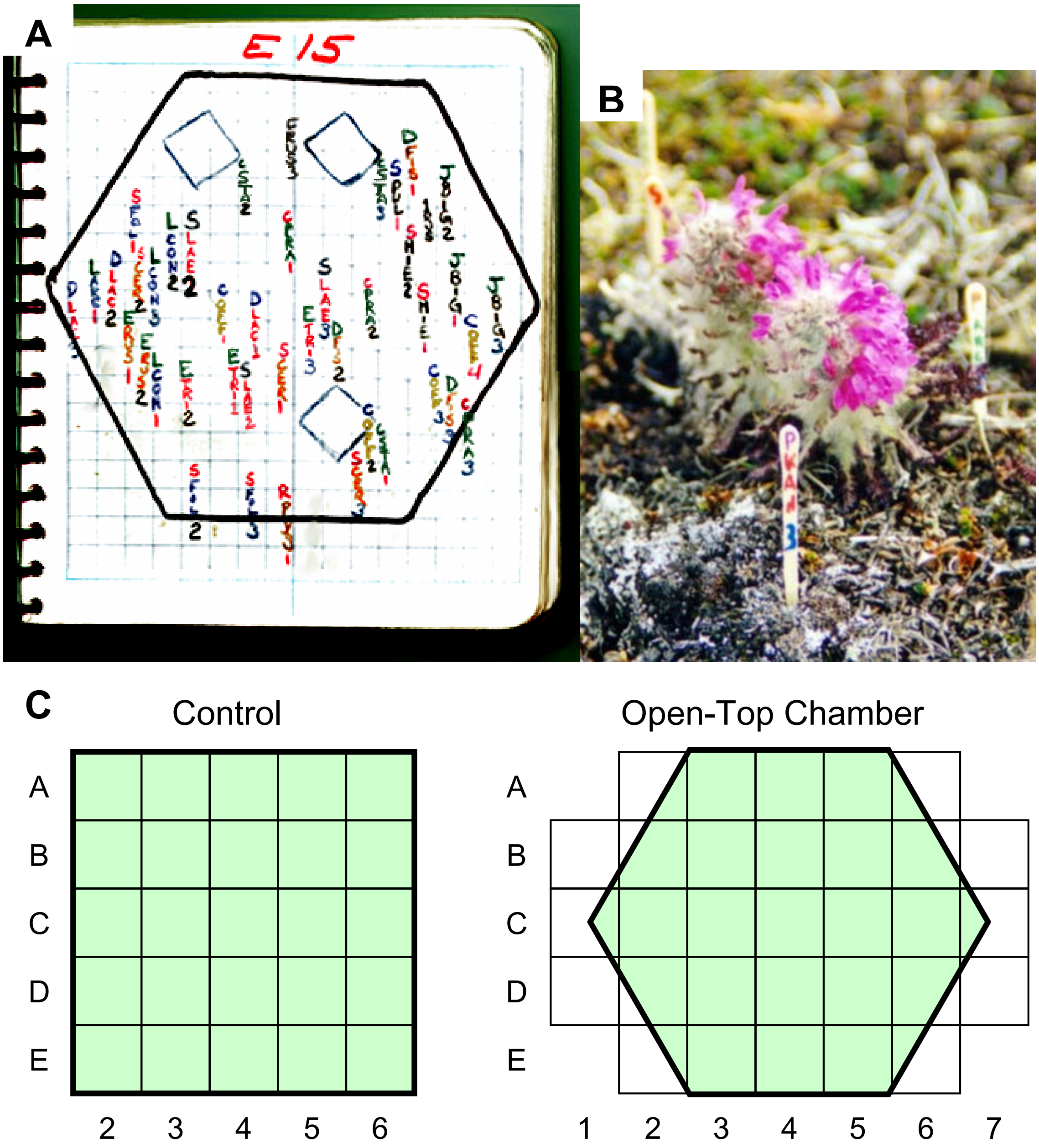

Figure I-22. The plant location scheme. ***A***) Photograph of a plot map. ***B***) Photograph of a marked plant. ***C***) Diagram of the assigned coordinates of each monitored plant within a plot.

I.5.4-5 Community Composition

The community composition was measured on the second summer of experimental warming at each site and then again during the summer of 2000. The data were gathered by placing a point frame (70x70 cm) over each plot and recording the top and bottom species at 100 grid locations on the frame (Figure I-23). Species were grouped into growth forms according to Webber (1978) and Vitt *et al*. (1988) (Figure I-24). More details are provided in Chapter V. The data set is considered to be of high quality and virtually error free (Appendix B.5).

Figure I-23. Photograph of vegetation sampling using the point frame method in the Atqasuk Dry Heath (AD) site.

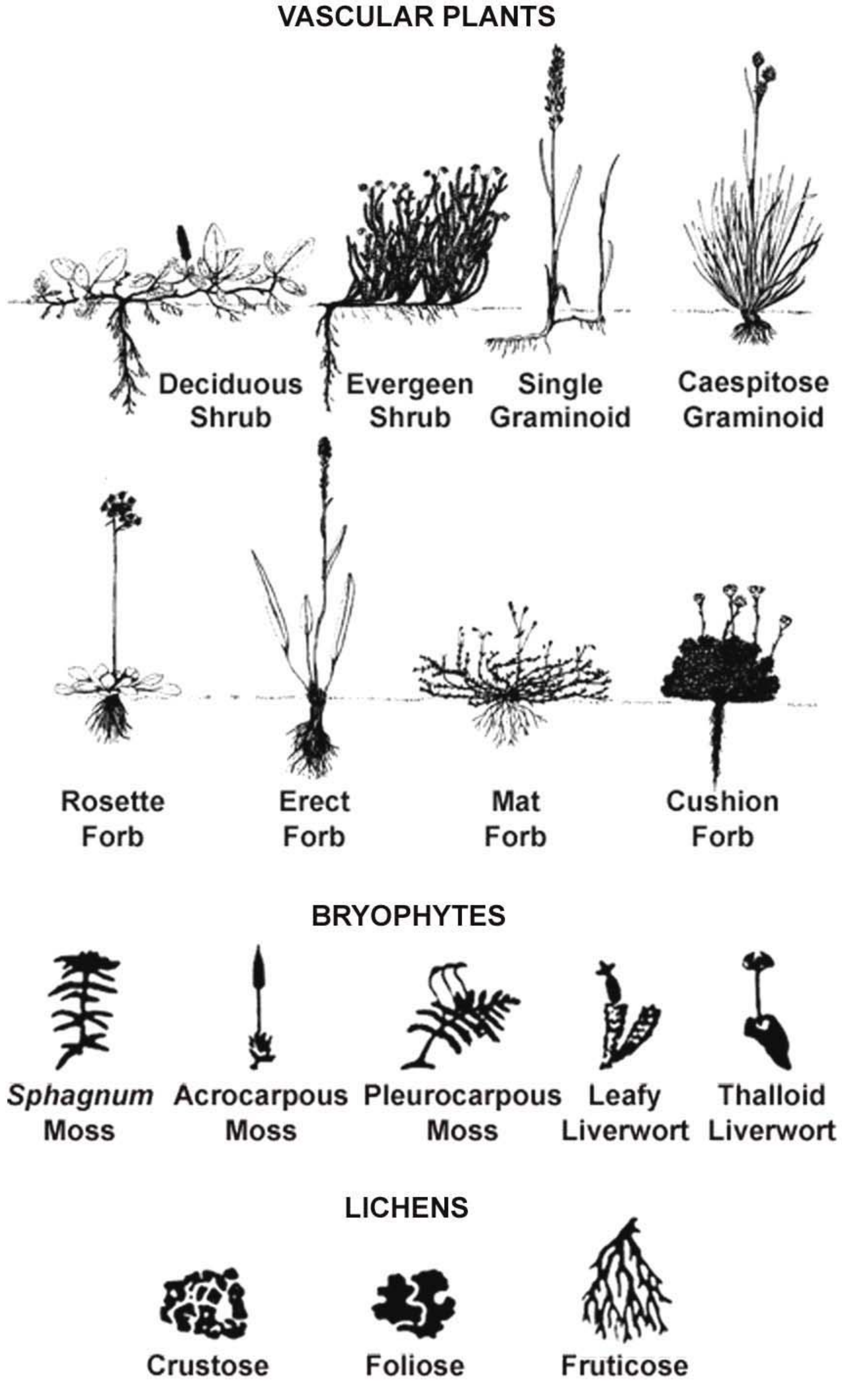

Figure I-24. Drawings of the growth forms used in the community composition analysis (redrawn from Webber 1978, Vitt *et al*. 1988).

I.6 SUMMARY

This project and dissertation attempt to determine the response of tundra plants to variation in temperature in northern Alaska. Chapters were written to become stand alone papers. This introductory chapter provides a comprehensive review of the relevant literature and addresses the broad experimental design and approach so that subsequent chapters could be streamlined. This format made repetition between chapters unavoidable.

Much is known about the relationship between vegetation and temperature, yet reasonable forecasts of vegetation response due to climate change are difficult due to the individualistic nature of the species that comprise natural plant communities. Arctic tundra is an important region to examine plant response to climate change because the Arctic is predicted to warm more than other regions of the world and the Arctic is believed to be the most vulnerable biome to changes in temperature. There are many recently documented changes in the abiotic environment of the Arctic that can be attributed to climate change. For example, in Barrow, Alaska, snowmelt is on average about 8 days earlier and the average annual temperature is about 1.6 ^{o}C warmer than it was 50 years ago. While there is a growing body of research documenting biotic changes that are consistent with anticipated changes associated with climate change, there are also studies that show little biotic change despite well documented warming. Recent manipulative warming studies in tundra systems have observed changes in vegetation, however the results have varied greatly between years, locations, and species. The larger changes in vegetation characteristics commonly reported in the literature are often biased by interactions between warming and fertilization. The most consistent changes due exclusively to warming have been a trend toward increased photosynthesis, CO_2 efflux, growth, reproductive effort, and cover and decreased tissue nitrogen. When changes occurred at the species or growth form level vascular plants, particularly graminoids and shrubs, generally fared better in the warmer environment while non-vascular plants fared worse. In general, vegetation has changed more in mesic than dry or wet communities and more in low arctic than high arctic regions. Changes in below ground processes will likely influence climate driven vegetation change but probably less than is commonly believed.

The research presented in this dissertation is a contribution to the International Tundra Experiment (ITEX). The project began 1994 when an ITEX site was established in a dry heath community in Barrow. The author of this dissertation joined the project in 1995 and expanded the project by adding a wet meadow study site in Barrow and two physiognomically equivalent study sites in Atqasuk in 1996. The focus of the research has evolved over time but the fundamental constructs were established in 1994. The North Slope of Alaska, particularly the Barrow region, is an ideal place to study tundra plant response to warming because of the rich history of research in the region on all aspects of tundra ecosystems. The project uses variation in temperature due to experimental warming, the natural temperature gradient between Barrow and Atqasuk, and interannual variability to address plant temperature relations. The project collects detailed abiotic data (temperature, soil moisture, thaw depth) in order to interpret the biotic data (plant growth, reproductive effort, and changes in cover).

The overarching goal of the dissertation is to describe the response of tundra vegetation to temperature to improve vegetation change forecasts for the Arctic. The three main objectives are to: 1) evaluate the validity of using the open-top chambers to simulate climate change (Chapters II, III, and IV); 2) describe the phenological and morphological responses of plants to temperature (Chapter IV); and 3) describe the community changes due to warming (Chapter V).

Chapter II

THE MICROENVIRONMENTS OF FOUR EXPERIMENTALLY WARMED ARCTIC TUNDRA COMMUNITIES

II.1 ABSTRACT

Arctic tundra communities were experimentally warmed with open-top chambers (OTCs) near Barrow (71°18'N 156°40'W) and Atqasuk (70°29'N 157°25'W), Alaska. Chambers have been widely used to warm tundra communities in order to forecast biotic change due to climate warming. The goal was to describe the microenvironments of four study sites over time and to compare the performance of the OTCs in each site. The study is unique because it provides descriptions of the microenvironments of multiple sites recorded over 3-8 years with the same methods. The study found approximately no differences in above ground temperatures within a geographic region (Barrow or Atqasuk), however it did find large differences in the below ground microenvironments between study sites within a region. The OTCs warmed average growing season air temperature between 0.6 and 2.2 °C depending on the site and year. The change in average July soil temperature recorded at 10 cm depth due to the OTCs varied between ⁻0.8 and 0.9 °C depending on the site and year. The OTCs generally did not change the thaw depth or soil moisture content. There were consistent differences in air and soil warming due to the OTCs between sites. Differences in warming between study sites must be considered when interpreting biological responses to experiment warming, particularly when speculating on mechanisms for observed changes.

II.2 INTRODUCTION

The microenvironments of tundra organisms have been described to improve the understanding of species distributional patterns and to interpret plant physiological response (Sørensen 1941, Mooney and Billings 1961, Corbet 1972, Tieszen 1973). Recently there has been an increased focus on understanding the relationship between species and temperature due to concern about the regional impacts of climate change (McCarthy *et al*. 2001, Walther *et al*. 2001). Most interest to date has focused on climate warming due to the significance of temperature on many biological processes (Long and Woodward 1988, Minorsky 2002) and the increase in temperature being experienced globally (Houghton *et al*. 2001), especially in high northern latitudes including northern Alaska (Serreze *et al*. 2000).

There are now many groups of researchers experimentally warming plant and animal communities to forecast change. The largest of these groups are the International Tundra Experiment (ITEX, *e*. *g*. Molau and Mølgaard 1996, Henry and Molau 1997, Arft *et al*. 1999), and the Global Change and Terrestrial Ecosystem Network of Experimental Warming Studies (GCTE-NEWS, *e*. *g*. Shaver *et al*. 2000, Rustad *et al*. 2001). Researchers associated with these groups manipulate microclimates in a way intended to simulate regional climate warming. Warming experiments are now prevalent in many community types but are greatest in number (over 30 in ITEX alone, Table I-5) and longest (*e*. *g*. over 20 years Chapin *et al*. 1995, Chapin and Shaver 1996) in tundra environments. This is partly because the Arctic is predicted to warm more than other regions of the world (Cattle and Crossley 1995, Rowntree 1997, McCarthy *et al*. 2001) and tundra communities are believed to be vulnerable to changes in temperature (Bliss *et* *al*. 1973, Billings 1987, Everett and Fitzharris 1998). Currently more than 69 published papers report vegetation change resulting from small (generally ~1 m^2) warming manipulations in tundra systems (for details see Section I.4.3-2).

The most widely used mechanism to warm patches of tundra has been passive chambers. Passive chamber warming is ideal for remote regions with harsh climates because there is no need for electrical power or other technical equipment. An undesirable characteristic of chamber warming is the lack of direct control of the amount of temperature change. For these and other reasons, the performance of chambers used to experimentally warm the plant canopy has been reviewed critically (*e. g*. Debevec and MacLean 1993, Kennedy 1995b, Marion *et al*. 1997, Wookey and Robinson 1997). In a review of several passive chamber designs, Marion *et al*. (1997) found that chambers warm the average daily temperature, increase the daily range of temperatures, reduce canopy turbulence, lower light levels, and reduce relative humidity. They do not change gas concentrations (namely CO_2), soil moisture, or thaw depths. They have a variable effect on soil temperatures and may interfere with herbivory and pollination. Marion *et al*. (1997) found that there was an offset between warming and experimental artifacts. Generally as the design of chambers became increasingly closed the warming potential of the chamber increased as did the potential impact from unwanted experimental artifacts. For the above reasons preference has been given to open-top chamber (OTCs). However, OTCs may affect the microclimate in numerous ways that are inconsistent with predicted climate change and it is important to carefully document chamber performance before interpretation of biological response to the warming manipulation (Kennedy 1995b,c).

This study experimentally warmed the microenvironment of arctic tundra using OTCs. It is unique in that it examined the microenvironment of control and experimentally manipulated plots in detail at four contrasting study sites that span temperature and moisture gradients and was conducted over 3-8 years using consistent methods. The goal of this chapter is: 1) to describe and contrast the microenvironments of the four study sites over time, and 2) to describe and contrast the performance of the OTCs in the four study sites over time.

II.3 METHODS

II.3.1 Study Sites

Study sites were established in wet and dry vegetation communities near Barrow (71^{o}18'N 156^{o}40'W) and Atqasuk (70^{o}29'N 157^{o}25'W) on the North Slope of Alaska (Figure II-1, Section I.5.1). A brief description of each site is presented in Table I-8 (Section I.5.3). A description of the vegetation of the Barrow and Atqasuk regions can be found in Webber *et al*. 1980 and Komárková and Webber 1980 respectively (also see Sections I.5.1-2 and I.5.1-3).

II.3.2 Experimental Design

At each site (Atqasuk Dry Heath – AD, Atqasuk Wet Meadow – AW, Barrow Dry Heath – BD, Barrow Wet Meadow – BW) 24 experimental warmed plots and 24 control plots were monitored. Each site was established by choosing plots and randomly assigning the treatment factor – warming with the use of OTCs (Section I.5.3). The

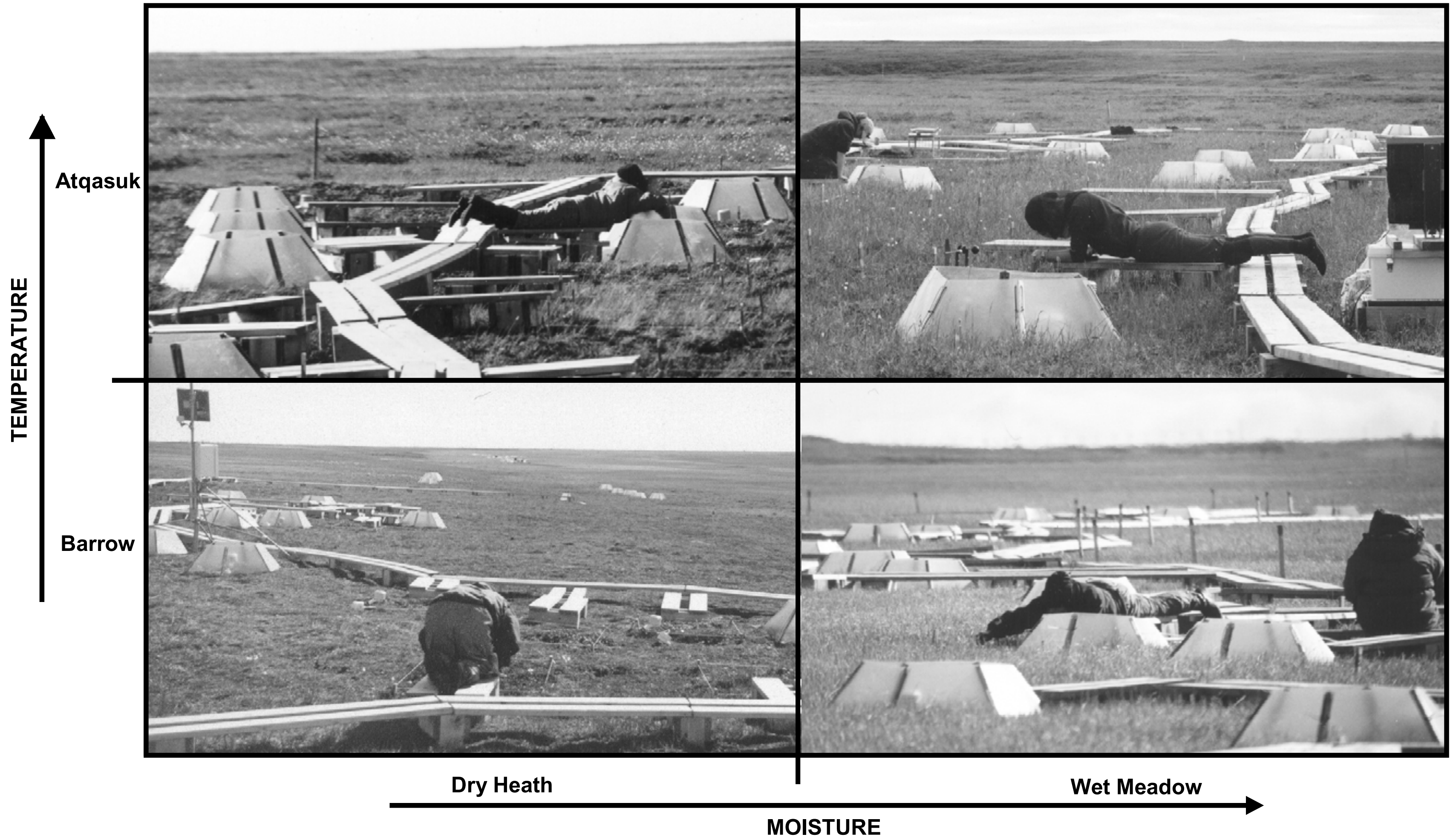

Figure II-1. Photographs of the four study sites in relation to their average summer temperature and soil moisture. Each site had an array of 24 experimentally warmed p1ots, with the use of open-top chambers (OTCs), and 24 control plots. One of the automated weather stations used to characterize macroclimate is shown in the photograph of the Barrow Dry Heath site.

OTCs were installed after snowmelt and removed at the end of each field season (after August 15th). The OTCs were hexagonal in shape with 35 cm high sloping sides constructed of Sun-Lite HPTM fiberglass (Solar Components Corporation, Manchester, New Hampshire). The distance between parallel sides was 103 cm at the base and 60 cm at the top. For additional details on the OTCs see Section I.5.2-3. Marion *et al*. (1993, 1997) described the general performance of the OTCs and Hollister 1998 and Hollister and Webber (2000, Chapter III) described the performance and established the validity of using the OTCs to simulate regional warming at the BW site.

II.3.3 Data Collection

II.3.3-1 Macroclimate

Automatic Weather Stations (AWSs) were established in 1998 at the dry heath sites at both Barrow and Atqasuk to provide climatic information for the region (Section I.5.4-1). Readings of temperature at screen height (2 m, 107 temperature probe), precipitation (35 cm, TE525 tipping bucket rain gage), and wind speed near the ground (35 cm, 03001 wind sentry) were taken every 15 minutes, averaged, and recorded every hour on a CR10X datalogger except for rain measures which were summed (the above instruments were produced by Campbell Scientific Inc., Logan, Utah). Light intensity, measured with StowAway™ light intensity loggers (Onset Computer Corporation, Pocasset, Massachusetts), was recorded every 10-20 minutes and averaged each hour. During times when the AWSs were not operational, data from the National Ocean and Atmospheric Association (NOAA) Climate Monitoring and Diagnostics Laboratory (CMDL) in Barrow (Stone *et al*. 1996) was used to estimate screen height temperature based on a correlation between locations (for more detail see Appendix D). Macroclimate information was collected in the dry heath sites; therefore, where it is reported for the wet meadow sites it is the same information reported for the adjacent dry heath sites.

II.3.3-2 Site Temperature and Relative Humidity

Site temperature and relative humidity measurements were made at the plot level with HOBO® and StowAway™ temperature and relative humidity dataloggers throughout the growing season (Onset Computer Corporation, Pocasset, Massachusetts, Section I.5.4-2). The growing season was defined as from snowmelt until the 15th of August. Measurements were recorded every 10 to 80 minutes (depending on the datalogger type) and averaged by the hour. When no data were recorded within an hour (for recording intervals of greater than 1 hour) or if the data were considered erroneous the average of the hour before and the hour after was used. The placement of temperature sensors in plots was determined randomly each year. The recording of relative humidity was systematically chosen from plots already chosen for recording temperature. Generally the number of plots measured per site and treatment was 5-10 for temperature and 3-5 for relative humidity. Sensors were housed in radiation shields placed at canopy height: approximately 13 cm above the ground (Figure I-17).

II.3.3-3 Plot Microenvironment

At each of the four sites an additional two warmed and two control plots were established in 1998 to provide more detailed information on the effect of the OTCs on the aerial and soil microenvironment (Section I.5.4-2). Plots were monitored hourly throughout the growing seasons of 1999 and 2001 for canopy height temperature (13 cm, Hobo® temperature dataloggers), soil temperature at depths 0, 5, 10, 15, 30, 45 cm (TP101M temperature probe, Measurement Research Corporation, Gig Harbor, Washington), and soil moisture at 7.5 cm depth (HYD-10-A hydra probe, Stevens Vitel Hydrological & Meteorological Systems, Chantilly, Virginia). Soil temperatures were measured every 15 minutes, averaged, and recorded every hour. Voltages from the soil moisture probe were recorded every hour and were converted to water fraction by volume (WFV). Readings were not calibrated with more traditional methods, namely gravimetric, because the focus of the measurements was relative change between years and treatments. Canopy height temperatures were recorded every 10-18 minutes and averaged hourly.

II.3.3-4 Thaw Depth and Snow Melt

The depth of thaw was measured daily to seasonally for each plot at all four sites (Section I.5.4-3). Thaw depths were measured to the nearest cm by inserting a graduated metal rod into the ground until the frozen surface was reached. The day of snowmelt was recorded for a plot when all the snow within the plot had melted. If the site installation was after snowmelt, then the day plots became snow free was estimated based on nearby soil temperatures and the snowmelt pattern of other years.

II.3.4 Data Analysis

All temperature and relative humidity data were first averaged per treatment and point in time. This made comparisons between treatments and data from the AWSs possible despite differences in the number of recording devices.

Thawing degree-day totals since snowmelt (TDD_{sm}) were calculated by plot based on hourly data. Hourly temperature data have been found to provide a better estimation of degree-days than daily averages (Raworth 1994). When canopy height temperatures were not recorded screen height temperatures were used to estimate the missing data prior to calculating TDD_{sm}. Between snowmelt and site set-up a linear model was used to calculate canopy height temperatures based on correlations with screen height temperatures (for more detail see Appendix D). After August 15th screen height temperatures substituted canopy height temperatures. It was considered unnecessary to make an adjustment for canopy temperature late in the season due to the square root relationship between degree-day totals and thaw depth. All the plots within a treatment were then averaged to represent the average TDD_{sm} per treatment on any given day for each site.

An index of wind speed, solar intensity, and precipitation was calculated on a relative scale based on daily conditions. If the daily mean wind speed or solar intensity was more or less than the average it was classified as more or less, respectively. Wind was classified as average if the average daily wind speed near the ground was between 2.4 and 3.9 m/sec. Solar intensity was classified as average sunny if the average solar intensity from 8:00-16:00 was between 3.40 and 3.55 lum/m^2. Precipitation was classified as no rain, trace, or rainy (more than trace). Rain was classified as trace if the daily sum was between 0 and 1 mm.

A variation of the Stefan solution for thaw depth (*e. g.* Jumikis 1977) was used to describe the relation between temperature and thaw at the four sites. The basic form of the Stefan equation for depth of thaw is given by

$$Z_t = \mathrm{sqrt}[(2\ \lambda\ n\ S\ DDT)/(\rho\ w\ L)]$$

where *Z* represents the thaw depth at time t, λ is thermal conductivity (W m^{-1} $^{o}C^{-1}$), n is the dimensionless ratio between surface and air thawing degree-day indices (Klene *et al*. 2001a), S is a temporal scaling factor (86,400 s d^{-1}), DDT is the thawing index at standard screen height (^{o}C days), ρ is soil density (kg m^{-3}), w is water content expressed in dimensionless form, and L is the latent heat of fusion (J kg^{-1}).

The Stefan solution can be simplified and rewritten in linear form as

$$Z_t = E\ C,$$

where *Z* represents the thaw depth at time t, E is an "edaphic term" representing soil thermal, textural, surface, and moisture properties and C is a "climatic term" defined as the square root of DDT (Nelson and Outcalt 1987). The close dependence of thaw progression on the square root of the thawing index facilitates treatment of the thaw problem through linear regression, wherein the edaphic factor represents the rate of thaw progression. This approach has been used in northern Alaska by Nelson *et al*. (1997), Klene *et al*. (2001b), Brown *et al*. (2000), and Shiklomanov and Nelson (2002); these studies indicate that well-defined vegetation/soil associations develop characteristic values of E and that the values are relatively stable on an interannual basis. Thawing degree-days from snowmelt (TDD_{sm}) measured at canopy height was considered to be a better representation of climate than DDT. Therefore we rewrite the formula as

$$Z_t = E\ \mathrm{sqrt}(TDD_{sm})$$

where *Z* represents the thaw depth at time t, and E is the "edaphic term", TDD_{sm} is the thawing degree-day totals since snowmelt measured at canopy height. For interpretation, the higher the E value the stronger the influence of temperature on thaw depth (Nelson and Outcalt 1987).

Thaw depth data were analyzed as a single factor repeated ANOVA using SAS (2000). The analyses were run separately for each site and an overall analysis was run on all sites by blocking for site.

II.4 RESULTS

II.4.1 Site Temperature and Relative Humidity

The average date of snowmelt and growing season temperature was variable among sites, years, and treatments (Table II-1). Recorded screen height growing season temperature at Atqasuk was on average 3.8-5.2 ^{o}C warmer than at Barrow depending on the year (1999-2001). Average screen height growing season temperatures were up to 0.9 ^{o}C warmer in the wet communities than the dry communities within a region (Barrow or Atqasuk) due to later snowmelt and therefore a later recording interval. Average growing season screen height temperatures were 0.4-0.9 ^{o}C lower than canopy height temperatures except where temperatures were estimated. The average growing season temperature was between 0.6 and 2.2 ^{o}C higher in the warmed plots that the controls depending on the site and year.

Comparisons between sites and years during the same recording interval were made by examining average July temperatures (Table II-2). The average July temperature recorded at canopy height over the control plots was approximately the same temperature within a geographic region (Barrow or Atqasuk) and year. The average minimum July temperatures were approximately the same regardless of height or treatment within a geographic region and year except where temperatures were estimated. Most of the increase in temperatures at canopy height and in warmed plots was due to increases in daily maximum temperatures. The amount of experimental warming varied among sites and years of the experiment. The pattern was not consistent over time but the trend was that the site with the least amount of experimental warming at canopy height relative to the control plots was AW (0.6-1.2 ^{o}C increase in average; 1.3-2.9 ^{o}C increase in maximum), followed by AD (1.0-1.6 ^{o}C increase in average; 2.4-4.4 ^{o}C increase in maximum), BD (1.1-2.0 ^{o}C increase in average; 2.4-4.6 ^{o}C increase in maximum), and BW (1.4-2.7 ^{o}C increase in average; 3.2-5.7 ^{o}C increase in maximum) (calculated from Table II-2).

The TDD_{sm} varied between 169 and 854 depending on the site, year, height, and treatment (Figure II-2). The relative difference in TDD_{sm} between sites, heights, and treatments was also variable between years. The TDD_{sm} was higher in Atqasuk than Barrow, higher in dry heath sites than wet meadow sites, higher when measured at screen height than canopy height, and higher in warmed plots than control plots. The average growing season TDD_{sm} estimated at screen height at each site was 569, 555, 243, and 227 for the AD, AW, BD, and BW sites, respectively. The average difference between canopy and screen heights for TDD_{sm} at sites AD, AW, BD, and BW was 11.5, 10.9, 22.9 and 20.5 % and the average difference between warmed and control plots was 15.5, 9.1, 36.8, and 34.4 %, respectively. The percentage increase in TDD_{sm} was much greater at Barrow than Atqasuk, due to fewer TDD_{sm} at Barrow.

The average and minimum daily relative humidity for the growing season varied from 80.0 to 96.9 % depending on the site, year, and treatment (Table II-3). The relative humidity in the warmed plots was on average for the growing season 1.5 to 12.8 % lower than in the control plots depending on the year and site. These differences were greatest for average daily minimum (up to 8.7 %). The average maximum daily relative humidity varied little and was over 90 % for all sites, years, and treatments. The average relative humidity was higher in Barrow than Atqasuk, higher in the wet meadow sites than the dry heath sites, and higher in the control plots than the warmed plots.

Table II-1. Average calendar day of OTC installation (set-up) and snowmelt and average daily temperatures (^{o}C) from installation until August 15 recorded at screen height (S, 2 m) and at canopy height (13 cm) over control (C) and experimentally warmed (W) plots from years 1994-2001 at the four study sites. Information in italics is estimated.

Site	Dry Heath						Wet Meadow					
Year	Snowmelt	Set-up	S	C	W	W-C	Snowmelt	Set-up	S	C	W	W-C
Atqasuk												
1996	*May 22*	Jun 12	*9.0*	9.3	11.1	1.8	*May 29*	Jun 12	*9.0*	9.2	10.2	1.0
1997	*Jun 09*	Jun 18	*8.4*	9.9	11.6	1.7	*Jun 16*	Jun 18	*8.4*	10.0	10.9	0.9
1998	*Jun 02*	Jun 04	*8.5*	9.9	11.5	1.6	*Jun 09*	Jun 09	*8.7*	10.2	11.1	0.9
1999	Jun 09	Jun 09	9.3	10.0	11.6	1.6	Jun 10	Jun 09	9.3	10.0	11.1	1.1
2000	Jun 06	Jun 06	7.1	7.7	9.2	1.5	Jun 11	Jun 10	7.4	8.2	8.8	0.6
2001	Jun 04	Jun 04	6.4	7.1	8.1	1.0	Jun 10	Jun 17	7.2	7.6	8.4	0.8
Average	Jun 03	Jun 08	8.1	9.0	10.5	1.5	Jun 09	Jun 12	8.3	9.2	10.1	0.9
Barrow												
1994	Jun 15	Jun 20	*4.2*	6.1	8.0	1.9	·	·	·	·	·	·
1995	Jun 14	Jun 20	*3.1*	3.1	4.9	1.8	*Jun 19*	Jul 07	*3.5*	3.4	5.4	2.0
1996	May 30	Jun 01	*3.7*	4.3	6.1	1.8	Jun 10	Jun 07	*3.8*	4.8	6.2	1.4
1997	Jun 08	Jun 05	*3.2*	4.0	5.9	1.9	Jun 25	Jun 25	*4.1*	5.1	7.3	2.2
1998	Jun 03	Jun 03	*3.9*	5.2	6.9	1.7	Jun 20	Jun 20	*4.8*	6.3	7.8	1.5
1999	Jun 16	Jun 14	4.1	4.9	6.9	2.0	Jun 27	Jun 26	4.7	5.5	7.4	1.9
2000	Jun 12	Jun 09	3.3	4.2	5.3	1.1	Jun 18	Jun 19	3.6	4.4	5.7	1.3
2001	Jun 12	Jun 08	2.5	3.2	4.7	1.5	Jun 21	Jun 18	2.7	3.5	5.4	1.9
Average	Jun 09	Jun 10	3.5	4.4	6.1	1.7	Jun 20	Jun 21	3.9	4.7	6.5	1.8

· no data

Table II-2. Average, maximum, and minimum daily July temperatures (^{o}C) recorded at screen height (S, 2 m) and at canopy height (13 cm) over control (C) and experimentally warmed (W) plots from years 1994-2001 at the four sites (AD - Atqasuk Dry Heath; AW - Atqasuk Wet Meadow; BD - Barrow Dry Heath; BW - Barrow Wet Meadow). Temperatures in italics are estimated.

		1994			1995			1996			1997			1998			1999			2000			2001		
		avg	max	min	avg	max	min	avg	max	min	avg	max	min	avg	max	min	avg	max	min	avg	max	min	avg	max	min
AD	S	·	·	·	·	·	·	*10.1*	*15.3*	*5.8*	*8.7*	*12.9*	*5.0*	*10.5*	*15.1*	*6.7*	10.3	15.1	5.8	7.1	10.7	3.8	7.6	11.3	3.9
AD	C	·	·	·	·	·	·	10.1	15.4	5.1	9.7	15.9	4.9	12.5	18.0	7.6	11.1	17.0	5.7	7.5	11.8	3.6	8.4	12.9	3.7
AD	W	·	·	·	·	·	·	11.7	19.8	5.4	11.5	20.0	5.1	14.1	21.8	7.9	12.6	20.6	5.9	8.7	14.4	3.8	9.4	15.3	3.9
AW	C	·	·	·	·	·	·	9.9	15.3	4.9	9.8	15.8	5.1	12.6	18.0	7.7	11.1	17.2	5.8	7.8	11.9	4.1	8.2	12.5	3.6
AW	W	·	·	·	·	·	·	10.8	18.0	5.0	10.8	18.0	5.2	13.6	20.9	7.8	12.3	19.9	6.0	8.4	13.2	4.1	9.1	14.3	3.9
BD	S	*3.8*	*7.2*	*1.4*	*3.6*	*6.1*	*1.5*	*4.8*	*8.2*	*1.9*	*3.6*	*6.1*	*1.5*	*5.1*	*8.0*	*2.8*	4.4	7.1	1.9	3.1	5.6	1.0	2.6	5.5	0.2
BD	C	5.5	10.9	0.9	3.8	7.4	0.8	5.7	9.6	1.8	4.4	8.0	1.4	6.6	10.0	3.8	5.2	9.2	1.9	3.9	7.3	1.0	3.3	7.3	0.0
BD	W	7.5	15.5	1.4	5.6	11.5	1.3	7.3	13.3	2.2	6.4	12.4	1.8	8.2	13.3	4.1	7.1	13.4	2.2	5.0	9.7	1.2	5.2	11.3	0.4
BW	C	·	·	·	3.8	7.5	0.8	6.0	10.1	1.8	4.5	8.1	1.4	6.6	10.0	3.7	5.2	9.1	1.9	4.0	7.3	1.1	3.7	7.8	0.2
BW	W	·	·	·	6.0	12.2	1.2	7.4	13.6	2.0	7.2	13.8	1.9	8.5	13.9	4.1	7.3	13.4	2.4	5.5	10.5	1.4	6.1	12.4	0.9

· no data

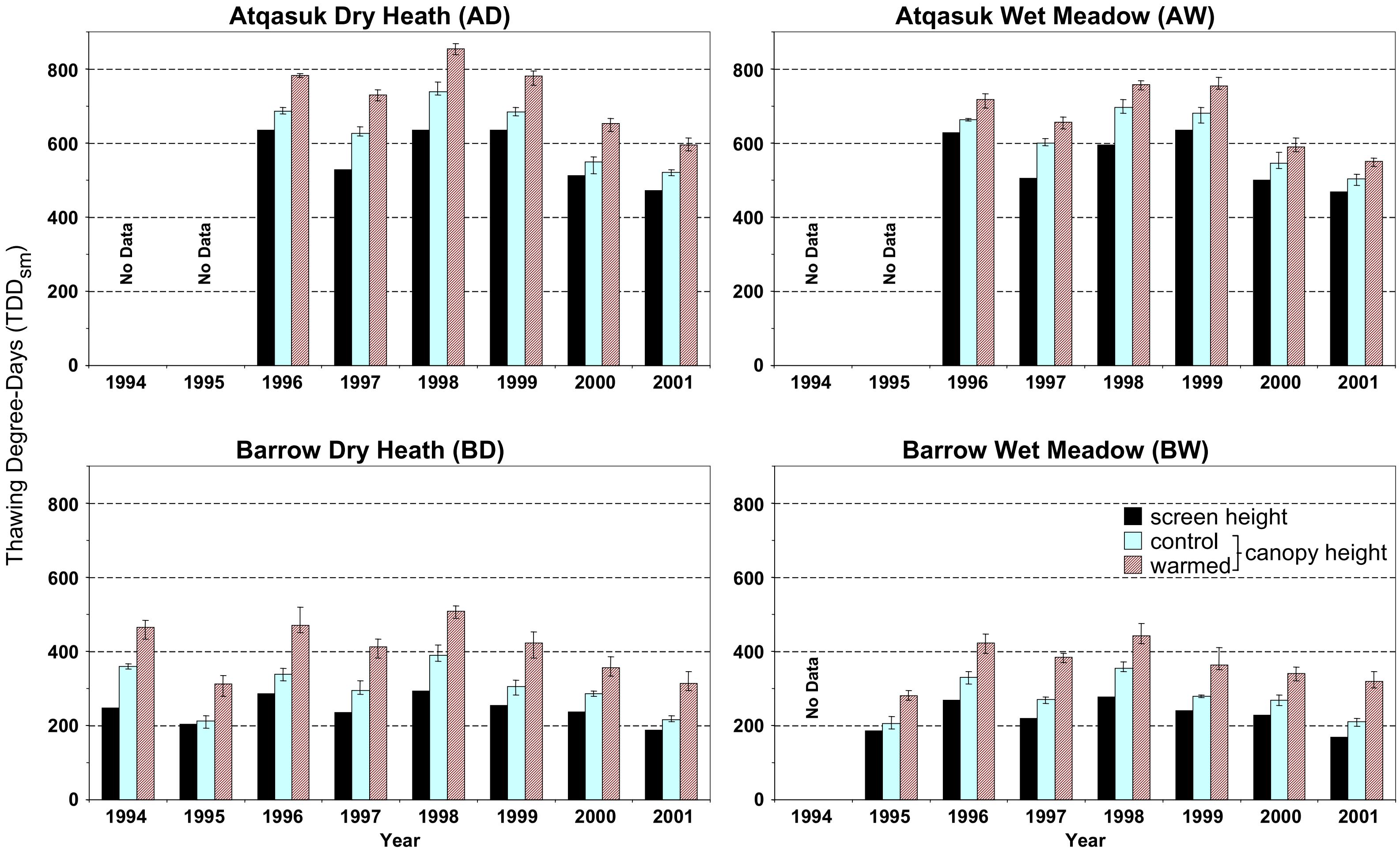

Figure II-2. Thawing degree-day totals from snowmelt until August 15 (TDD$_{sm}$) measured at screen height (2 m) and canopy height (13 cm) over control and experimentally warmed plots at the four study sites during years 1994-2001. Error bars represent the maximum and minimum.

Table II-3. Average and minimum daily relative humidity from site set-up until August 15 recorded at the plant canopy height (13 cm) over control (C) and experimentally warmed (W) plots from years 1994-2001 at the four study sites.

Site	Dry Heath						Wet Meadow					
	C		W		W-C		C		W		W-C	
Year	avg	min	avg	min	avg	min	avg	min	avg	min	avg	min
Atqasuk												
1996	·	·	·	·	·	·	·	·	·	·	·	·
1997	85.1	65.8	76.1	54.8	-9.0	-11.0	86.3	69.2	84.8	66.2	-1.5	-3.0
1998	83.5	66.6	75.7	54.1	-7.8	-12.5	85.1	69.6	82.5	64.8	-2.6	-4.8
1999	80.0	62.1	74.2	52.3	-5.8	-9.8	87.2	70.2	82.9	65.2	-4.3	-5.0
2000	89.6	73.9	76.8	59.6	-12.8	-14.3	90.2	77.9	88.5	75.1	-1.7	-2.8
2001	88.1	74.6	82.3	65.7	-5.8	-8.9	·	·	·	·	·	·
Average	85.3	68.6	77.0	57.3	-8.3	-11.3	87.2	71.7	84.7	67.8	-2.5	-3.9
Barrow												
1994	·	·	·	·	·	·	·	·	·	·	·	·
1995	90.6	75.1	79.7	56.6	-10.9	-18.5	·	·	·	·	·	·
1996	86.9	77.4	79.8	64.6	-7.1	-12.8	·	·	·	·	·	·
1997	93.6	85.4	82.0	67.1	-11.6	-18.3	92.9	84.9	82.0	66.2	-10.9	-18.7
1998	95.3	87.5	85.8	70.7	-9.5	-16.8	94.6	86.7	84.6	68.5	-10.0	-18.2
1999	89.9	80.0	83.8	67.0	-6.1	-13.0	91.7	82.3	82.0	67.5	-9.7	-14.8
2000	93.1	85.3	88.8	74.6	-4.3	-10.7	96.9	90.3	89.0	75.1	-7.9	-15.2
2001	91.7	82.9	88.3	76.0	-3.4	-6.9	95.4	88.7	83.6	72.7	-11.8	-16.0
Average	91.6	81.9	84.0	68.1	-7.6	-13.8	94.3	86.6	84.2	70.0	-10.1	-16.6

· no data

II.4.2 Plot Microenvironments

A more detailed description of the microenvironment was performed on two plots from each site and treatment from years 1999-2001. These data showed that the average daily July temperature increased from screen height to ground surface and gradually decreased with soil depth except for the AD site, which was cooler at the ground surface than at canopy height during some years (Table II-4, Figure II-3). The change in temperature with depth was variable between sites, treatments, and years. The OTCs, on average, warmed the soils except in the AW site, where the OTCs cooled the soils. The difference in temperatures due to the OTCs was generally greatest at canopy height or the ground surface and decreased with depth. The site with the largest change in average July soil temperature at ground surface associated with the OTCs was BW (0.4-2.4 °C increase), followed by AW (1.2-1.7 °C decrease), then AD (0.1-1.7 °C increase), and finally BD (¯0.1-0.6 °C increase) (calculated from Table II-4). The average difference between treatments in July soil temperature at 10 cm depth was between 0.4-0.6 °C for the AD site, ¯0.8 °C for the AW site, 0.2-0.4 °C for the BD site, and 0.3-0.9 °C for the BW site.

Average soil moisture data (Table II-4) were difficult to interpret owing to large differences in soil moisture between plots within a treatment and site. In the AW and BD sites there was less than a 5% difference between years or treatments. In the BW site there was no consistent difference between treatments and a small difference between years. In the AD site there were up to 14 and 8% differences between years and treatments, respectively; in the two drier years control plots had lower soil moisture than warmed plots, while in the wettest year there was no difference.

The average July hourly course of temperature at canopy height, ground surface, and below ground showed a similar pattern at the four sites: the maximum temperatures occurred in the afternoon while minimum temperatures occurred in the morning and the ground surface showed the greatest hourly fluctuation, followed by canopy height, and then below ground (Figure II-4). The average daily maximum and minimum temperatures displayed in Figure II-4 were damped compared with Figure II-3 because actual daily maximum and minimum occurred at various times during the day. The AW site had a distinctly lower hourly fluctuation in ground surface temperature from the other sites. This difference was likely due to a shallow layer of standing water in the AW site.

In the wet sites the temperature below ground was on average cooler than at the surface, while in the dry sites the temperatures below ground was the same or even warmer than at the surface during the early morning. The dry sites showed a greater fluctuation in hourly soil temperatures. The decline in ground surface temperature in the afternoon in the dry sites is likely due to instrument shading. Most of the OTC warming of the plant canopy occurred during mid-day. The relative change in ground surface temperatures associated with the OTCs varied greatly by site.

The average daily temperatures in July varied greatly by day (Figure II-5). The overall pattern of above ground temperatures was similar between sites within a year, this was particularly true for control plots within a geographic region (Barrow or Atqasuk). Below ground temperatures generally followed above ground temperatures, but the relationship lessened with increasing depth. The relative OTC warming varied greatly by day and the patterns were different between sites. The largest warming at canopy height due to the OTCs occurred during days that were sunny, had no rain, and were windy.

II.4.3 Thaw Depths

The average thaw depth at the end of the field season varied significantly between sites and years (*p*-value <0.001) but not treatments (*p*-value = 0.567)(Table II-5). The same results were true when analyses were run by site: years were significant (*p*-value <0.001) but treatments were not (*p*-value: AD = 0.818, AW = 0.279, BD = 0.635, BW = 0.132). The strong relationship between thaw depth and sqrt(TDD_{sm}) confirms that temperature is strongly correlated with the progression of thaw depth at the four sites (Figure II-6). The correlation between thaw depth and sqrt(TDD_{sm}) was strongest when

Table II-4. Average daily July temperatures (^{o}C) recorded at screen height (S, 2 m), canopy height (13 cm), ground surface (0 cm) and 5 depths below the surface (5, 10, 15, 30, 45 cm) and average water fraction by volume (wfv) measured at 7.5 cm depth in control (C) and experimentally warmed (W) plots during the years 1999-2001. Temperatures in italics are estimated. Estimated canopy height temperatures were taken site from data presented in Table II-2.

	Atqasuk Dry Heath (AD)						Atqasuk Wet Meadow (AW)						Barrow Dry Heath (BD)						Barrow Wet Meadow (BW)					
	1999		2000		2001		1999		2000		2001		1999		2000		2001		1999		2000		2001	
	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W
S	10.3	10.3	7.1	7.1	7.6	7.6	*10.3*	*10.3*	*7.1*	*7.1*	*7.6*	*7.6*	4.4	4.4	3.1	3.1	2.6	2.6	*4.4*	*4.4*	*3.1*	*3.1*	*2.6*	*2.6*
13	*11.1*	*12.6*	7.8	8.8	8.4	9.6	*11.1*	*12.3*	7.9	8.5	8.6	9.0	5.6	7.3	3.9	5.5	3.8	5.8	*5.2*	7.9	4.2	6.4	3.9	6.1
0	12.9	13.0	9.3	9.9	9.5	11.2	10.4	8.7	8.0	6.8	8.8	7.2	7.6	8.2	6.3	6.5	6.7	6.6	6.3	8.7	6.3	7.9	6.3	6.7
-5	8.7	9.5	6.6	7.1	6.6	7.8	7.3	6.0	6.0	4.9	6.2	5.0	5.6	6.1	4.6	5.0	4.4	4.8	3.2	5.0	4.0	5.2	3.4	4.1
-10	7.7	8.4	5.8	6.2	5.9	6.5	5.9	5.1	4.9	4.1	4.8	4.0	4.8	5.1	4.0	4.2	3.6	4.0	1.7	2.8	2.7	3.4	2.1	2.4
-15	6.8	7.5	5.1	5.6	5.0	5.7	4.9	4.4	4.0	3.6	3.7	3.3	3.8	4.3	3.3	3.6	2.8	3.2	0.8	1.5	1.5	2.1	1.0	1.4
-30	5.0	5.4	3.9	4.1	3.6	4.1	3.3	2.7	2.6	2.1	2.2	1.8	2.0	2.8	1.9	2.3	1.3	1.9	-0.5	0.2	0.0	0.7	-0.3	0.2
-45	3.4	3.6	2.5	2.7	2.2	2.6	1.8	1.1	1.2	0.7	0.9	0.5	1.0	1.4	1.1	1.1	0.5	0.6	-1.1	-0.8	-0.8	-0.5	-0.9	-0.7
wfv	0.12	0.20	0.26	0.27	0.15	0.19	0.42	0.40	0.43	0.40	0.43	0.40	0.35	0.39	0.36	0.40	0.36	0.39	0.55	0.55	0.64	0.60	0.60	0.57

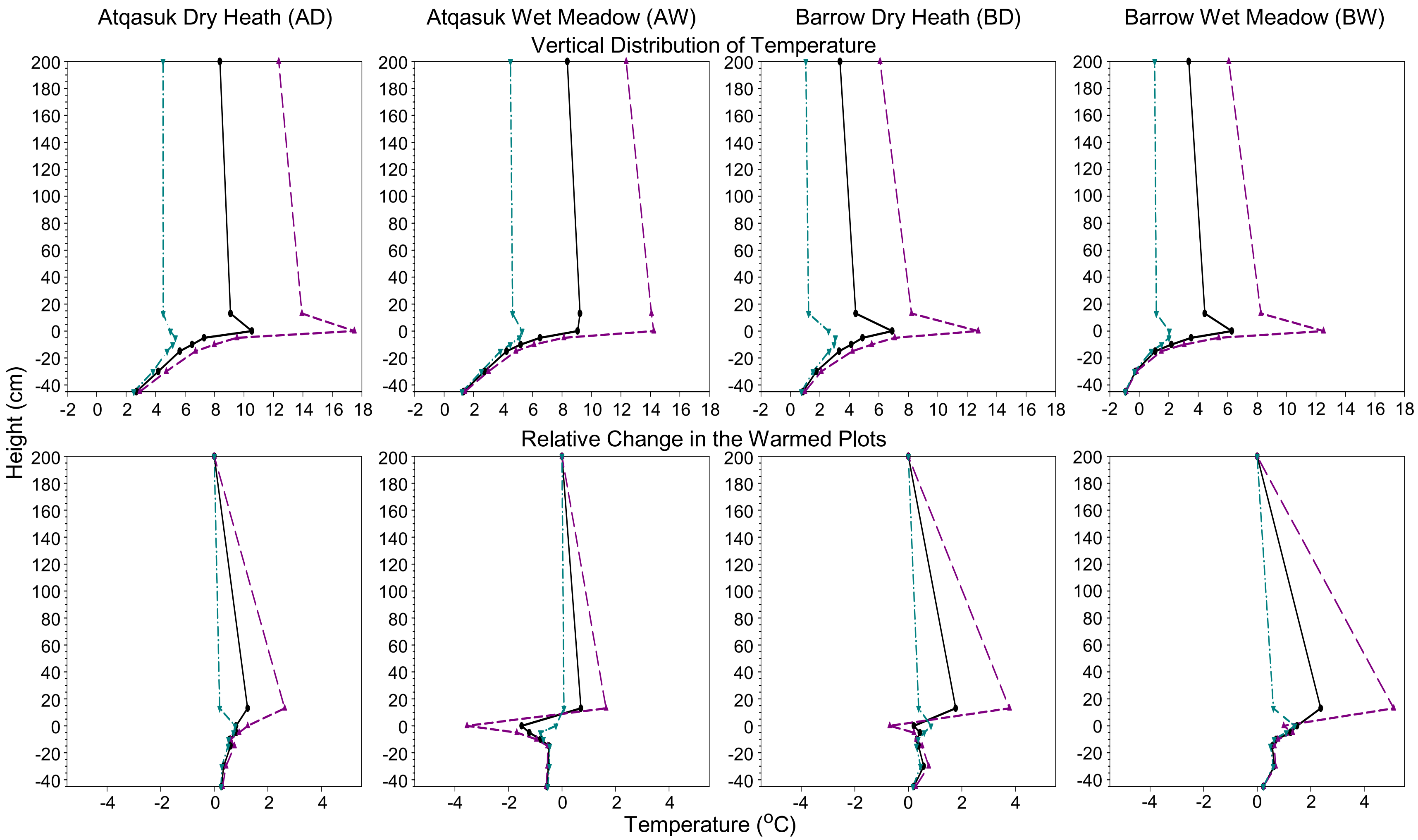

Figure II-3. Average daily vertical distribution of minimum (*dotted dashed line*), average (*solid line*), and maximum (*dashed line*) temperature in July for the years 1999-2001 at the four study sites and the change in these temperatures with height in the warmed plots relative to the control plots.

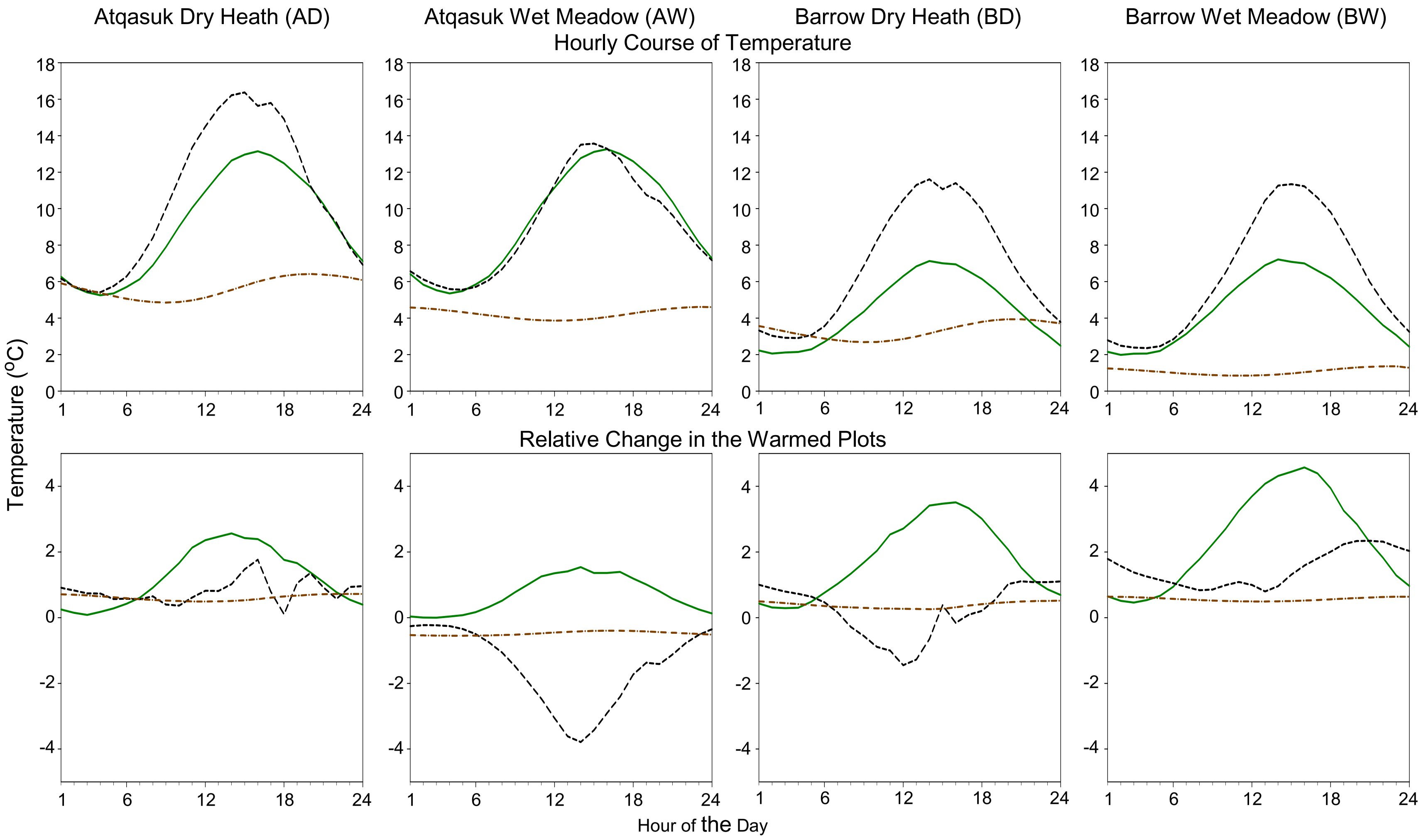

Figure II-4. Average daily course of temperature in July recorded at canopy height (13 cm, *solid line*), ground surface (0 cm, *dashed line*), and below ground (15 cm, *dotted dashed line*) for the years 1999-2001 at the four study sites and the change in temperature in the warmed plots relative to the control plots.

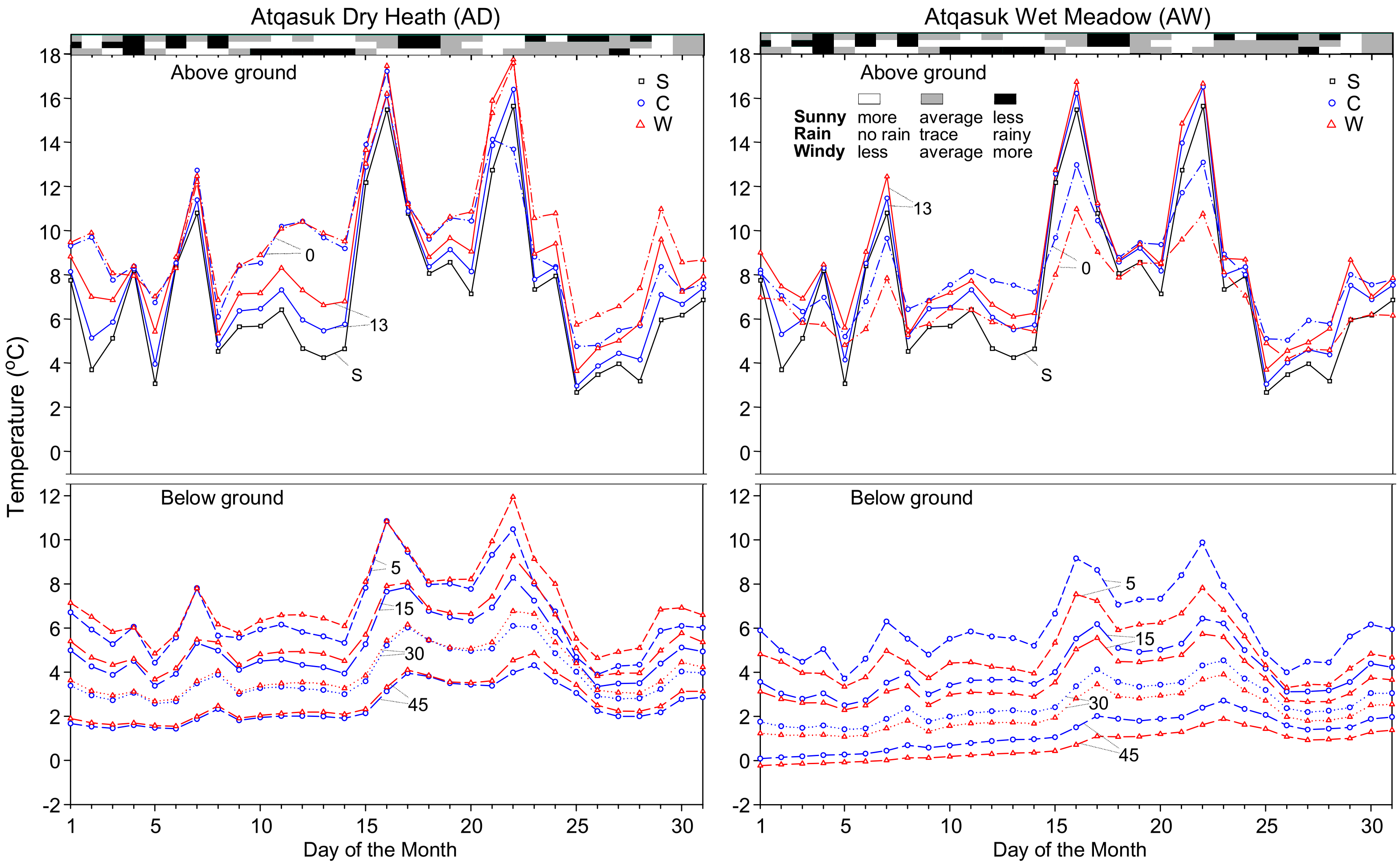

Figure II-5. Progression of daily average temperatures recorded in July of 2000 above (S - screen height 2 m, 13 cm, 0 cm) and below (5, 15, 30, 45 cm) control (C) and experimentally warmed (W) plots at the four study sites. The daily sun (***top***), rain (***middle***) and wind (***bottom***) conditions are displayed above the temperature graph according to the legend displayed in the figure.

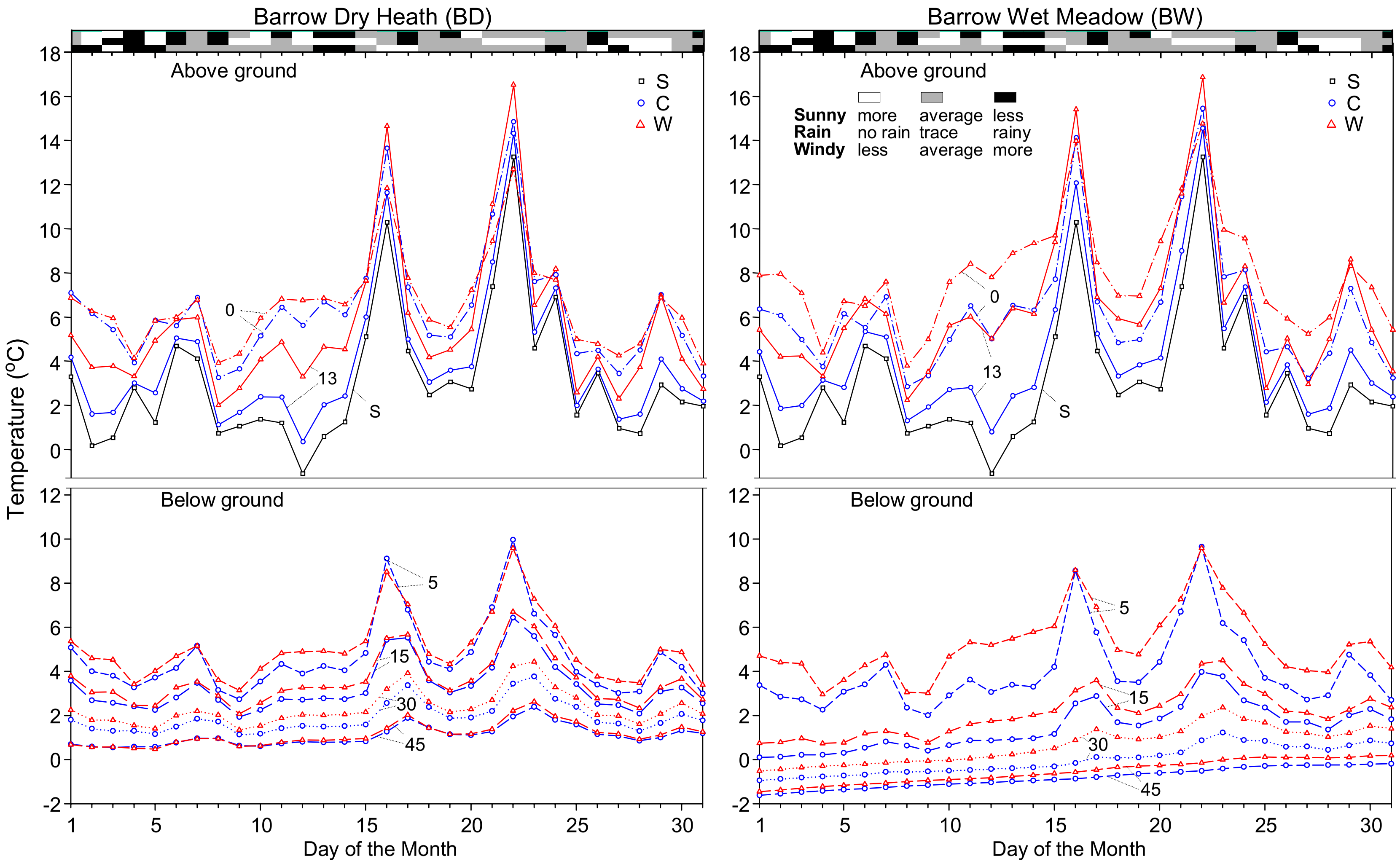

Figure II-5. Continued.

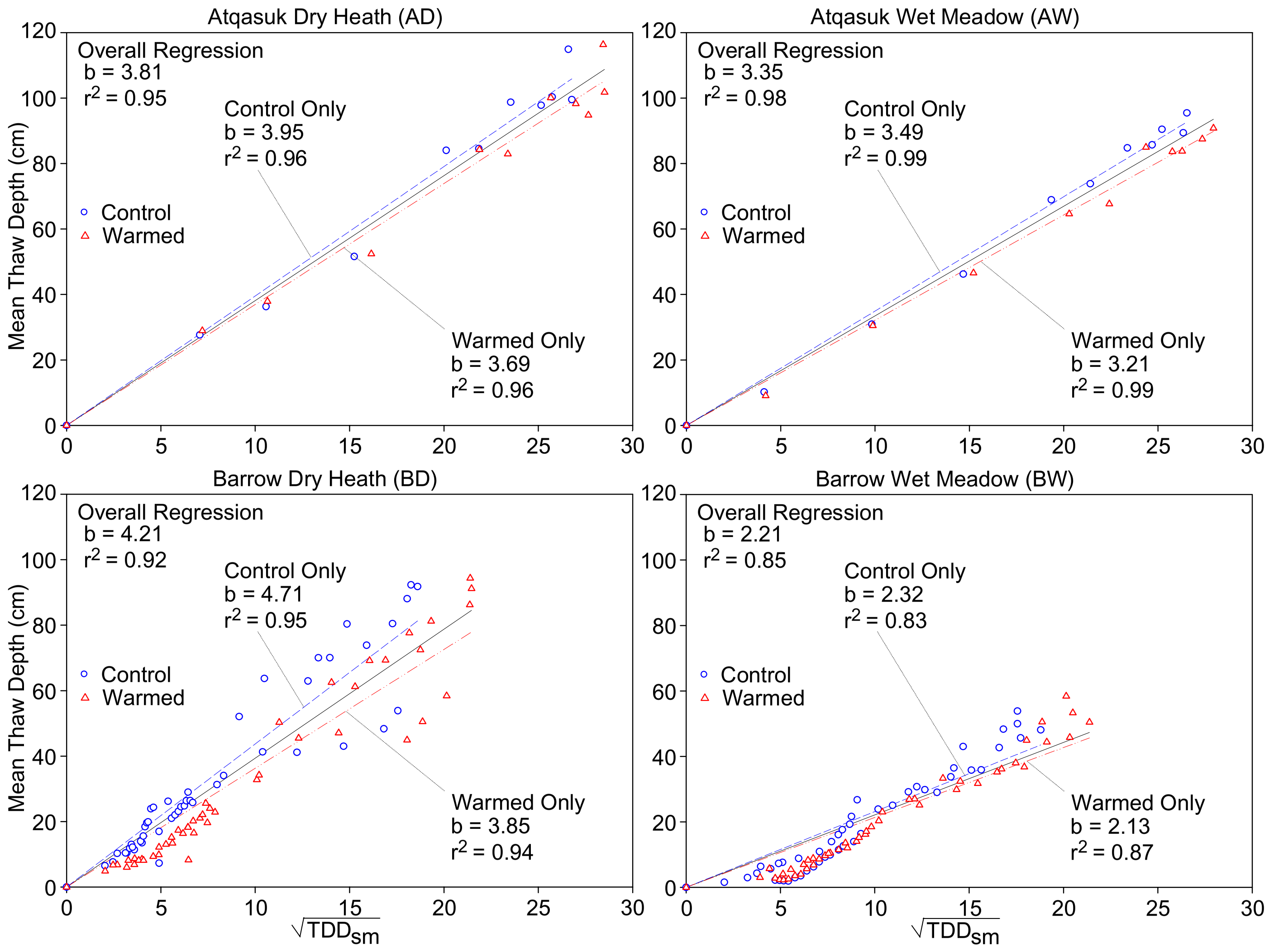

Figure II-6. The relationship between thaw depth and thawing degree-day totals since snowmelt (TDD_{sm}) recorded at canopy height (13 cm) at the four study sites. Thaw depths and TDD_{sm} are the average for each treatment on a given day.

analyzed by treatment. The site with the strongest relationship between thaw depth and sqrt(TDD_{sm}) was AW, followed by AD, BD, and BW. The slope of the line describing the relationship between thaw depth and sqrt(TDD_{sm}), used to calculate the edaphic factor or E value, was greatest for BD, followed by AD, then AW, and finally BW and within a site the slope was lower for the warmed plots relative to the control plots.

Table II-5. Average depth of thaw (cm) recorded at the end of the field season at all four sites (AD - Atqasuk Dry Heath; AW - Atqasuk Wet Meadow; BD - Barrow Dry Heath; BW - Barrow Wet Meadow) for control (C) and experimentally warmed (W) plots during the years 1994-2001. Values in parentheses are standard deviations.

	AD		AW		BD		BW	
	C	W	C	W	C	W	C	W
1994	·	·	·	·	·	·	·	·
1995	·	·	·	·	73.9(4.7)	72.5(4.8)	35.9(4.6)	36.8(5.5)
1996	99.5(6.9)	101.8(10.0)	89.4(11.7)	87.5(12.3)	88.1(5.2)	86.2(6.1)	48.1(7.3)	50.5(7.5)
1997	100.3(9.0)	94.8(17.0)	90.4(19.2)	83.8(19.6)	92.3(5.4)	91.2(6.7)	50.0(7.8)	53.3(9.2)
1998	·	·	·	·	·	·	·	·
1999	114.9(16.8)	116.3(9.1)	95.4(19.0)	90.8(15.6)	91.8(6.1)	94.3(6.4)	53.9(7.1)	58.4(7.2)
2000	98.7(11.5)	100.1(7.9)	84.8(11.1)	85.0(10.0)	80.5(5.0)	81.2(5.9)	48.3(8.9)	50.5(7.2)
2001	84.5(18.1)	82.9(7.9)	73.8(10.1)	67.7(19.9)	80.4(5.6)	77.6(5.5)	43.0(6.8)	44.9(6.8)
Avg	99.6	99.2	86.8	83.0	84.5	83.8	46.5	49.1

· no data

II.5 DISCUSSION

II.5.1 Site Microenvironments

A summary of the results characterizing the microenvironments of the four sites is provided below:

- Atqasuk growing seasons were on average 3.8-5.2 ^{o}C warmer than at Barrow.
- The total number of growing season TDD_{sm} was larger at Atqasuk than Barrow.
- Within a geographic region the temperature at 13 cm height and above was similar among community types.
- Canopy height temperatures were on average 0.4-0.9 ^{o}C higher than screen height temperatures during the growing season, yet there was little difference in daily minimum temperatures.
- The July average vertical profile of all the sites showed temperatures generally became warmer closer to the ground surface and became cooler with increasing depth below the surface.
- The dry study sites had earlier snowmelt and higher TDD_{sm} than the wet study sites within both regions.
- The average hourly temperature profile during July was different for each site. The largest difference was in the AW site where temperatures at the ground surface were damped due to standing water.
- The vertical distribution of average daily temperatures fluctuated throughout the growing season as did the relation between temperatures at various depths.
- The correlation between thaw depth and the square root of TDD_{sm} varied from a r^2 of 0.83 to 0.99 depending on the site.

The general description of summer temperatures for Barrow and Atqasuk was similar to the findings of Haugen and Brown (1980) who examined this relationship between 1975 and 1978. This study found Atqasuk to be on average 4.9 °C warmer at screen height than Barrow in July for the years 1999-2001, while Haugen and Brown found Atqasuk to be 5.3 °C warmer in years 1975-1978. The relationship between July average, maximum, and minimum temperatures recorded at canopy and screen height was similar even during years when Atqasuk screen height data were estimated from Barrow temperatures. This confirms that a strong relationship between Atqasuk and Barrow temperatures continues to exist. During both time periods there was considerable variation in July temperatures between years, but there was no warming trend in growing season temperatures from years 1994-2001 that may have been expected due to the documented 1.0-1.5 °C increase in summer air temperatures from 1949-1998 for the region (Stafford and Wendler 2000).

The similarity of canopy temperatures between sites was not anticipated due to the differences in site characteristics, particularly vegetation (*cf*. Ng and Miller 1977). Even at the ground surface temperatures were similar between sites within Barrow. The true effect of vegetation on temperature at the ground surface may have been under represented because the temperature probe was placed in a way that generally allowed direct exposure to sunlight. Tundra plant tissues have been shown to be 20 °C or more higher than screen temperatures during clear sky conditions, yet the range differences varies by organ and species (*e. g*. Bliss 1956, Warren Wilson 1957, Corbet 1972, Hansen 1973, Mølgaard 1982, Fischer and Kuhn 1984), and their influence on air temperatures likely diminishes greatly with distance. The temperatures recorded in this study may have been insulated from true plant canopy warming by height and the radiation shield that housed the sensor. The vertical and temporal distribution of temperatures was similar to previously reported tundra studies (*e. g*. Bliss 1956, Kelley and Weaver 1969, Corbet 1972, Weller and Holmgren 1974, Rouse 1984a,b,c), although detailed comparisons were not usually possible because previous studies usually presented only daily or weekly average temperature data for the vertical temperature profiles from one site in a geographic region.

Nearly all the detectable differences in microenvironment between sites occurred below ground. The transfer of heat within the soil varied greatly between sites. This was likely due to differences in soil thermal properties and soil moisture (Lord *et al*. 1972, Andersland and Ladanyi 1994, Paetzold *et al*. 2000). These differences resulted in different progressions of thaw between sites and consequently different relationships between thaw depth and TDD_{sm}. As expected, due to soil moisture content the dry heath sites thawed faster and more deeply than the wet meadow sites given the same amount of heating (as shown by the value of their edaphic factor – E value). The changing relationship between ground temperatures and screen height temperatures at the four sites is consistent with another study conducted in the region (Klene *et al*. 2001a). The daily variability in soil temperatures was also consistent with earlier work conducted in the region (*e. g*. MacLean and Ayres 1985). These daily and annual differences are important to consider when accurately characterizing the air or soil temperature profiles (Myers and Pitelka 1979). The variability in temperatures between days and years suggest that long monitoring periods are necessary to accurately portray average temperatures for a site particularly for ground surface temperatures.

II.5.2 Open-Top Chamber (OTC) Performance

A summary of the results necessary to characterize the performance of the OTCs in the four sites is provided below:

- The OTCs warmed average growing season air temperatures at canopy height between 0.6-2.2 °C depending on the site and year.
- Most of the OTC warming occurred during daily maximums and there was little to no change in daily minimums.
- The amount of relative change in growing season TDD_{sm} associated with OTC warming was greater in Barrow than Atqasuk due to fewer TDD_{sm} in Barrow.
- The OTCs decreased average growing season relative humidity at canopy height between 1.5-12.8% depending on the site and year.
- Most of the OTC decrease in relative humidity occurred during daily minimums and there was little or no change in daily maximums.
- The effect of the OTCs on soil temperatures was variable. In the AW site the OTCs cooled the soils, in the AD and BW sites the OTCs warmed the soils, and in the BD site the OTCs showed little difference in soil temperatures.
- The OTCs generally did not affect soil water content.
- The OTCs did not affect thaw depth.
- The amount of OTC canopy warming varied greatly by day presumably due to differences in sky conditions, wind, and precipitation.
- The amount of daily OTC soil warming or cooling responded to different cues than canopy warming.

- Differences seasonal weather conditions resulted in differences in the amount of OTC warming between years within a site.

The review of OTC performance by Marion *et al*. (1997) reported observations similar to those documented in this study (see Section II.2). Unlike previous studies, this study found many of the observed differences in chamber performance were due to differences in the microenvironments of the communities on which they were placed. Previous studies were unable to make this determination because of difficulties in comparing different chamber types and different measurement protocols. Although not empirically tested in this study, the relative importance of direct solar radiation and wind on ground surface temperatures is probably very different within the four sites. In all four sites, OTCs warmed the canopy temperatures and most of the warming occurred during mid-day with very little warming occurring during the night. Yet, at ground surface the effect of the OTCs was different. These differences were likely primarily due to differences in plant cover and standing water. Where plant cover was nearly complete in the BW site, ground surface temperatures were on average higher in the OTCs. Where plant cover was lower and there was exposed ground in the BD site, the ground surface temperatures in the OTCs was lower during mid-day probably due to partial shading by the chamber walls. The AD site also had bare ground but the lighter color and presumably higher albedo of the sandy soils probably reduced the direct impact of radiative warming due to higher reflectivity. Where there was standing water the reduction of wind and shading of the OTCs probably contributed to cooling. Other studies have also found differences in chamber soil warming between field sites (Coulson *et al*. 1993, Wookey *et al*. 1993, Marion *et al*. 1997).

The performance of chambers is of greatest interest when comparing the biological response from chamber warming experiments. When making comparisons, it is important to recognize that the treatments themselves may have performed differently between sites and year. For example, based on the variable amount of OTC warming, one would predict that the response of plants would be least in the AW site and greatest in the BW site and all sites would have had the least response in year 2000. The mechanisms contributing to observed biological response might also vary between sites. Several researchers believe below ground processes leading to increased nutrient availability contribute greatly to observed plant response to warming (Chapin 1983, Wookey and Robinson 1997, Shaver and Jonasson 1999). Yet, in these four sites the below ground response to chambers varied considerably making it difficult to generalize about the influence of below ground dynamics. Therefore, when differences between treatments are not addressed in analysis of multiple sites the variability in the results may be inflated and this may lead to misinterpretation of mechanisms driving plant response.

The most likely reason why OTCs appear to have little to no effect on depth of thaw is the small size of the chambers. When soil temperatures were changed under OTCs, the effect decreased with depth and is commensurate with other studies (Zhang and Welker 1996, Marion *et al*. 1997). Under larger close-top chambers thaw depths have been shown to increase (Chapin *et al*. 1995, Bret-Harte *et al*. 2001). The apparent disconnection between canopy and soil warming could be considered a drawback of OTC warming. However, there is not a constant natural association between regional temperatures measured at screen height and soil temperature (Kennedy 1997, Klene *et al*. 2001a). Therefore, the disconnection between soil and canopy temperatures observed in many chamber studies may not conflict with future climate scenarios. Furthermore, where canopy warming occurs in the absence of soil warming this allows a unique opportunity to study direct temperature effects that are less altered by indirect temperature effects on below ground processes.

The effects of herbivores and pollinators were not explicitly tested in this study. However, chambers have been shown to influence herbivores or pollinators at several locations (*e. g*. Jones *et al*. 1997, Totland and Eide 1999, Richardson *et al*. 2000, Molau 2001) and a few general comments are warranted. In Barrow and Atqasuk herbivory in the sites was primarily due to lepidoptera and lemmings, was patchy, and was not noticeably influenced by the OTCs (personal observations). The only exception was that occasionally in Atqasuk ptarmigan would visit the sites and eat the inflorescences of plants growing in control plots but they would not enter an OTC or graze on the plants within them. Caribou are present in both regions but avoided the sites during the growing season due to the continual presence of researchers. In the winter their disturbance was equally distributed among treatments. There were no obvious differences in pollination between treatments in any of the sites (personal observations). The influence of OTCs on herbivores and pollinators is variable among sites and may need to be accounted for in interpretation of plant response to OTC warming (Totland and Eide 1999, Richardson *et al*. 2000). However, in these four sites it was not considered necessary.

The amplification of the range of daily temperatures due to a disproportional increase in daily maximum temperature, the reduction of wind, and the potential uncoupling of soil and canopy temperatures in the chambers are inconsistent with climate change forecasts (Kennedy 1995b,c, Houghton *et al*. 2001). Experimental artifacts are not unique problems of OTC warming. Even continually monitored mechanical heating devices such as soil heating cables (Hiller *et al*. 1994, Oberbauer *et al*. 1998) and infrared heaters (Nijs *et al*. 2000) have their drawbacks beyond the obvious financial costs and necessary infrastructure to maintain. These devices can provide a specified amount of warming, but they may also create non-natural vertical temperature profiles, and other unwanted experimental artifacts such as soil drying (Harte *et al*. 1995). The lack of true control and the propensity for experimental artifacts is a tradeoff inherent to *in situ* field studies. As with all field studies it is important to properly document and address any potential experimental artifacts.

Clearly OTCs and other chambers modify microenvironments in ways that are inconsistent with future climate change scenarios and results from warming experiments should not be applied *en bloc* toward biological change forecasts. Yet results from warming experiments can provide valuable insight into mechanisms of biological change if interpreted correctly. The interpretation of results from warming experiments is severely hampered if the performance of the warming mechanism is not well documented. Therefore, all warming experiments should continually monitor the performance of the warming manipulation.

II.5.3 Concluding Remarks

It is important to monitor microclimate over several years because the relationships between various components of the microenvironment change with different weather conditions. Even when the relationships between regional weather and microenvironment have been established, regional weather can often only be used to approximate the microenvironment of interest because the relationships are intricately related to many weather parameters.

When using chambers to manipulate microenvironments, it is important to document the response in each site and each year, because the response can be highly variable. Interpretation of biological response to chamber warming must consider all potential chamber effects when theorizing about underlying mechanisms and forecasting change.

II.6 ACKNOWLEDGEMENTS

We thank the US National Science Foundation, Office of Polar Programs, Arctic System Science Program for its support of this work (OPP # 9714103), and the many people responsible for collecting and organizing the data particularly Christian Bay, Lisa Walker, and Steve Rewa. We also thank our many ITEX colleagues for sharing their insights.

Chapter III

BIOTIC VALIDATION OF SMALL OPEN-TOP CHAMBERS IN A TUNDRA ECOSYSTEM

III.1 ABSTRACT

Small open-top chambers (OTC) are widely used in ecosystem warming experiments. The efficacy of the open-top chamber as an analog of climatic warming is examined. Twenty-four small OTCs were used to passively warm canopy temperatures in wet meadow tundra at Barrow, Alaska during two consecutive summers with contrasting surface air temperatures. Fortuitously, the seasonal average temperature regime within chambers in the colder year (1995) was similar to the controls of the warmer year (1996); this allowed a comparison of natural versus chamber warming. Measured plant responses behaved similarly to both year and treatment 68% of the time. A comparison of the populations of the warmer summer's control with the cooler summer's OTC found no statistical difference in 80% of the response variables measured. A meta-analysis also found no significant difference between the responses of the two populations. These results give empirical biotic validation for the use of the OTC as an analog of regional climate warming.

III.2 INTRODUCTION

Recently, there has been considerable interest in temperature relations of species in response to predicted global temperature rise (Henry and Molau 1997, Thornley and Cannell 1997, Sykes *et al.* 1999, Walker *et al.* 1999b). Increasingly researchers are using devices to manipulate temperature in a variety of habitats in order to forecast responses of species to climate change (Farnsworth *et al.* 1995, Harte & Shaw 1995, Kennedy 1995, Marion *et al.* 1997). This is particularly true in arctic tundra in light of the magnitude of predicted temperature change in this region (Houghton *et al*. 1996, Maxwell 1997) and the perceived dominant role of temperature in structuring tundra communities (Bliss *et al.* 1973, Wielgolaski 1997).

This report arises from an ongoing study of the response of tundra plants to warming. It was begun in 1994 (Bay 1995). This study uses open-top chambers (OTCs) to create the desired warming.

The use of chambers has been one of the favored manipulative tools to experimentally increase temperatures in the field (Kennedy 1995b). This is particularly true in relatively inaccessible localities such as the Arctic and Alpine (Debevec and MacLean 1993, Molau and Mølgaard 1996). OTCs have the desirability of being passive warming devices that do not require technological maintenance. The open-top design, which is not sealed to the ground, allows free air exchange and minimizes undesirable chamber effects including low light levels, temperature extremes, unnatural precipitation, unnatural gas and humidity concentrations, exclusion of pollinators, and access of herbivores (Marion 1996). Yet, it is known that OTCs do modify the microenvironment in a multitude of ways and, as such, this makes it imperative to document the performance of the chamber in the environment of its use in order to interpret plant response (Kennedy 1995b, Marion 1996, Hollister 1998). Kennedy (1995b) urged that the use of passive greenhouses for testing the biological effects of environmental perturbations requires careful *a priori* testing and evaluation without which doubts are cast on the usefulness of the measured biotic responses and their application in extrapolation. The objective of this chapter is to address these concerns and to assess the validity of using the OTC as an analog of regional climate warming in a tundra system.

Fortuitously, the warming caused by chambers in this study was similar in magnitude to the natural difference in temperatures between the two summers of 1995 and 1996. This created an opportunity to test the efficacy of the chambers as a temperature enhancement device. If the plants respond similarly to both treatment and year, then it is reasonable to conclude that the plants are responding primarily to temperature. This work is part of the International Tundra Experiment (ITEX) (see Global Change Biology Volume 3, Supplement 1, December 1997).

III.3 METHODS

III.3.1 Study Site

The study site was located on the Barrow peninsula of Alaska (71°18'N 156°40'W) within a wet meadow community dominated by *Carex aquatilis/stans*, *Eriophorum* sp., *Dupontia fisheri*, *Calliergon giganteum*, and *Sarmenthypnum sarmentosum* (Section I.5.1-2). The site is referred elsewhere in the dissertation as the Barrow Wet Meadow (BW) site. The site was in a transition zone between a drained lake basin and a former raised beach ridge. The site elevation above mean sea level was 3 ± 0.5 m. The substrate was fine silt and the soil was a histic pergelic cryaquept with poor drainage (Section I.5.3-2). The vegetation of the Barrow region is described by Britton 1957 and Webber *et al.* 1980 (also see Section I.5.1-2).

III.3.2 Experimental Plots and Chamber Design

The data presented here were collected during the growing seasons of 1995 and 1996. Twenty-four control and 24 experimental designations were assigned randomly from predetermined plots within a distance of 300 meters (Section I.5.3).

The open-top chambers (OTCs) are hexagonal with sloping sides constructed of Sun-Lite HP^{TM} fiberglass (Solar Components Corporation, Manchester, New Hampshire). This material is commonly used in horticultural applications due to its high transmittance of visible wavelengths (86%) and low transmittance of infrared (<5%) (Molau and Mølgaard 1996). The chambers are 35 cm tall and the distance between parallel sides is 103 cm at the base and 60 cm at the top (Figure I-17). For additional details on the OTCs see Section I.5.2-3. Marion *et al.* (1993, 1997) described the general performance of the OTCs and Hollister (1998) documented their performance at Barrow (also see Chapter II).

III.3.3 Vascular Plant Monitoring

Three individuals, where possible, of each species present were permanently tagged and monitored in each plot. The date of first flowering along with other plant developmental attributes was followed throughout the field season (Section I.5.4-4). Vigor measurements (length of inflorescence, length of longest leaf, and number of leaves) were measured at the end of each field season which is approximately August 18 and when species began to enter dormancy or senescence (Miller *et al.* 1980). The average rosette diameter was substituted for the length of longest leaf in *Draba lactea* and *Saxifraga foliolosa*. Measurements where collected in accordance with established protocols (ITEX Manual, Molau 1993). A vegetative response measure was calculated from the product of leaf length and number of leaves per plant.

III.3.4 Microenvironment Monitoring

Hobo® and StowAway™ temperature thermistors and loggers (Onset Inc., Pocasset, Massachusetts) were installed in ventilated radiation shields at approximately 13 cm above the ground (Section I.5.4-2). The number of sensors varied but was not less than 7 per treatment. Data loggers were set to record at 12 to 80 minute intervals, depending on the sensor type, from the date of snowmelt or soon after until August 18. [Note: August 18 was the last day in common that data were collected in the BW site in 1995 and 1996; August 15 was the last day in common that data were collected in all the sites during every year.] Soil thaw depths were measured at least every 10 days by penetration with a slender metal rod (Section I.5.4-3).

III.3.5 Thawing Degree-Day Calculation

Thawing degree-days were used to represent seasonal heat accumulation. This was based on the observation that at Barrow 0 °C is generally the cardinal temperature at which growth begins (Dennis *et al.* 1978, Miller *et al.* 1980). Thawing degree-day totals from snowmelt ($\mathrm{TDD}_{\mathrm{sm}}$) was calculated by using the temperature data collected from selected plots measured at the finest time scale available. Degree-day totals from snowmelt until thermistor installation were estimated from standard screen temperature data provided by the National Ocean and Atmospheric Association (NOAA) Climate Monitoring and Diagnostics Laboratory (CMDL)(Stone *et al.* 1996).

III.3.6 Data Analysis

The experiment used a non-orthogonal randomized design with subsampling. Plots were used as experimental units and multiple individuals within a plot were used as observational units. Analysis of variance (ANOVA) was run on a species per variable basis. The homogeneity of the variances for all analyses was tested. In many cases this assumption was violated and the analyses were rerun with weighted averages adjusted by the population's standard deviation. In no cases were the conclusions different for the two analyses. An outcome was deemed statistically significant if the probability for a Type I Error was 5% or less. Statistical tests at the species level were performed using SAS (SAS Institute 1996a). Analyses of the response variables were run identically for all species.

An analysis of variance with unbalanced sample sizes was used to compare populations from the 1995 OTCs with the 1996 controls. Multiple comparisons were performed with Fisher's LSD (least significant difference) and Tukey's HSD (honestly significant difference) (SAS Institute 1996b). In all cases the significances were similar for the two analyses.

Meta-analyses were run in MetaWin 2.0 (Rosenberg *et al.* 2000). Meta-analysis has recently gained favor in ecology due to their ability to integrate a variety of existing and published analyses (Gurevitch *et al.* 1992). Meta-analysis is able to analyze net responses rather than the original data, and is of benefit in this case where individual species responses may not be comparable due to large differences in species morphology. All analyses were run using Hedge's D and a random effects model. The mean effect size was calculated for all analyses; it represents the magnitude of the experimental effect. Effect sizes of 0.2, 0.5, and 0.8 represent small, medium, and large response, respectively (Gurevitch *et al.* 1992). The meta-analysis for all measures for all species excluded the metric Julian day of flowering, instead flowering was accounted for in terms of TDD_{sm}; this was based on the assumption that the large differences in Julian day of flowering was directly attributable to a 10 day earlier snowmelt in 1996.

The percentage of individuals that responded similarly were calculated by summing the number of occurrences for the appropriate category from the data presented in Tables III-2 (excluding the TDD_{sm} data) or III-3 and dividing by the total number of occurrences.

III.4 RESULTS

III.4.1 Microenvironment

Table III-1 compares the temperature of the standard meteorological screen with the microclimate of controls and chambers for the two years of the experiment. The 1996 growing season began two weeks earlier than that of 1995 (Figure III-1). The 1996 growing season was also warmer with the average screen temperature greater by 0.5 °C and the canopy temperature greater by 1.2 °C. The mean and maximum temperatures in the plant canopy were greater than those of the screen by 0.4 and 1.1 °C respectively. The mean minimum temperatures of the canopy in controls and OTCs are between 0.3 and 1.0 °C less than the minimum screen temperature. The chambers increased canopy temperature on average by 1.9 °C in 1995 and 1.4 °C in 1996. There was also an increased temperature variation in the OTCs (Walker 1997, Hollister 1998).

Table III-1. A comparison of summer average, maximum, and minimum daily temperature and relative humidity of OTC plots, control plots, and climate data of the nearby National Ocean and Atmospheric Administration (NOAA) station in Barrow. Control and OTC measurements were made at *ca*. 13 cm above soil surface. NOAA data is from a standard meteorological screen. Data are from snowmelt until August 18 for 1995 and 1996.

		NOAA		Control		OTC	
		1995	1996	1995	1996	1995	1996
Precipitation (mm)		18	33	·	·	·	·
Temperature (^{o}C)	mean	3.2	3.7	3.6	4.8	5.5	6.2
	max	6.0	7.7	7.7	9.4	12.2	13.2
	min	1.4	1.0	0.4	0.7	0.8	0.7
Relative Humidity	mean	89.8	89.1	·	89.1	·	76.5
	max	98.8	98.2	·	95.6	·	89.3
	min	·	·	·	80.5	·	63.1

· no data

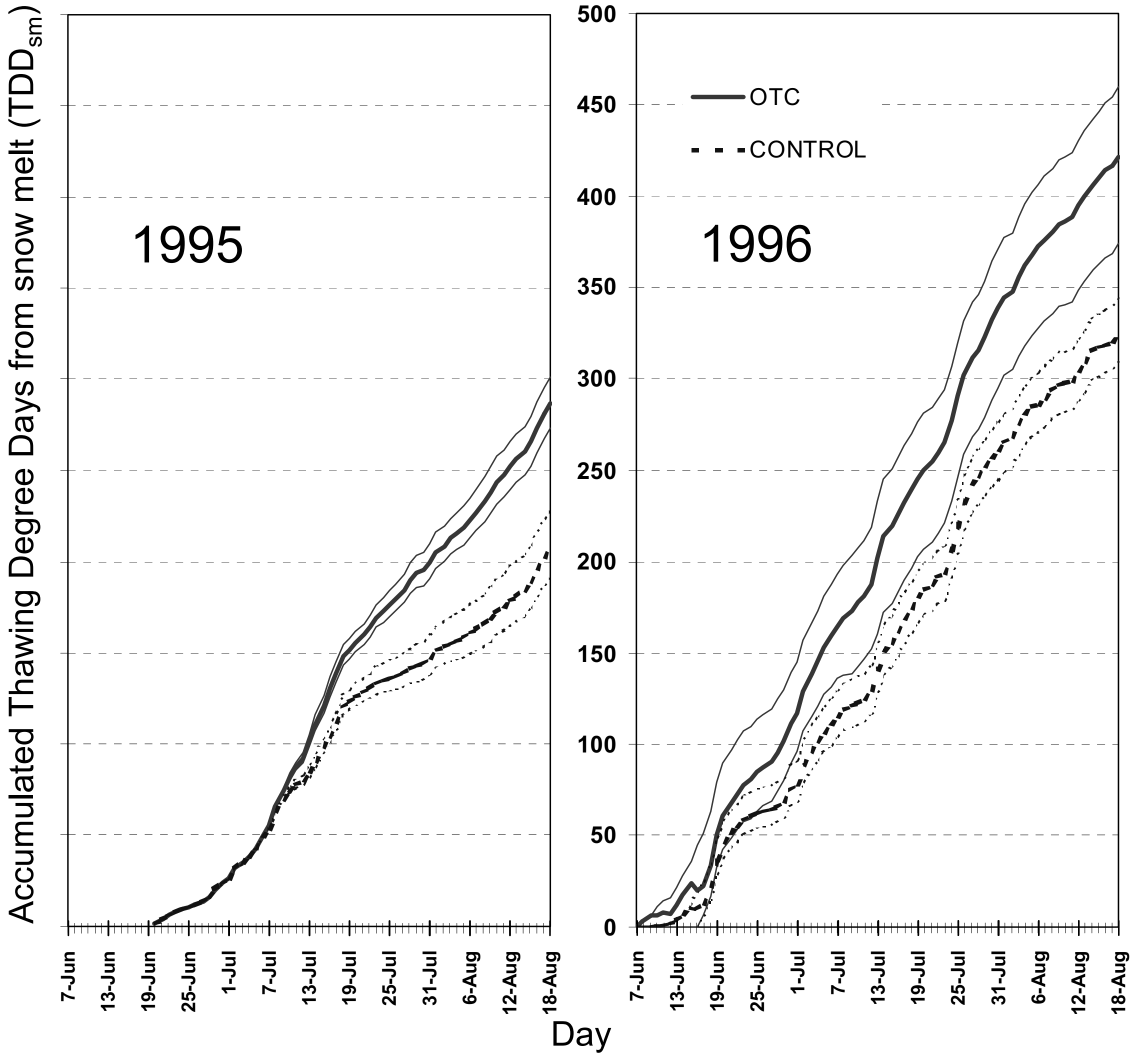

Figure III-1. Mean (*thick line*) and range (*thin lines*) thawing degree-day totals from day of snow melt (TDD$_{sm}$) for the field seasons 1995 and 1996 for the control plots and the chamber plots (OTC) in a wet meadow tundra in Barrow, Alaska ($n \geq 7$).

The earlier snowmelt and higher canopy temperature within the chambers caused approximately 38% and 30% increase in total thawing degree-days from snowmelt (TDD_{sm}) until 18 August in the years 1995 and 1996 respectively (Figure III-1). Differences in TDD_{sm} among plots were greater in the OTCs than in the controls.

The thermal regimes of the 1995 OTCs and 1996 controls as shown by temperature and TDD_{sm} are similar. Mean temperature and mean end-of-season TDD_{sm} for the 1995 OTCs and 1996 controls were 5.5 and 4.8 ^{o}C and 287 and 324 TDD_{sm}, respectively. This compared with the contrasting values of 3.6 and 6.2 ^{o}C and 208 and 422 TDD_{sm} for 1995 controls and 1996 OTCs, respectively.

Precipitation was greater during the growing season of 1996 than that of 1995 (Table III-1). The canopy relative humidity (RH) of the controls is similar to the RH of the screen while the canopy RH for the OTC is less than that of the control, which is in accordance with the higher temperatures. Depth of soil thaw was greater in 1996, but there was no significant difference in depth of thaw between treatments in either year (Hollister 1998).

III.4.2 Plant Response to Years and Chambers

All species flowered significantly earlier in 1996 than in 1995, and 50% of the species flowered significantly earlier in the chambers during those years (Table III-2). The meta-analysis of all species found that year and treatment differences were significant. In all but two species, *Eriophorum triste* and *Juncus biglumis,* the average date of flower opening was earlier in chambers than the control of that season. This difference was significant for *Dupontia fisheri*, *Luzula arctica*, *Luzula confusa*, *Hierochloe pauciflora*, and *Saxifraga hirculus*. The two species that flowered later in the chambers in 1995, *E. triste* and *J. biglumis*, flowered earlier in the OTCs in 1996. *Juncus biglumis* was the only species to show a significant year-treatment interaction.

Interannual variability was found to be less significant across species for the date of flower opening when analyses were run using TDD_{sm} instead of Julian day (Table III-2). *Draba lactea, D. fisheri, H. pauciflora*, *J. biglumis*, *Saxifraga hieracifolia*, and *S. hirculus* showed that year had a significant effect on the TDD_{sm} of flowering. The meta-analysis of all species found year and treatment to be significant. For all species in a given year it took, on average, more TDD_{sm} for flowering to occur in chambers. For 50% of the species this effect was statistically significant. The difference between treatment and controls were similar in mean effect size when flowering was calculated in terms of Julian day or TDD_{sm} with values of 0.89 and 0.67 respectively. The mean effect size for year was greater when calculated in terms of Julian day with values of 0.34 and 2.68 for TDD_{sm} and Julian days, respectively.

Of the species for which the number of flowers was counted, 71% responded to either interannual variability or to chambers, but none responded to both (Table III-2). The three species, *D. fisheri, Saxifraga cernua*, and *Saxifraga foliolosa* produced significantly more flowers in the warmer year and *Carex aquatilis/stans* and *H. pauciflora* flowered significantly more in the chambers. *Cardamine pratensis* and *S. hirculus* did not respond to the chambers or to interannual variation. The meta-analysis of all species found year and treatment effects to be significant. The average number of flowers was found to be greater in the controls than in chambers for *D. fisheri* and *S. hirculus* in 1996.

The length of inflorescence was consistently greater during the warmer field season and within the chambers (Table III-2). The meta-analysis of all species found both year and treatment to be significant; the mean effect size for year and treatment was 0.86 and 0.89, respectively. All but two species, *E. triste* and *S. hirculus*, responded significantly to both treatment and year. For all species the average inflorescence was longer in the chambers and during the warmer summer.

There was no consistent pattern in leaf length response to chambers or years across species (Table III-2). Only *C. pratensis* responded significantly to chambers and year but the magnitude of response was small. *Saxifraga hieracifolia* and *C. aquatilis/stans* responded significantly to year but not chambers. The meta-analysis of all species found no effect of treatment or year.

In terms of the vegetative measure (leaf length x leaf number), *C. pratensis* and *E. triste* showed significant response to both year and treatment while *C. aquatilis/stans* and *S. hieracifolia* showed significant responses to year but not treatment (Table III-2). The meta-analysis of all species found a significant difference between treatment and year.

The meta-analysis of all the measures of all the species found year and treatment to be significant and of moderate effect size. The mean effect size was calculated to be 0.43 (0.31-0.55 Confidence Interval of 95%) for year and 0.49 (0.39-0.59 Confidence Interval of 95%) for treatment. Of the 44 response variables measured for both year and treatment there were 17 cases where species responded similarly to both year and treatment, 1 case where a species responded to year and treatment but in opposite directions, 13 cases where species responded to year but not treatment, 1 case where the species responded to treatment but not year, and 13 cases where species did not respond to either year or treatment (calculated from Table III-2 excluding TDD_{sm} data). Thus, for all the measures recorded 68% of the time a species behaved similarly to year and treatment (either responded similarly or did not respond to both). If a species responded to treatment or year, then in 53% of the cases it responded to both.

Table III-2. Differences between years (1995 and 1996) and treatments (OTC and control) for species monitored in wet meadow tundra at Barrow, Alaska. All responses were positive in relation to warmth (i.e., earlier flowering, greater numbers of flowers, longer inflorescence, longer leaf, and greater leaf length x no. of leaves) except for one instance (Γ). The meta-analysis (*last line*) determines if there is a net difference across all the species. Mean effect size is shown when the results from the meta-analysis were significant. Effect sizes of 0.2, 0.5, and 0.8 represent small, medium, and large responses, respectively.

	Julian Date of Flowering		TDD_{sm} of Flowering		Number of Flowers /plot		Length of Inflorescence		Length of Leaf		Leaf Length x no. of Leaves	
Species	Year	OTC	Year	OTC	Year	OTC	Year	OTC	Year	OTC	Year	OTC
Cardamine pratensis	—	—	—	—	nsd	nsd	—	—	Θ	Θ	Θ	Θ
Carex aquatilis/stans	Θ	nsd	nsd	nsd	nsd	Θ	Θ	Θ	Θ	nsd	Θ	nsd
Draba lactea	Θ	nsd	Θ	Θ	—	—	Θ	Θ	nsd	nsd	—	—
Dupontia fisheri	Θ	Θ	Θ	Θ	Θ	nsd	Θ	Θ	nsd	nsd	nsd	nsd
Eriophorum triste	Θ	nsd	nsd	Θ	—	—	nsd	nsd	nsd	nsd	Γ	Θ
Hierochloe pauciflora	Θ	Θ	Θ	Θ	—	Θ	Θ	Θ	—	—	—	—
Juncus biglumis	Θ	nsd	Θ	Θ	—	—	Θ	Θ	—	—	—	—
Luzula arctica	Θ	Θ	nsd	nsd	—	—	Θ	Θ	nsd	nsd	—	—
Luzula confusa	Θ	Θ	nsd	nsd	—	—	Θ	Θ	nsd	nsd	—	—
Saxifraga cernua	—	—	—	—	Θ	nsd	Θ	Θ	nsd	nsd	nsd	nsd
Saxifraga foliolosa	—	—	—	—	Θ	nsd	Θ	Θ	nsd	nsd	—	—
Saxifraga hieracifolia	Θ	nsd	nsd	Θ	—	—	Θ	Θ	Θ	nsd	Θ	nsd
Saxifraga hirculus	Θ	Θ	Θ	Θ	nsd	nsd	Θ	nsd	—	—	—	—
Meta-Analysis	2.68	0.67	0.34	0.89	0.63	0.33	0.86	0.89	nsd	nsd	0.27	0.20

— no comparison possible nsd no statistical difference Θ or Γ statistical difference (*p*-value <0.05)

III.4.3 Comparison of Plant Response of the 1995 Chambers with the 1996 Controls

The meta-analysis of all measures for all species found that there was no significant difference between the 1995 OTC data set and the 1996 control data set (mean effect size of $^{-}$0.07 with a 95% Confidence Interval of $^{-}$0.22-0.09). Of the 44 response variables measured for each species there were only 9 cases where the 1995 OTC population was significantly different from the 1996 control population; thus, 80% of the cases there was no difference in response between the two populations (Table III-3).

Table III-3. Population means of the 1995 OTC compared with the 1996 control in wet meadow tundra at Barrow, Alaska. The meta-analysis (*last line*) determines if there is a net difference across all the species. Mean effect size from the meta-analysis is shown when the result of the analysis is significant.

Species	TDD$_{sm}$ of Flowering	Number of Flowers /plot	Length of Inflorescence	Length of Leaf	Vegetative Measure
Cardamine pratensis	—	nsd	—	nsd	nsd
Carex aquatilis/stans	nsd	nsd	nsd	Θ	Θ
Draba lactea	Θ	—	nsd	nsd	—
Dupontia fisheri	nsd	Θ	nsd	nsd	nsd
Eriophorum triste	nsd	—	nsd	nsd	nsd
Hierochloe pauciflora	nsd	—	nsd	—	—
Juncus biglumis	Θ	—	nsd	—	—
Luzula arctica	nsd	—	nsd	nsd	—
Luzula confusa	nsd	—	Θ	nsd	—
Saxifraga cernua	—	Θ	nsd	nsd	nsd
Saxifraga foliolosa	—	nsd	nsd	nsd	—
Saxifraga hieracifolia	nsd	—	Θ	nsd	Θ
Saxifraga hirculus	nsd	nsd	nsd	—	—
Meta-Analysis	0.11	nsd	nsd	nsd	nsd

— no comparison possible   nsd no statistical difference   Θ statistical difference (*p*-value <0.05)

III.5 DISCUSSION

The phenological and growth responses to warming reported here are generally commensurate with those reported by other studies (e.g., Sørensen 1941, Chapin *et al.* 1995, Arft *et al.* 1999). Nevertheless, these findings are site specific and the interpretation and application of plant responses to OTCs must be considered with caution (Kennedy 1995b, Hollister 1998).

The date of flowering appears to be closely controlled by temperature. When flowering was examined in terms of calendar date (Julian days) there was a very large effect of year and a moderate effect of treatment. The large year effect was likely more of a response to the date of snowmelt than to temperature. If the only variable controlling flowering was heat accumulation, then flowering should occur on the same TDD_{sm}. Clearly this is not the case, but the effect size of year is notably less in terms of TDD_{sm} than calendar date; this indicates that TDD_{sm} is a better predictor of flowering than Julian day. The effect size of treatment increased when expressed in terms of TDD_{sm}. This could be a result of the increase in the daily range of chamber temperatures towards the maximum, which may infer a different pattern of heat accumulation encountered by plants in the chambers. It could also be due to a balance between warmth accumulation and developmental time requirements or biological cues in the plants that the chambers do not affect. Higher TDD_{sm} for phenologic progression were also reported for the dry heath community at Barrow (Walker 1997).

The vigor indices show that the species responded similarly to the warmer canopy temperatures whether this was due to interannual variability or chambers. All vigor indices except for leaf length appeared to respond to temperature. This is in agreement with other studies (e.g., Graglia *et al*. 1997, Jones *et al*. 1997, Stenström and Jónsdóttir 1997, and Welker *et al*. 1997). Elsewhere we have shown that an increase in plant stature was the most consistent plant response to increased temperature (Hollister 1998). The mean effect size of the length of inflorescence was large and nearly identical for both year and treatment (year = 0.86, treatment = 0.89). Variability in inflorescence length was greatest in chambers (Hollister 1998). This may be due to the increased variability of temperature in chambers.

The response in the number of flowers was variable. No species responded significantly to both chambers and the warmer year. This may be due to the fact that most arctic plant species have extended bud formation requirements and flower episodically (Sørensen 1941, Savile 1972). If a plant flowered in the chambers in the cooler year of 1995 in response to chamber warming, then it may have been unable to produce significantly more pre-formed flowers for the following year. All species measured had more flowers in the chambers during the first year of the experiment. In addition, all of the species that were monitored in the control plots had more flowers during the warmer field season of 1996. This suggests that preformation is important and may explain the lack of response in the chambers relative to the controls in the second year of the experiment.

Overall, species responses to chambers and interannual variability in temperature were similar. Both show a modest response, with a mean effect size of 0.43 and 0.49 for year and treatment, respectively. For all measured responses 68% of the time a species behaved similarly to year and treatment (i.e. a species either responded to both or did not respond to both; Table III-2). If a species responded significantly to year or treatment, then 53% of the time the species responded to both. Furthermore, from a comparison of the populations of the 1995 chambers with the 1996 controls, for all the species-measures combinations, 80% of the responses were not different (Table III-3). The meta-analysis of all the measures for all the species found no significant difference between the 1995 OTC and 1996 control data sets.

The similarity of results is remarkable considering the interannual differences in active layer thickness, date of snowmelt, precipitation, and other climatic attributes such as varying sky conditions that may have caused differences between year and treatment effects. These findings also indicate that chamber deficiencies including shading, access of pollinators and herbivores, changes in daily temperature range, soil-air relations, and wind were not dominant factors in this community during this short-term experiment. Nevertheless, in long-term experiments artifacts introduced by the chambers may be significant.

III.5.1 Concluding Remarks

This study found that the short-term response of the studied species was similar to their response to natural temperature interannual variability and concurs with the general observation that tundra vascular plant species respond directly or indirectly to increased temperature particularly by flowering earlier and growing larger. These results empirically validate the use of chambers as an analog of regional warming in wet meadow tundra at Barrow, Alaska. Therefore, it is reasonable to conclude that the long-term plant response to chambers may be useful in forecasting plant responses to regional warming, although since they are not perfect surrogates of natural variation caution is warranted. Information gained from warming experiments such as this should be synthesized with information on natural temperature gradients and plant biology. The combination of these results is necessary to form fundamental biological understanding of plant temperature relations, which can subsequently be used to forecast plant response to global climate change.

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Chapter IV

PLANT RESPONSE TO TEMPERATURE IN NORTHERNMOST ALASKA: IMPLICATIONS FOR PREDICTING VEGETATION CHANGE

IV.1 ABSTRACT

The response of tundra vegetation to variation in temperature due to natural temperature gradients, interannual variability, and experimental warming was examined at sites near Barrow ($71^{o}18'$N $156^{o}40'$W) and Atqasuk ($70^{o}29'$N $157^{o}25'$W) in northern Alaska. At each of the four sites 24 plots were experimentally warmed with small open-top chambers and plant growth and phenology were monitored; an equal number of un-manipulated control plots were monitored. The response of 7 traits from 32 plant species occurring in at least one of four sites is reported when there were at least 3 years of recordings. Plants responded to temperature in 130 of 267 observations (49%) of a trait of a species in a site. The most common response to warming was earlier phenological development and increased growth and reproductive effort. The response of a species was individualistic and varied among sites. In 37 of 267 observations (14%) the plant trait was correlated with thawing degree-day totals from snowmelt (TDD_{sm}) and temperature was considered the dominant factor. In 73 of 267 observations (35%) the plant trait responded to warming but the interannual variation in the trait was not correlated with TDD_{sm} and temperature was considered subordinate to other factors. It is well established that temperature affects the functioning and ultimate distribution of plants, yet the magnitude of influence should be considered in the context of other fluctuating factors within a given location. Prediction of plant response to temperature that does not account for natural fluctuations may over estimate the importance of temperature and lead to unrealistic projections of the rate of vegetation change.

IV.2 INTRODUCTION

The response of plants to temperature, particularly tundra plants, has been studied for many decades. Traditionally, research has emphasized the role of temperature on plant distribution (*e. g.* de Candolle 1855, Clements 1916) and physiology (*e. g.* Mooney and Billings 1961, Larcher 1995). Recent climate change scenarios and observed decadal climate trends have caused a renewed interest in the interaction between plants and temperature with a focus on the dynamics of community change due to warming at decadal time scales (Foley *et al.* 2000, Cramer *et al.* 2001, Malcolm *et al.* 2002, Minorsky 2002). This work was done in the Arctic because it is predicted to warm more than other regions of the world (Cattle and Crossley 1995, Rowntree 1997, McCarthy *et al.* 2001) and tundra is believed to be one of the biomes most vulnerable to change in temperature (Bliss *et al.* 1973, Billings 1987, Everett and Fitzharris 1998). Furthermore, the arctic system has already been shown to be changing (Overpeck *et al.* 1997, Serreze *et al.* 2000, Morison *et al.* 2000). There have also been observed biotic changes in the Arctic (Suarez *et al.* 1999, Sturm *et al.* 2001b, Kullman 2002, Lucht *et al.* 2002) that have contributed to the growing number of worldwide studies showing changes of organisms consistent with regional trends associated with climate warming (McCarthy *et al.* 2001, McCarty 2001, Walther 2001, Walther *et al.* 2002, Parmesan and Yohe 2003, Root *et al.* 2003).

Concomitant with the above, there has been emphasis on warming experiments in tundra systems over the past decade. There have been over 69 papers from 50 studies in

34 community types in 18 geographic regions (Section I.4.3-2). When vegetation change has been detectable, there has been a trend toward increased photosynthesis, CO_2 efflux, growth, reproductive effort and cover and decreased tissue nitrogen (Section I.4.3-2). These studies have been used to predict the state of tundra communities in response to observed and forecast climate change (*e. g*. Epstein *et al*. 2000, Epstein *et al*. 2001) and they have contributed to the widely held belief that tundra communities will respond more than most other biomes to warming (Everett and Fitzharris 1998, McCarthy *et al*. 2001).

The objective of this chapter is to describe the relationship between temperature and the phenological development, growth, and reproductive effort of tundra plant species in northernmost Alaska and to evaluate the usefulness of this relationship in predicting the response of tundra to climate warming. To simplify the interpretation of this complex data set, each trait of each species is characterized according to its response to temperature. This research integrates results from natural variation in temperature between four field sites, interannual variability, and experimental warming to characterize the relationship between plants and temperature. This chapter reports results from the first 7 years of the study. For this study, it was assumed that interannual variability in the response of a measured trait was due to natural fluctuations in a host of causative factors important to plant species in their natural environment such as non-temperature components of climate, light availability, nutrient availability, soil moisture, or biotic interactions. The inclusion of multiple years in the study allowed a characterization of each species response to temperature in relation to other factors. This research focuses on the response of tundra plants to a magnitude of warming that is within the natural range of interannual variability and similar to forecast and observed climate change with the Alaskan Arctic of approximately 0.5 ^{o}C per decade (Stafford *et al*. 2000, Houghton *et al*. 2001).

IV.3 METHODS

IV.3.1 Study Sites

The four study sites were located on the north slope of Alaska near Barrow (71^{o}18'N 156^{o}40'W) and Atqasuk (70^{o}29'N 157^{o}25'W) (Section I.5.1). In both regions sites were established in physiognomically equivalent wet meadow and dry heath community types (Section I.5.3). The Barrow Dry Heath (BD) site was on a former raised beach ridge with moderately well drained xeric pergelic cryaquept soils. The Barrow Wet Meadow (BW) site was in a transition zone between a drained lake basin and the former raised beach ridge (the BD site) with poorly drained histic pergelic cryaquept soils. The Atqasuk Dry Heath (AD) site was on the rim of a partially drained lake margin with well-drained pergelic cryopsamment soils. The Atqasuk Wet Meadow (AW) site was near a pond margin with poorly drained histic pergelic cryaquept soils. A more comprehensive description of each of site is presented in Chapters I and II.

IV.3.2 Experimental Warming

At each study site 24 experimental warmed plots and 24 control plots were monitored. Sites were established in 1994, 1995, 1996 and 1996 for the BD, BW, AD, and AW sites respectively. Each site was established as a completely randomized experimental design with one treatment factor – warming (Section I.5.3). Warming was achieved with the use of open-top chambers (OTCs). The OTCs were hexagonal with sloping sides constructed of Sun-Lite HPTM fiberglass (Solar Components Corporation, Manchester, New Hampshire). The OTCs were 35 cm tall and the distance between parallel sides was 103 cm at the base and 60 cm at the top. For a detailed description of the OTCs see Section I.5.2-3. The OTCs warmed the plant canopy between 0.6 and 2.2 ^{o}C on average throughout the growing season (Chapter II). This moderate amount of warming resulted in large increases between treatments in thawing degree-day totals from snowmelt (TDD_{sm}) until the 15 of August. A description of the performance of the OTCs at the four sites is provided in Chapter II. A test of the validity of using the OTCs to simulate regional warming in Barrow, Alaska is provided in Chapter III.

IV.3.3 Plant Traits

The plant traits measured were chosen on the basis of species morphology and ease of quantification. All vascular plant species were monitored, but the frequency and types of observations varied among sites and years due to logistical constraints. Within each plot individual plants were permanently marked and monitored each year of the experiment. Some species, such as clonal graminoids, do not form distinct individuals. In these cases unit areas were established to monitor change over time. Due to the low percentage of flowering, data on reproductive traits required the measurement of non-marked plants.

The measured plant traits included: phenological development (day of first - leaf emergence, inflorescence emergence or visible flower bud, and flower opening); annual growth (leaf length and change in size); and annual reproductive effort (number of inflorescences per plot and inflorescence length). The measurement used to monitor “changes in size” varied by species but was the number of branches for shrubs, the number of ramets for graminoids and most forbs, or the average diameter of the rosette for some forbs. For across-site phenological development the day the trait first occurred was replaced with the seasonal progression of leaf growth (average length of leaf on a given day), inflorescence growth (average length of inflorescence on a given day), and flowering (number of inflorescence in flower per plot on a given day). Measurements were collected daily, weekly, or yearly at all plots within each of the four sites during the summers of 1994-2000.

When more than one measurement of a species was recorded per plot the average was used in subsequent analysis. Only plant traits that were recorded in three or more years at three or more plots per treatment at a single site are reported here. A more comprehensive explanation of the plant traits examined is provided in Section I.5.4-4.

IV.3.4 Use of Thawing Degree-Days

Thawing degree-day totals from snowmelt (TDD_{sm}) were used to express seasonal differences in temperature. It was calculated for each plot where temperature was recorded and then averaged by treatment at each site for each year (Chapter II). Annual growth and reproductive effort was correlated with whole growing season TDD_{sm} (snowmelt-August 15th). For phenological traits the mean Julian day that the event occurred was correlated with the TDD_{sm} of that day.

IV.3.5 Data Analysis

In all cases the outcome of a statistical test was considered significant if the *p*-value was less than 0.05. In order to simplify the presentation of multiple years of data collection the results are represented by a three-letter sequence according to the relationship with temperature and the statistical significance associated with experimental warming, interannual variability, and the overall correlation between TDD_{sm} and the observed trait. The first letter represents the overall correlation between the trait and TDD_{sm} irrespective of year or treatment. If the correlation was significant, then the direction of the relationship with temperature was determined by the sign of the correlation (positive [P] or negative [N]), otherwise it was considered uncorrelated [U]. The second letter represents the response of the trait to interannual variability. If there was a significant year effect, determined from a two factor repeated ANOVA, then the direction of the response in relation to temperature was determined by a correlation between TDD_{sm} and the trait measured in the control plots only (significant positive [P], significant negative [N], no correlation or inconsistent [I]), otherwise it was considered unresponsive [U]. The third letter represents the response of the trait to experimental warming. If there was a significant warming effect or an interaction between year and warming, determined from a two factor repeated ANOVA, then the direction of the response in relation to temperature was determined by the direction of the prevailing difference between the warmed and control plots within a given year (positive [P] or negative [N]), otherwise it was considered unresponsive [U]. If there was a significant interaction between year and treatment but the difference in the warmed plots was clearly in one direction, then it is denoted in small case letters (positive [p] or negative [n]); if in some years the difference was positive and others negative, then the direction was considered inconsistent [I]. The response patterns associated with each category of the response characterization scheme described above is portrayed in Figure IV-1.

IV.3.6 Formation of Temperature Response Types

A plant species response to warming within a site is presented as a response type rather than a summary value for each year. Data tables containing the seasonal mean values for species and each trait can be found in Appendix E. Temperature response types were determined using the overall correlation with TDD_{sm} and the response to warming. If the trait was significantly correlated with TDD_{sm}, then temperature was considered to dominate the response enough to override other factors. In the few cases where there was a significant correlation with TDD_{sm} but no treatment difference, temperature was still considered a dominant factor. The temperature difference was larger between years than between treatments; therefore, the correlation with TDD_{sm} across treatments and years could detect a small but significant response. If a trait responded to warming but the interannual variation in the trait was not significantly correlated with TDD_{sm}, then temperature did not override other factors and was considered a subordinate factor. If there was no overall correlation with TDD_{sm} and no response to warming, then the trait was considered unresponsive to temperature. A positive response to temperature represents an increase in growth or reproductive effort or earlier phenological development with warming, a negative response to temperature represents the opposite. The response was considered inconsistent if it was positive in some years and negative in others. For phenological traits there was no objective method to identify a dominant negative response to temperature because there is an inherently strong positive correlation between Julian days and TDD_{sm} due to the way TDD_{sm} is calculated. The distinction between a temperature response that is dominant or subordinate to other factors was specific to the site examined and the amount of fluctuation in other factors that occurred during the years of recording. Comparisons between sites were used to further support the temperature response types and to identify differences in response between geographic regions or community types.

For plant species that were present in more than one site, the response of each trait was evaluated by its relationship with temperature when the information across the sites where the species occurred was pooled. Phenological information in this analysis consisted of weekly measurements of leaf and inflorescence lengths and the number of inflorescences in flower. These traits were graphed against TDD_{sm} and Julian days to visually determine which variable produced a more similar pattern in flowering between years. The variable (Julian day or TDD_{sm}) that displayed a more similar pattern between years or had the stronger correlation with the response was considered the better predictor of the response. For seasonal growth and reproductive traits the correlation of the trait with TDD_{sm} was expanded to include values from more than one site.

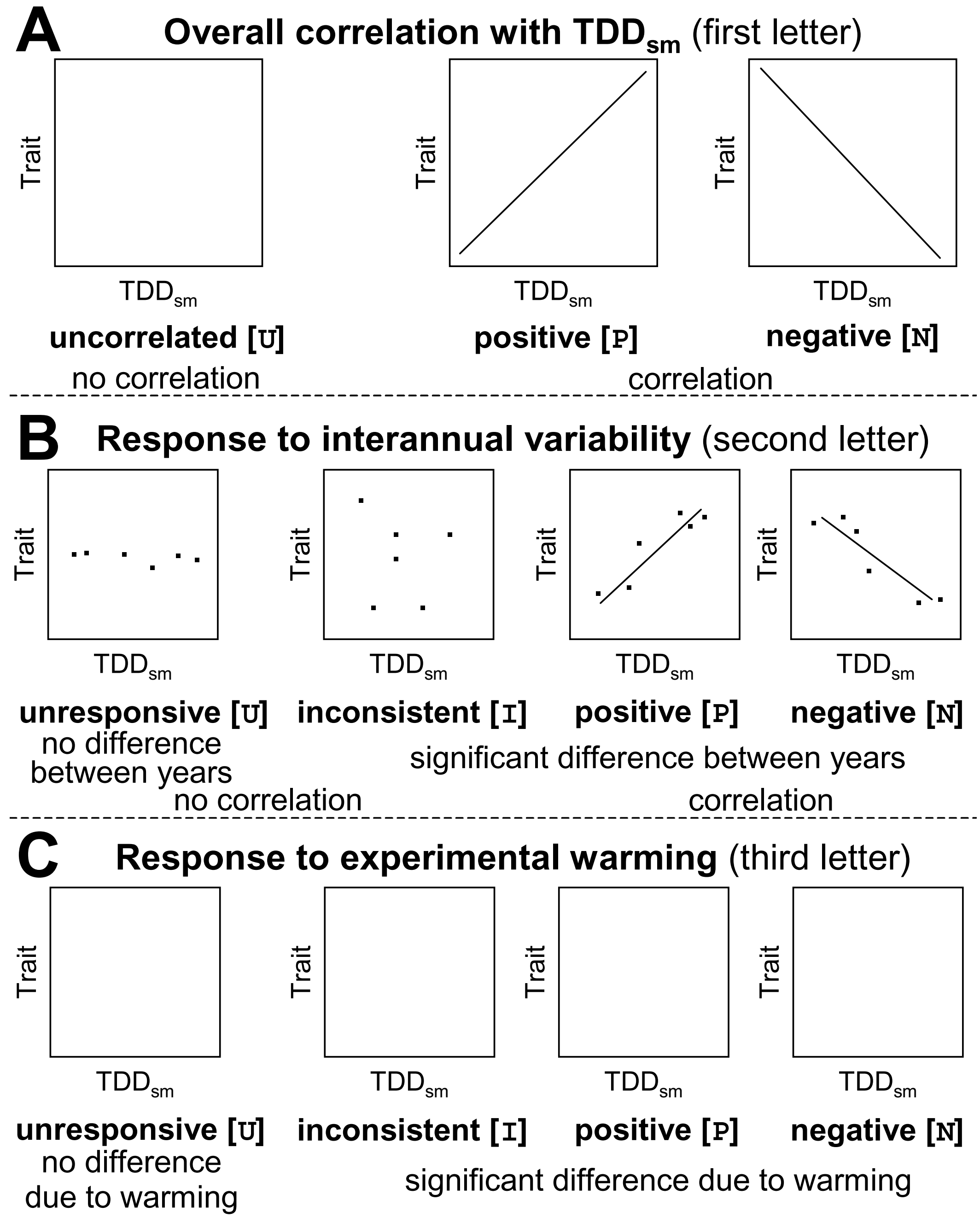


Figure IV-1. Conceptual response patterns of the trait of a species to thawing degree-day totals from snowmelt (TDD_{sm}). The relationship between the observed trait and TDD_{sm} is characterized by: ***A***) the overall correlation with TDD_{sm} irrespective of year or treatment; ***B***) the response to interannual variability; and ***C***) the response to experimental warming. Lines represent significant correlations. Arrows represent the mean difference from the control to the warmed plots in a given year. Dots represent the mean value of the control plots in a given year. Each response was coded as unresponsive or uncorrelated [U], inconsistent [I], positive [P], or negative [N].

IV.4 RESULTS

IV.4.1 Within-Site Temperature Response Types

The relationship with temperature and the statistical significance of the overall correlation of the seven observed traits of all species at the four study sites with TDD_{sm} and the response of the traits to interannual variability and experimental warming is presented in Table IV-1. The temperature response types determined for the seven observed traits of all species at the four study sites are presented in Table IV-2. An example of each temperature response type is provided in Figures IV-2 and IV-3 for phenological, growth, and reproductive traits respectively. Plants responded to temperature in 130 of 267 observations (49%). The most common response to warming was earlier phenological development (44/116 38%), increased growth (22/72 31%), and increased reproductive effort (33/79 42%). In 37 of 267 observations (14%) temperature was considered the dominant factor driving the response of the plant trait. In 73 of 267 observations (35%) the response to temperature of the plant trait was considered subordinate to other factors. The overall response of some traits was distinctly different. The traits leaf length and inflorescence length had a higher proportion of observations assigned to the dominant positive response type (17/36 47%) than other traits. There were also distinct differences between sites. In the BW site the inflorescence length showed a dominant positive response to temperature in 13 of 15 observations (87%). Whole plant response to temperature was individualistic. Of the 46 observations of a species in a site, there were 44 combinations of the 7 response variables. Every species that was measured in more than one site responded differently between sites in at least one trait.

IV.4.2 Across-Site Temperature Response Types

The temperature response types determined by examining the pooled observations for each trait from all the sites where a species occurred are presented in Table IV-3. Examples of the phenological temperature response types are provided in Figures IV-4 and IV-5 for seasonal growth and flowering, respectively. Examples of the annual growth and reproductive effort types are provided in Figure IV-6. From a tabulation of Table IV-3, observed traits were correlated with TDD_{sm} in 19 of 40 observations (48%) and TDD_{sm} was a better predictor of response than Julian day in 15 of 20 observations (75%). The relationship between TDD_{sm} and a plant trait was more pronounced when the range of TDD_{sm} was greater. The four species studied in two sites within the same geographic region (Barrow), *Draba lactea*, *Poa arctica*, *Saxifraga foliolosa*, and *Stellaria laeta*, showed less relationship with temperature than the species measured at sites in both Barrow and Atqasuk. The percentage of observations where Julian day was a better predictor of phenological development across sites (5/20 25%)(Table IV-3) was about half the percentage of phenological observations unresponsive to temperature within a site (62/116 53%)(Table IV-2). The percentage of growth and reproductive observations not correlated with TDD_{sm} (21/40 52%)(Table IV-3) was approximately the same percentage characterized as unresponsive to temperature in each site (75/151 50%)(Table IV-2); however, the number of observations correlated with TDD_{sm} (19/40 48%) was more than double that examined at an individual site (33/151 22%). The subset of species occurring at more than one site was representative of all the species sampled in relation to the percentage of observations assigned to the three major temperature response types within a site (14% dominant, 35% subordinate, 51% unresponsive).

Table IV-1. The relationship with temperature and statistical significance associated with the overall correlation of each observed trait with TDD_{sm} and the response of the trait to interannual variability and experimental warming is shown using letter codes (see footnote for letter meanings). See text for a description of the analyses used to make the determination.

Trait Type	Phenological			Growth		Reproductive	
Trait	Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flower Emergence	Leaf Length	Change in Size	No. of Inflorescences / plot	Inflorescence Length
Species by Site							
Atqasuk Dry Heath							
Carex bigelowii	PIU	PIU	●	UUU	NIN	●	●
Cassiope tetragona	●	●	●	UIn	PPP	UIn	●
Diapensia lapponica	PIU	PII	UIU	UIP	●	NIn	UIU
Hierochloe alpina	PIU	UIU	UPn	PIP	UUU	UIP	UIP
Ledum palustre	UIU	UIU	UIU	●	●	UIU	●
Luzula arctica	UIU	●	UIU	UIU	UUU	UUI	UUU
Luzula confusa	PII	UIn	UIN	UIU	UUU	UII	UIN
Polygonum bistorta	UIU	●	●	PIU	UUU	UUU	PIU
Vaccinium vitis-idaea	UIU	UIU	UIU	UIU	PIU	UIn	●
Atqasuk Wet Meadow							
Carex aquatilis	PIU	PPI	PIn	UIP	●	UII	UIP
Dupontia fisheri/psilosantha	PPP	●	●	UIU	UUU	UUU	UIU
Eriophorum angustifolium	PIU	●	●	PIU	UUU	UIU	UUI
Eriophorum russeolum	PIU	●	●	PPP	NIU	UIU	UUP
Luzula wahlenbergii	UUI	●	●	PIU	●	●	●
Pedicularis sudetica	PIU	●	●	UIP	●	UUU	●

First letter – overall correlation with TDD_{sm} (P-positive, N-negative, U-uncorrelated)
Second letter – year response (P-positive, N-negative, I-inconsistent, U-unresponsive)
Third letter – warming response (P-positive, N-negative, I-inconsistent, U-unresponsive)
● – not enough information for analysis

note: small case letters (n, p) represent an interaction between warming and years where the response was always in the same direction but its magnitude was inconsistent. "Change in Size" was generally the change in the number of ramets (graminoids and most forbs), number of branches (shrubs), or average diameter of rosette (some forbs) between years.

Table IV-1. Continued.

Trait Type		Phenological			Growth		Reproductive	
Trait		Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flower Emergence	Leaf Length	Change in Size	No. of Inflorescences / plot	Inflorescence Length
Species by Site								
Barrow Dry Heath								
Arctagrostis latifolia		UIU	UIN	•	UIU	UUP	UIU	UIp
Cassiope tetragona		UIU	UIn	UIn	UII	UIU	UIp	•
Draba lactea		UII	•	UUU	UNU	•	UUU	UIU
Draba micropetala		UIU	PIn	UIU	UUU	UUU	UIP	UIP
Luzula arctica		UIU	PPU	UIU	UIU	UII	UIU	UIp
Luzula confusa		UIN	PIN	UIn	UIP	UIU	UIU	UIP
Papaver hultenii		PIN	PPI	UIN	•	UUU	UIU	PIP
Poa arctica		PPU	UIN	UIU	UUP	UIU	UIU	UIP
Potentilla hyparctica		UIN	PPN	UIn	•	UIU	UIU	PPp
Salix rotundifolia	female	UIn	UIn	UIn	UIP	•	UII	UIP
	male	UIU	UIU	UIn	UIP	•	UII	•
Saxifraga foliolosa		PIU	•	•	UIU	•	•	UIU
Saxifraga punctata		PPn	PPU	UIN	UIP	UIU	UIU	PIp
Senecio atropurpureus		PPU	PIU	PPN	UIU	UIU	UUI	UIU
Stellaria laeta		UIN	UIn	UIN	•	UIU	PIU	•
Barrow Wet Meadow								
Cardamine pratensis		NIU	UIn	UIN	PIP	•	PIU	PIP
Carex aquatilis/stans		UIU	UIn	UIN	UIP	UII	UIU	PIP
Draba lactea		UIU	UIU	UIU	UUU	UUU	UUU	PIP
Dupontia fisheri		UIP	UIU	NIN	UIU	UUP	UII	PIp
Eriophorum angustifolium/triste		UIU	NIU	UIN	UIU	UIU	UIU	UIP
Eriophorum russeolum		PIU	UIU	UIn	UIP	UUU	UIU	PIU
Hierochloe pauciflora		PIU	UIN	UIN	PPP	•	UIn	UII
Juncus biglumis		PIU	UIU	PIU	UIU	UIU	UIU	PPP
Luzula arctica		UIU	UIn	UIN	UIU	UIU	UUU	PPP
Luzula confusa		PIU	UIU	UIU	UIU	UIU	UUU	PIP
Poa arctica		PII	UIU	•	UIU	•	UIU	PIP
Saxifraga cernua		UIU	UIU	UNU	UII	•	UIU	PIP
Saxifraga foliolosa		UIN	UIU	NUN	UIU	UUU	UIU	PIp
Saxifraga hieracifolia		UIU	PIU	UIN	PPU	UUU	UIU	PIP
Saxifraga hirculus		PIp	PIU	UIN	•	•	UIU	PPP
Stellaria laeta		UIU	UIU	UIU	•	UIU	PPU	•

Table IV-2. Response of species traits to temperature at the four study sites. See text for a description of each of the response types.

Trait Type	Phenological			Growth		Reproductive	
Trait	Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flower Emergence	Leaf Length	Change in Size	No. of Inflorescences / plot	Inflorescence Length
Species by Site							
Atqasuk Dry Heath							
Carex bigelowii	U	U	●	U	N	●	●
Cassiope tetragona	●	●	●	n	P	n	●
Diapensia lapponica	U	i	U	p	●	N	U
Hierochloe alpina	U	U	p	P	U	p	p
Ledum palustre	U	U	U	●	●	U	●
Luzula arctica	U	●	U	U	U	i	U
Luzula confusa	i	p	p	U	U	i	n
Polygonum bistorta	U	●	●	P	U	U	P
Vaccinium vitis-idaea	U	U	U	U	P	n	●
Atqasuk Wet Meadow							
Carex aquatilis	U	i	p	p	●	i	p
Dupontia fisheri/psilosantha	n	●	●	U	U	U	U
Eriophorum angustifolium	U	●	●	P	U	U	i
Eriophorum russeolum	U	●	●	P	N	U	p
Luzula wahlenbergii	i	●	●	P	●	●	●
Pedicularis sudetica	U	●	●	p	●	U	●

note: "Change in Size" was generally the change in the number of ramets (graminoids and most forbs), number of branches (shrubs), or average diameter of rosette (some forbs) between years.

P positive dominant response
p positive subordinate response
N negative dominant response
n negative subordinate response
i inconsistent response
U unresponsive or no significant response
● not enough information to determine

Table IV-2. Continued.

Trait Type		Phenological			Growth		Reproductive	
Trait		Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flowering	Leaf Length	Change in Size	No. of Inflorescences / plot	Inflorescence Length
Species by Site								
Barrow Dry Heath								
Arctagrostis latifolia		U	p	●	U	p	U	p
Cassiope tetragona		U	p	p	i	U	p	●
Draba lactea		i	●	U	U	●	U	U
Draba micropetala		U	p	U	U	U	p	p
Luzula arctica		U	U	U	U	i	U	p
Luzula confusa		p	p	p	p	U	U	p
Papaver hultenii		p	i	p	●	U	U	P
Poa arctica		U	p	U	p	U	U	p
Potentilla hyparctica		p	p	p	●	U	U	P
Salix rotundifolia	female	p	p	p	p	●	i	p
	male	U	U	p	p	●	i	●
Saxifraga foliolosa		U	●	●	U	●	●	U
Saxifraga punctata		p	U	p	p	U	U	P
Senecio atropurpureus		U	U	p	U	U	i	U
Stellaria laeta		p	p	p	●	U	P	●
Barrow Wet Meadow								
Cardamine pratensis		P	p	p	P	●	P	P
Carex aquatilis/stans		U	p	p	p	i	U	P
Draba lactea		U	U	U	U	U	U	P
Dupontia fisheri		n	U	P	U	p	i	P
Eriophorum angustifolium/triste		U	P	p	U	U	U	p
Eriophorum russeolum		U	U	p	p	U	U	P
Hierochloe pauciflora		U	p	p	P	●	n	i
Juncus biglumis		U	U	U	U	U	U	P
Luzula arctica		U	p	p	U	U	U	P
Luzula confusa		U	U	U	U	U	U	P
Poa arctica		i	U	●	U	●	U	P
Saxifraga cernua		U	U	U	i	●	U	P
Saxifraga foliolosa		p	U	P	U	U	U	P
Saxifraga hieracifolia		U	U	p	P	U	U	P
Saxifraga hirculus		n	U	p	●	●	U	P
Stellaria laeta		U	U	U	●	U	P	●

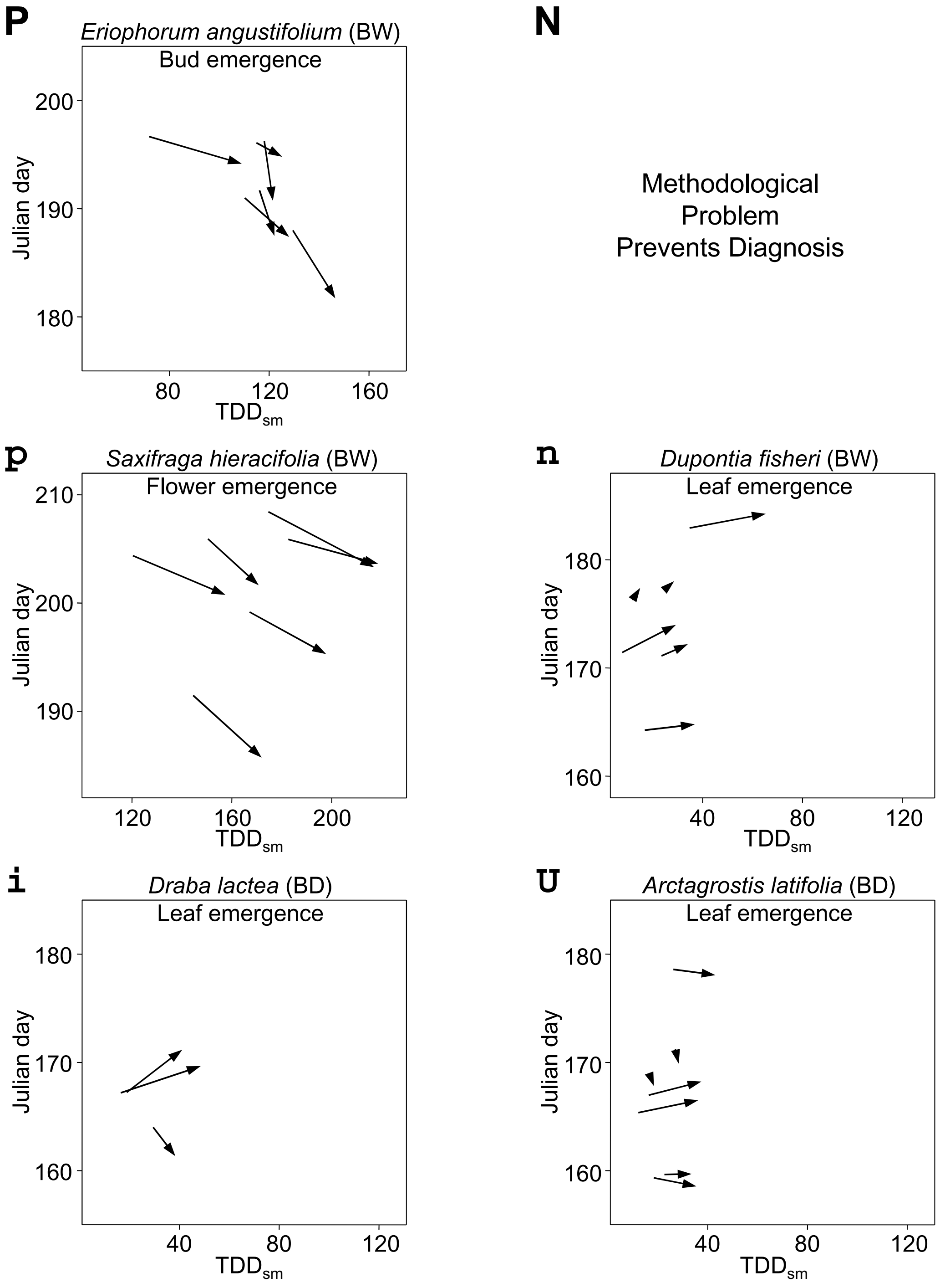


Figure IV-2. The Julian day that a phenological stage was reached versus the thawing degree-day totals from snowmelt (TDD$_{sm}$) of species representing the six temperature response types. Arrows represent the mean difference from the control to the warmed plots in a given year (arrow heads only represent small change). The site the species occurred in is presented in parentheses (AD - Atqasuk Dry Heath, BD - Barrow Dry Heath, BW - Barrow Wet Meadow). The temperature response types are: P - positive dominant response, p - positive subordinate response, N - negative dominant response, n - negative subordinate response, i - inconsistent response, and U - unresponsive.

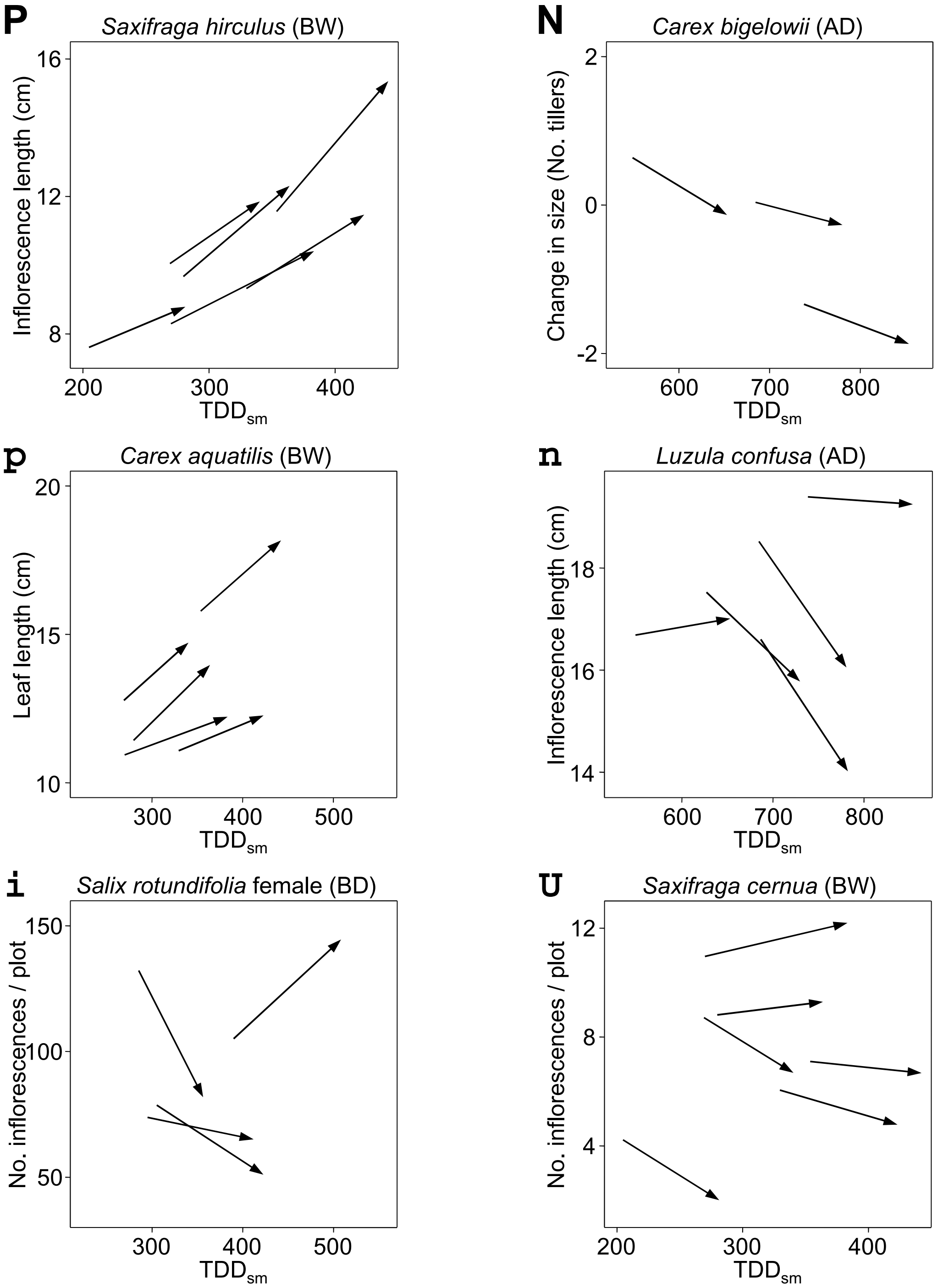
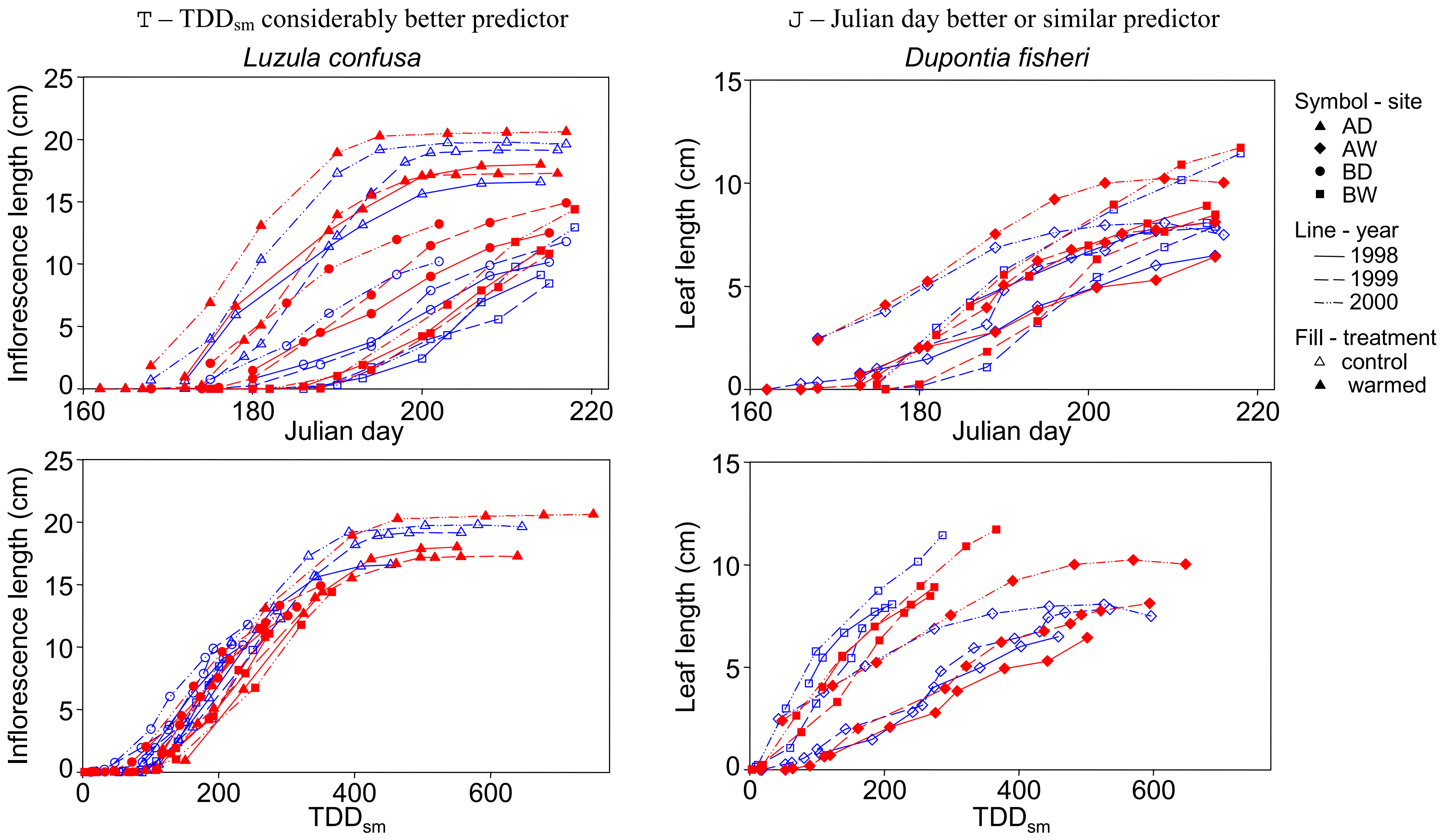


Figure IV-3. Growth or reproductive effort versus the thawing degree-day totals from snowmelt (TDD_{sm}) of species representing the six temperature response types. The trait of the species is shown on the y-axis and the site is presented in parentheses (AD - Atqasuk Dry Heath, BD - Barrow Dry Heath, BW - Barrow Wet Meadow). Arrows represent the mean difference from the control to the warmed plots in a given year. The temperature response types are: P - positive dominant response, p - positive subordinate response, N - negative dominant response, n - negative subordinate response, i - inconsistent response, and U - unresponsive.

Table IV-3. Response of species traits to temperature examined at more than one site (AD - Atqasuk Dry Heath, AW - Atqasuk Wet Meadow, BD - Barrow Dry Heath, BW - Barrow Wet Meadow). See text for a description of each of the response types.

Trait Type					Phenological			Growth		Reproductive	
					Seasonal Progression of						
Trait					Leaf Growth	Inflorescence Growth	Flowering	Leaf Length	Change in Size	No. of Inflorescences / Plot	Inflorescence Length
Study Sites	AD	AW	BD	BW							
Species											
Carex aquatilis		x		x	T	T	T	P	–	N	P
Cassiope tetragona	x		x		●	●	T	–	P	N	●
Draba lactea			x	x	●	●	●	–	–	–	–
Dupontia fisheri		x		x	J	J	T	–	–	N	P
Eriophorum angustifolium		x		x	T	T	T	P	–	N	P
Eriophorum russeolum		x		x	●	●	T	P	–	–	P
Luzula arctica	x		x	x	T	T	T	–	–	N	P
Luzula confusa	x		x	x	T	T	J	P	–	–	P
Poa arctica			x	x	●	●	J	–	●	–	P
Saxifraga foliolosa			x	x	●	●	T	–	–	–	P
Stellaria laeta			x	x	●	●	J	●	–	P	●

x the species occurred in that site
T TDD_{sm} considerably better predictor of phenology
J Julian day better or similar predictor of phenology
P positive correlation with TDD_{sm}
N negative correlation with TDD_{sm}
– no correlation with TDD_{sm}
● not enough information to determine


T – TDD$_{sm}$ considerably better predictor

J – Julian day better or similar predictor

Figure IV-4. Seasonal growth versus thawing degree-day totals from snowmelt (TDD$_{sm}$) or Julian day. The graphs on the ***left*** are representative of a trait of a species (*Luzula confusa*) that is better predicted by TDD$_{sm}$ than Julian day, the graphs on the ***right*** are representative of a trait of a species (*Dupontia fisheri*) that does not show a considerable improvement in prediction when represented by TDD$_{sm}$.

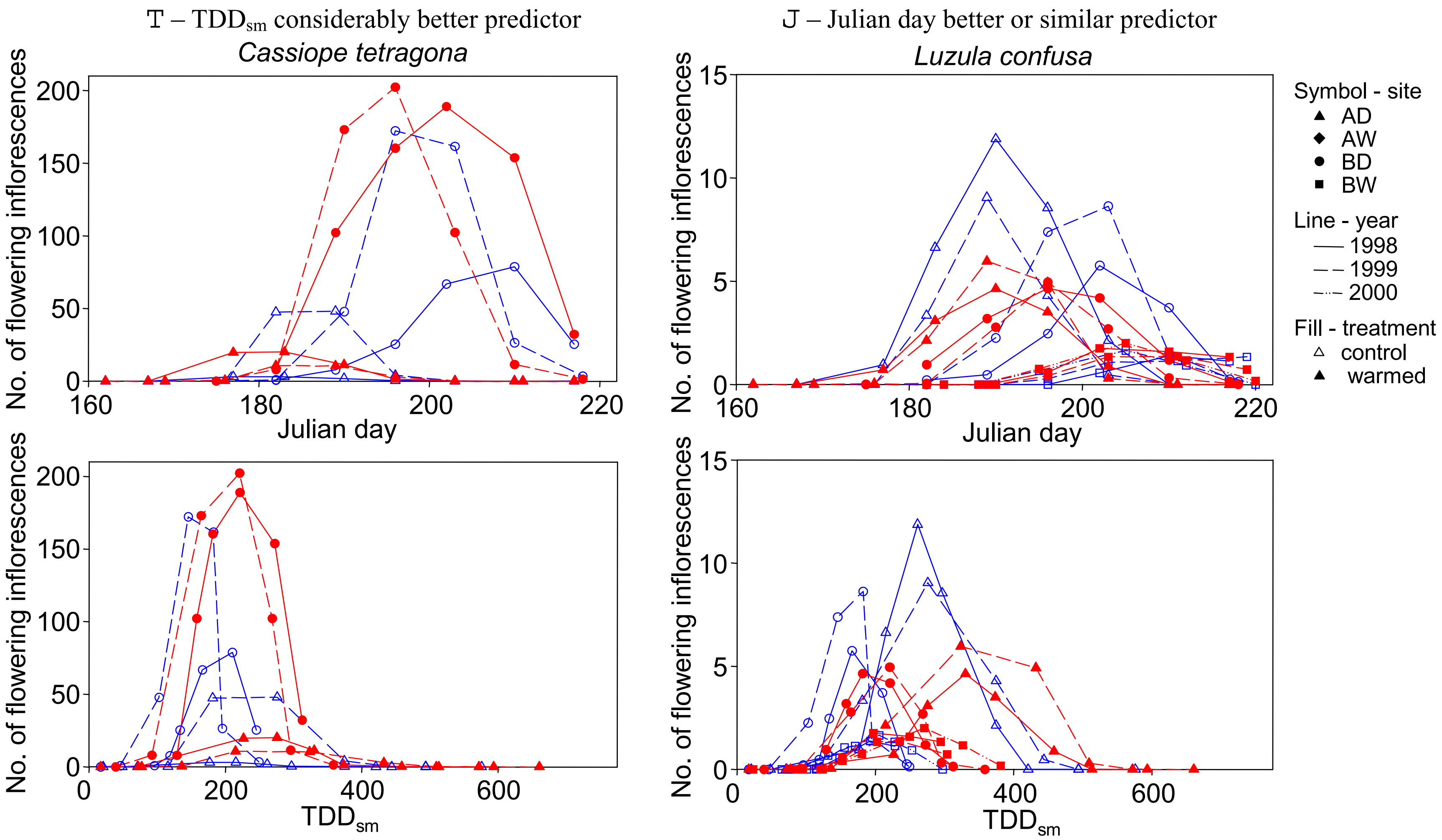


Figure IV-5. Flowering versus thawing degree-day totals from snowmelt (TDD$_{sm}$) or Julian day. The graphs on the ***left*** are representative of a trait of a species (*Cassiope tetragona*) that is better predicted by TDD$_{sm}$ than Julian day, the graphs on the ***right*** are representative of a trait of a species (*Luzula confusa*) that does not show a considerable improvement in prediction when represented by TDD$_{sm}$.

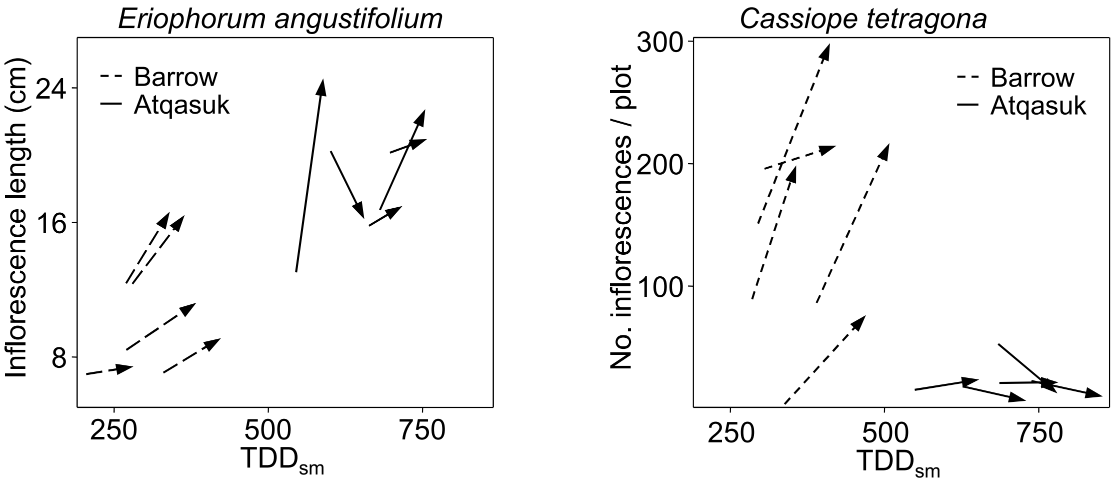


Figure IV-6. Growth or reproductive effort versus thawing degree-day totals from snowmelt (TDD_{sm}) for traits of species observed at both Barrow and Atqasuk. The graphs on the ***left*** are representative of a trait of a species that is positively correlated with TDD_{sm}, the graphs on the ***right*** are representative of a trait of a species that is negatively correlated with TDD_{sm}. Arrows represent the mean difference from the control to the warmed plots in a given year at a given site. *Eriophorum angustifolium* was present in the wet meadow communities and *Cassiope tetragona* in the dry heath communities.

IV.5 DISCUSSION

There were clear differences in TDD_{sm} between treatments (warming experiment), sites (natural temperature gradients), and years (interannual variability). Results obtained from the three independent sources of temperature variation were used to verify results obtained from each method and to characterize the response of a species to temperature. Furthermore, the response of a species to temperature was characterized in relation to its response to other naturally fluctuating factors in the environment such as non-temperature components of climate, light availability, nutrient availability, soil moisture, or biotic interactions. The characterization of plant response to temperature relative to other factors is important for application of the findings toward predictions of vegetation change in response to ongoing warming of the region. It is believed that these temperature response groups could lend themselves to predictive modeling of future states of plant cover in a warming Arctic.

IV.5.1 Utility of Natural Temperature Gradients, Interannual Variability, and Experimental Warming

Long-term descriptive studies have been used to predict the response of plant species to temperature (*cf*. Walker *et al*. 1994b, Walker *et al*. 1995). However, this study found that certain responses of plants to warming were difficult to identify without experimental warming. The inclusion of a warming experiment allows for comparisons of plant response to two different seasonal temperature regimes within a single growing season which essentially doubles the number of replicates available for correlational studies and expands the natural range of seasonal temperatures toward warmer seasons.

Warming experiments also allow for the identification of traits where the temperature response was subordinate to other factors. It would take many years to identify effects of temperature that are subordinate to other factors based exclusively on interannual variability because other factors mask temperature effects. In fact, this study found in most cases 3-7 years of interannual variability without inclusion of the experimentation was not sufficient to assess plant response to temperature.

Across-site trends in trait responses correlated with TDD_{sm} in 19 of 40 observations (48%). This was essentially the same percentage of observations that responded to temperature when examined at a single site, but within a site the responses were mostly subordinate to other factors. Therefore, correlations based on natural temperature gradients over estimated the importance of temperature. For example, the inflorescence length of *Eriophorum angustifolium* was correlated with TDD_{sm} when examined at Barrow and Atqasuk, but within a site the warming response of the trait was subordinate to other factors (Table IV-3, Figure IV-6). Across-site comparisons span complex gradients and the response of a trait may be related to factors that are difficult to dissect from temperature. The reduced amount of flowering of several species in Atqasuk relative to Barrow is probably based on factors other than temperature (Table IV-3, Figures IV-5 and IV-6). For example, the reduction in flowering in *Cassiope tetragona* from cooler Barrow to warmer Atqasuk is more likely due to differences in water availability than temperature. In fact, in Barrow *C. tetragona* flowered more in response to warming. Therefore, the use of multiple sites indicates that a species may vary its response over its range.

The warming experiment provided empirical evidence for the importance of temperature on particular traits. It is possible, although unlikely, that responses to temperature that were considered subordinate to other factors were artifacts of the warming method. Where across-site comparisons were available, there usually was agreement between natural temperature gradients and results from the experimental warming. Furthermore, there generally was a consistent relationship between TDD_{sm} and the response of plant traits irrespective of treatment for many observations. Thus, it is concluded that experimental differences within a year were due primarily to differences in seasonal temperature and, therefore, that the method of warming is a reasonable analog of regional climate warming. This finding is also supported by the detailed examination of plant response to warming presented in Chapter III.

IV.5.2 Plant Response to Temperature

The finding that nearly every species showed an individualistic response to warming was commensurate with other studies examining the response of multiple species to warming (Chapin and Shaver 1985b, Henry and Molau 1997). There were no clear patterns of plant response within growth forms or phylogenic groups. The most consistent pattern was among species within the same community. Nearly all species occurring in the wet meadow community of Barrow increased their inflorescence length in response to warming. However, this similarity of response was only for one trait and there were no clear groups of species with similar response when multiple traits were examined.

The finding that the response of plant phenological development to temperature was unresponsive in 62 of 116 observations (53%) or subordinate to other factors in 50 of 116 observations (43%) was somewhat contradictory to what was expected from an examination of the literature. This illustrates the importance of examining several traits of many species to avoid making generalizations based on the most responsive traits of the most responsive species. Many studies have generally found phenological development to be connected to temperature, particularly in tundra ecosystems (Sørensen 1942, Holway and Ward 1965, Fitter *et al*. 1995, Thórhallsdóttir 1998). In fact, the connection between development and temperature (Lindsey and Newman 1956, Lieth 1974) was the foundation for the use of degree-days in this study. It is not surprising that in most cases TDD_{sm} was a better predictor of plant phenological development than Julian days, particularly for traits of species with many years of recordings and where observations were gathered at multiple sites.

Many recent studies have reported accelerated phenological development of organisms and attributed these changes to regional climate warming (Bradley *et al*. 1999, Menzel and Estrella 2001, Peñuelas and Filella 2001, Fitter and Fitter 2002, Sparks and Menzel 2002). Many of these increases have been attributed primarily to an earlier onset of spring. An explanation for the lack of major change in phenological development in this study is that the warming manipulation did not include lengthening the growing season, rather warming began after snowmelt occurred. Phenologic events that generally occur later in the growing season were accelerated more than events characteristic of the early season. For example, flower emergence was accelerated in 22 of 35 observations (63%).

In cases where there was a negative correlation between TDD_{sm} and Julian day it took more cool days to reach the same phenological stage as fewer warm days. The few cases where phenological development was slowed by warming may be due to what has been termed as an "exhaustion effect" (G.H.R. Henry, *personal communication*), where the plant optimizes growth or reproduction in the previous favorable year by drawing down its nutrient and carbohydrate reserves and this causes the initiation of growth the following spring to be delayed. In the two species where phenological development was delayed, *Dupontia fisheri* and *Saxifraga hirculus*, the delay was only in leaf emergence and this delay was greater in later years of the experiment. Both of these species are characteristic of High Arctic communities and this response may be considered maladaptive to warming.

The growth and reproductive responses to temperature were commensurate with the findings of other warming experiments of tundra plants (Henry and Molau 1997, Shaver and Jonasson 1999, Callaghan *et al*. 1999, Arft *et al*. 1999, Dormann and Woodin 2002). One explanation for the documented responsiveness of leaf and inflorescence length is the intercalary basal meristems of graminoids and many of the forbs allows the continual growth of leaves and inflorescences throughout the growing season. The general lack of change in size of plants between years due to warming conforms to the dogma that tundra plants exhibit conservative growth strategies (*cf*. Sørensen 1941, Billings and Mooney 1968). However, where permanently marked individuals are monitored, a bias exists against a decrease in growth due to the common practice of not including dead or unhealthy individuals from the analysis. Tundra plants allocate a proportionally higher amount of energy to reproduction than temperate plants and this contributes to the larger relative size and number of flowers characteristic of tundra communities (Chapin and Shaver 1985a, Philipp *et al*. 1990). This may explain why the response to warming of reproductive traits was generally greater than the response in vegetative traits, particularly in Barrow. The unresponsiveness and inconsistencies in the direction of the changes in the number of inflorescences in flower in a given year may have been due to the long preformation times associated with flowering in tundra plants (Sørensen 1941, Diggle 1997). In addition to the long preformation times, flowering is often episodic and may respond to a wide range of climatic and non-climatic factors (Rathcke and Lacey 1985, Philipp et al. 1990). Inflorescence lengths have been linked with seed development and dispersal (Savile 1972, Welker *et al*. 1997, Molau 2001); therefore, changes in inflorescence length may increase the probability of successful recruitment. This speculation may explain the frequency of significant increases in inflorescence length.

The most unexpected result was the high proportion of responses to temperature that were subordinate to other factors. When comparing between sites there were generally strong correlations between the measured traits and TDD_{sm}. Yet, in most cases, the amount of temperature variation between years and between control and warmed plots was not enough to override the natural fluctuations in trait response attributable to non-temperature factors.

IV.5.3 Implications for Prediction

Predicting the longer-term direct response of warming is the most straightforward for a single trait when temperature was considered a dominant driver of the response.

However, there were several cases where the response of a species varied among sites and in most cases the warming response within a site was subordinate to other factors. Inconsistent warming response suggests that temperature interacts with other factors and the ultimate effect will be difficult to predict. While temperature effects that were subordinate to other factors may ultimately lead to vegetation change, interannual fluctuations of these other factors will dampen the rate of change. The magnitude of the fluctuations in these other factors in relation to the warming effects will determine the amount of lag. It is also possible that sufficiently large fluctuations of these other factors may preclude any directional changes due to warming. Therefore, the importance of temperature in relation to other fluctuating factors in a given environment is essential to making realistic predictions that incorporate the dynamics of vegetation change at decadal time scales. Results from natural temperature gradients and short-term warming experiments tend to oversimplify both the long-term interactions between species and the indirect effects of warming. Incorporating lag times is necessary to forecast decadal scale plant community change as a result of warming.

The rationale for examining the immediate response of individual plant species was based on the assumption that changes in plant traits (phenological development, growth, and reproductive effort) in response to warming will change the competitive balance between species and ultimately lead to community change. Therefore, changes in plant traits due to warming should be an early indicator of future community change due to regional warming. However, there are a wide variety of plant traits that could be measured and it is difficult to know which traits of what species are key to successful reproduction and ultimately community change. Furthermore, the complex interactions between species and with the environment is likely to lead to many indirect warming effects that are difficult to predict and there remain many uncertainties involved with scaling from plant response to community response. In addition, the individuality of plant species response makes it difficult to lump species when examining multiple traits.

IV.5.4 Conclusions

The responsiveness of tundra plants growing in their natural environment to small increases in temperature underscores the importance of accounting for changing climate temperatures when predicting the state of arctic vegetation. Integration of findings from interannual variation, warming experiments, and natural temperature gradients was beneficial for characterizing plant response to temperature. Interannual variation alone generally under estimated the importance of temperature, while natural temperature gradients generally over estimated its importance. Warming experiments alone were not able to compare the temperature response of plant species with other naturally fluctuating factors. The most common plant response to warming was earlier phenological development and increased growth and reproductive effort. However, many of the responses were also affected by other factors in a given location. Warming effects that do not override other naturally fluctuating factors are likely to lag and to be difficult to identify. Many of the direct effects of warming may be masked by interannual variability and may take many years before they lead to, or could be attributable to, community change. Furthermore, the many possible indirect warming effects on communities resulting from factors such as nutrient availability and species interactions are poorly understood. To address possible indirect effects research efforts should focus on plant physiological processes and interactions of plant species with each other and changing environmental factors. Realistic forecasts of plant community change at the species level will need to account for both direct and indirect warming effects. The individualistic response of plant species necessitates the use of empirical information to assist in formulating predictions of plant community response.

IV.6 ACKNOWLEDGEMENTS

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Chapter V

DETECTION OF COMMUNITY CHANGE DUE TO MODERATE WARMING OF TUNDRA VEGETATION: SEPARATION OF INITIAL AND SECONDARY RESPONSE

V.1 ABSTRACT

Global climate models predict rapid warming of most Arctic regions during the next century. To further understand the response of Arctic tundra to climate warming, four community types in northern Alaska were warmed for 5 to 7 consecutive growing seasons using open-top chambers. Sites spanned a temperature gradient from Barrow to Atqasuk and a moisture gradient from well-drained dry heaths to frequently inundated wet meadows. Community composition was determined using a point frame. Significant changes in community composition occurred in the control plots of all four sites. Control plots declined in species diversity by up to 2.7 species/plot; other changes were site specific. Changes in relative cover in the control plots were generally larger at Barrow than Atqasuk and larger in the wet sites than dry sites. Responses to warming included increased canopy height (¯0.1-2.3cm), standing dead plant matter (1.5-6.0%) and relative cover of graminoids (1.8-5.8%) and decreased species diversity (0.1-1.7 species/plot) and relative cover of lichens (0.2-9.1%) and bryophytes (1.4-4.6%). The response to warming was separated into an initial response assessed after 2 summers of warming, and a secondary response assessed after an additional 3-5 summers of warming. The initial responses to warming were more uniform across sites, while the secondary responses were site specific. It is expected that longer-term responses to warming will more closely reflect changes associated with the secondary response. The response to warming was larger at Barrow than at Atqasuk due to a larger initial response at Barrow, however long-

term response to warming was projected to be greater at Atqasuk due to a larger secondary response at Atqasuk. These findings suggest that different tundra communities will respond differentially to warming and show that predictions of vegetation change due to climate warming based on manipulative experiments will differ depending on whether they are based on the initial or secondary responses to warming.

V.2 INTRODUCTION

For several reasons Arctic tundra is an ideal setting to experimentally examine the response of plant communities to warming. First, arctic tundra is perceived to be one of the most vulnerable biomes to changes in temperature (McCarthy *et al*. 2001) due to the prevalent role of temperature on the distribution of plants (Sørensen 1941, Bliss 1962, Chapin and Shaver 1985, Billings 1987). Second, arctic tundra has low species diversity, simple canopy structure, and few trophic levels (Warren Wilson 1957, Anderson *et al*. 1966, Bunnell 1981, Sonesson and Callaghan 1991, Walker 1995) making it easier to study whole communities than in most other biomes. Third, the small size and the fine scale distributional heterogeneity of species in arctic communities (Webber 1978, Walker 1995) allows the manipulation of a one meter square plot to be reasonably representative of whole plant community change. Furthermore, research on the effect of warming on the arctic region has been promoted because the Arctic is expected to warm more than other regions of the world over the next century (Cattle and Crossley 1995, Maxwell 1997, McCarthy *et al*. 2001) and the arctic system has already been shown to be changing (Overpeck *et al*. 1997, Serreze *et al*. 2000, Morison *et al*. 2000). Yet, there are conflicting hypotheses regarding the future rate of change of tundra vegetation due to regional warming (Table V-1). These considerations and others have led to recent research in understanding the relationship between temperature and tundra systems (Chapin *et al.*1992, Oechel *et al.* 1997, Lal *et al.* 2000).

Most of the recent experimental research on the relationship between plants and temperature has focused on plant physiology or morphology. These studies have documented increases in plant growth or reproductive effort in warmer environments (*e. g.* Wookey *et al.* 1993, Chapin *et al.* 1995, Graglia *et al.* 1997, Henry and Molau 1997, Arft *et al.* 1999) and that traits of species observed in the both high and low arctic sites generally respond more in the high arctic (Wookey *et al.* 1993, Henry and Molau 1997, Jonasson *et al.* 1999). The few studies that have examined community level response to temperature in tundra have found changes to be relatively small compared with other factors such as nutrient additions (*e. g.* Chapin *et al.* 1995, Molau and Alatalo 1998, Robinson *et al.* 1998).

This study examines the change of the tundra plant community due to moderate warming of 0.6-2.2 ^{o}C on average throughout the growing season (Chapter II). The project used open-top chambers (OTCs) to warm the summer plant canopy of four tundra communities. It has been suggested that the short-term response of tundra communities to warming may be different from longer-term response (Chapin *et al.* 1995, Arft *et al.* 1999, Callaghan *et al.* 1999, Hartley *et al.* 1999); therefore, the short-term initial plant response to warming was separated from the longer-term secondary response. The results presented here are part of a larger project examining the relationship between the

Table V-1. Theoretical arguments for and against rapid vegetation change in tundra systems in response to warming.

Topic	Arguments **for** rapid change	Arguments **against** rapid change
Daily temperatures	Tundra plants generally function below temperature optimums[1,2].	Tundra plants have evolved elaborate mechanisms to maintain life at variable temperatures[1,2,3,4,5].
Length of growing season	The short growing season limits annual growth and reproduction in tundra plants[1,2,6].	Many arctic tundra plants show periodic growth (thus, they may not always respond to a warmer environment)[4,7].
Nutrients	The warming of tundra soils will cause increased nutrient turnover[8,9].	Air and soil temperatures are poorly correlated[10,11], furthermore nutrient additions are often sequestered by microbes and unavailable to higher plants[12,13].
Plant Growth strategy	Many tundra plants exhibit a slow growing conservative strategy that will be less competitive in more favorable climates[14,15].	The conservative growth strategy of tundra plants is resistant to change[14,16].
Plant Reproduction	Success of sexual reproduction generally increases with increasing daily temperatures and growing season length in tundra plants[6,17].	The long distance dispersal of tundra plants and the dominance of clonal growth in tundra communities minimizes the importance of local changes in reproductive success[4].
Ecosystem Stability	Ecosystems with low diversity (i.e. tundra systems) are more susceptible to disturbance or change[18].	The inherent variability of tundra systems pre-adapts tundra plants to tolerate disturbance or change[19].
Interactions	There is expected to be a synergism in tundra systems between temperature and other factors including nutrients[20] and disturbance[16].	Tundra systems are often limited by multiple factors[21,22].

[1] Webber 1974
[2] Chapin and Shaver 1985
[3] Bliss 1962
[4] Savile 1972
[5] Billings 1974
[6] Molau 1993
[7] Sørensen 1941
[8] Melillo *et al.* 1990
[9] Nadelhoffer *et al.* 1997
[10] Kane *et al.* 1992
[11] Jonasson *et al.* 1993
[12] Shaver and Chapin 1980
[13] Jonasson and Chapin 1991
[14] McGraw and Fetcher 1992
[15] Callaghan and Carlsson 1997
[16] Jonasson 1997
[17] Molau and Larsson 2000
[18] Elton 1958
[19] Crawford 1997
[20] Parsons *et al.* 1994
[21] Chapin 1987
[22] Shaver and Kummerow 1992

tundra vegetation and temperature in Barrow and Atqasuk, Alaska (Bay 1995, Bay 1996, Walker 1997, Hollister 1998, Hollister and Webber 2000). The project is associated with a larger worldwide network examining the response of tundra vegetation to temperature known as the International Tundra Experiment (ITEX) (Molau & Mølgaard 1996, Henry 1997, Arft *et al*. 1999).

V.3 METHODS

V.3.1 Study Sites

Study sites were established in northern Alaska near Barrow (71°18'N 156°40'W) and 100 km south of Barrow near Atqasuk (70°29'N 157°25'W) (Section I.5.1). The mean July temperature of Barrow and Atqasuk is 3.7 °C and 9.0 °C respectively (Haugen and Brown 1980, Section I.5.1-1). In both regions sites were established in physiognomically similar well drained dry heath and frequently inundated wet meadow communities (Section I.5.3). The Barrow Dry Heath (BD) site was situated on a former raised beach ridge with moderately well drained xeric pergelic cryaquept soils. The Barrow Wet Meadow (BW) site was in a transition zone between the former beach ridge of the BD site and a drained lake basin, the soils were poorly drained histic pergelic cryaquept. The Atqasuk Dry Heath (AD) site was on the rim of a partially drained lake margin with well drained pergelic cryopsamment soils. The Atqasuk Wet Meadow (AW) site was near a pond margin with poorly drained histic pergelic cryaquept soils. The vegetation of the Barrow and Atqasuk regions is described by Webber *et al.* 1980 and

Komárková and Webber 1980, respectively (also see Sections I.5.1-2 and I.5.1-3). A more comprehensive description of each site is presented in Chapters I and II.

V.3.2 Experimental Warming

At each of the four study sites 24 warmed plots and 24 control plots were established using a randomized plot design (Section I.5.3). Warming was achieved with the use of open-top chambers (OTCs). The OTCs were constructed according to Molau and Mølgaard (1996) with Sun-Lite HPTM fiberglass (Solar Components Corporation, Manchester, New Hampshire). Chambers were hexagonal in shape with sides that are 35 cm in height and slope inward so that parallel sides were 103 cm apart at the base and 60 cm apart at the top. For additional details on the OTCs see Section I.5.2-3. Marion *et al.* (1993, 1997) described the general performance of OTCs and Hollister and Webber (2000, Chapter II) established the validity of using OTCs to simulate regional warming in Barrow. The OTCs warmed the plant canopy between 0.6 and 2.2 ^{o}C on average throughout the growing season (Chapter II). This moderate warming resulted in increases in total thawing degree-days throughout the growing season (Figure V-1).

V.3.3 Point Frame Sampling

The point frame sampling method was ideal for this long-term non-destructive study (Goodall 1952) and has been used in other studies to estimate plant biomass and leaf area index (Jonasson 1988, Groeneveld 1997). Vegetation at all sites was sampled twice, initially during the growing season following site establishment and in 2000 (see Figure V-1, Table V-2, Section I.5.4-5). All sites were sampled close to peak biomass

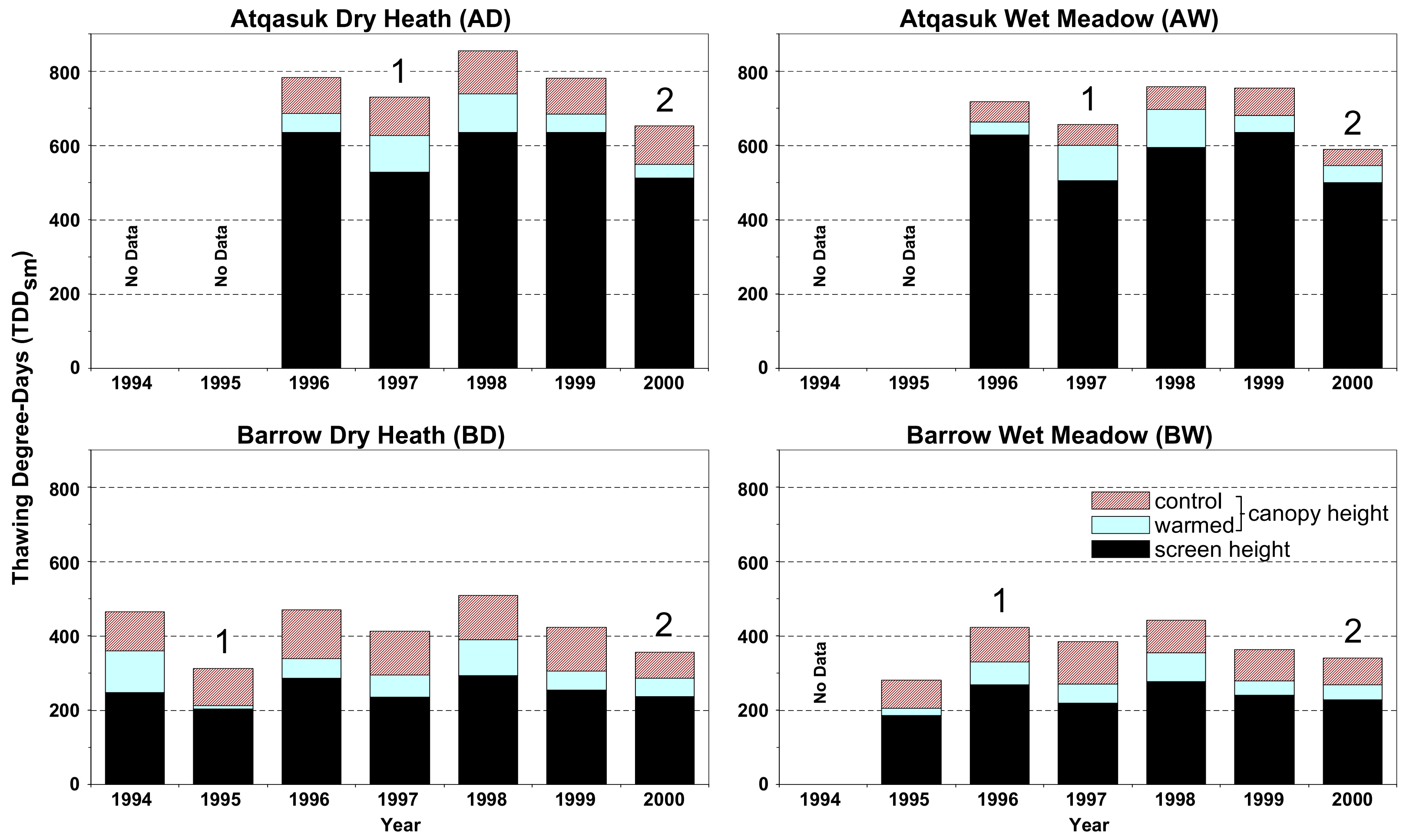

Figure V-1. Average thawing degree-days totals from snowmelt (TDD_{sm}) until August 15 for each site each year (modified from Chapter II). The year of the first and second vegetation sampling is noted with a 1 and 2 respectively, data were not collected before the site was established. Recordings were made at canopy height (13cm) over control and warmed plots and at screen height (2m).

between July and early August (Johnson and Tieszen 1976, Dennis *et al*. 1978). During 2000 plots were sampled within two weeks of the Julian day of the original sampling to minimize sampling variability due to seasonal phenological development. Vegetation sampling was performed according to procedures outlined in the ITEX Manual (Walker 1996). A 100 grid point frame strung with fine fishing line at 7 cm intervals was leveled above the height of the plant canopy. Below each grid point the uppermost contact was identified and the height was recorded. Where there were multiple contacts below a grid point, the lowermost contact was also identified. If a contact was a vascular plant or bryophyte, then the live/dead condition was recorded. When several species were intertwined, recording preference was given to vascular plants followed by lichens and then bryophytes. During the second sampling the total number of live and dead vascular plant or bryophyte contacts were counted below each grid point in order to estimate leaf area index (LAI). The location of the point frame was precisely relocated during the second sampling.

Table V-2. The year of site establishment and vegetation sampling of the four study sites. The researchers that did the sampling are denoted as follows: B - Bay; H - Hollister; N - Noyle; and W - Walker.

Site	Established	Sampling 1	Sampling 2
Atqasuk Dry Heath	1996	1997 H,N	2000 H
Atqasuk Wet Meadow	1996	1997 H,N	2000 H
Barrow Dry Heath	1994	1995 B,H,W	2000 H
Barrow Wet Meadow	1995	1996 H	2000 H

Where microscopic determination or reproductive characters were needed for taxonomic identification, classification was completed to the most detailed level possible in the field (Table V-3). The canopy profile of each community was composed of three relatively distinct strata. Contacts were assigned to strata based on growth form: ground strata (bare ground, leaf litter and non-vascular plants), short strata (all forbs, small graminoid species and prostrate shrubs), or tall strata (tall graminoids: *Alopecurus alpinus*, *Arctagrostis latifolia*, *Carex* sp., *Dupontia* sp., *Eriophorum* sp., *Hierochloe alpina*, and *Trisetum spicatum*; and erect shrubs: *Salix pulchra* and *Betula nana*).

V.3.4 Data Analysis

Point frame data were screened so that only grid points that were repeated during both samplings were used in the analysis (i.e., points occupied by markers or sensors were excluded). The analysis of each stratum was based on the uppermost contact only and included plant and non-plant contacts. For cover estimates of each taxon records of non-plant contacts (feces, litter, and bare ground) were removed. Cover information was converted to relative cover values. Species area curves were constructed to evaluate the number of grid points and plots sampled. The number of grid points sampled per plot was evaluated by graphing the cumulative number of species contacts against the number of grid points sampled after randomizing the grid point and averaging over all plots per site. Similarly, the number of plots sampled per treatment and site was evaluated by graphing the cumulative number of species encountered against the number of plots sampled after randomizing the plots.

Table V-3. The listing of all species included in each taxonomic group. The source for the species nomenclature was Hultén (1968) for vascular plants, Esslinger and Egan (1995) for lichens, Stotler and Crandall-Stotler (1977) for liverworts, and Anderson *et al.* (1990) and Anderson (1990) for mosses. The vascular and non-vascular species were assigned to growth forms according to Webber (1978) and Vitt *et al*. (1988) respectively.

Broad Growth Form **Narrow Growth Form** Species Grouping	Species
Algae	
Algae	
Nostoc	
Bryophyte	
Acrocarpous moss	
Aulacomnium	*Aulacomnium palustre* (Hedw.) Schwaegr.
	Aulacomnium turgidum (Wahlenb.) Schwaegr.
Bartramia	*Bartramia ithyphylla* Brid.
Bryoerythrophyllum	*Bryoerythrophyllum recurvirostre* (Hedw.) Chen
Bryum/*Mnium* complex	*Bryum cyclophyllum* (Schwaegr.) Bush & Schimp *in* B.S.G.
	Bryum pseudotriquetrum (Hewd.) Gaertn. *et al.*
	Bryum sp.
	Bryum subneodamense Kindb.
	Bryum teres Lindb.
	Cinclidium arcticum Buch & Schimp. *in* B.S.G.
	Cinclidium latifolium Lindb.
	Cinclidium subrotundum Lindb.
	Plagiomnium ellipticum (Brid.) T.Kop.
	Pohlia andrewsii Shaw
	Pohlia cruda (Hedw.) Lindb.
	Pohlia crudoides (Sull. & Lesq.) Broth.
	Pohlia drummondii (C.Müll.) Andrews
	Pohlia nutans (Hedw.) Lindb.
	Pseudobryum cinclidioides (Hüb.) T.Kop.
	Rhizomnium andrewsianum (Steere) T.Kop.
Conostomum	*Conostomum tetragonum* (Hedw.) Lindb.
Dicranum complex	*Dicranella crispa* (Hedw.) Schimp.
	Dicranella sp.
	Dicranella varia (Hedw.) Schimp.
	Dicranum angustum Lindb.
	Dicranum cf. acutifolium (Lindb. & Arnell.) C.Jens. *ex* Weinm.
	Dicranum elongatum Schleich. *ex* Schwaegr.
	Dicranum majus Sm.
	Dicranum sp.
	Dicranum spadiceum Zett.
	Distichium capillaceum (Hedw.) Buch & Schimp. *in* B.S.G.
	Distichium inclinatum (Hedw.) Bruch & Schimp. *in* B.S.G.
	Ditrichum flexicaule (Schwaegr.) Hampe
	Kiaeria glacialis (Berggr.) Hag.
Oncophorus	*Oncophorus virens* (Hedw.) Brid.
	Oncophorus wahlenbergii Brid.
Pogonatum	*Pogonatum dentatum* (Brid.) Brid.
Polytrichum complex	*Polytrichastrum alpinum* (Hedw.) G.L.Sm.
	Polytrichum commune Hedw.
	Polytrichum juniperinum Hedw.
	Polytrichum piliferum Hedw.
	Polytrichum strictum Brid.
	Timmia austriaca Hedw.

Table V-3. Continued.

Broad Growth Form **Narrow Growth Form** Species Grouping	Species
Bryophyte	
Acrocarpous moss	
Racomitrium	*Racomitrium canescens* (Hedw.) Brid.
	Racomitrium lanuginosum (Hedw.) Brid.
Tortella	*Tortella arctica* (Arnell) Crundw. & Nyh.
Pleurocarpous moss	
Brachythecium	*Brachythecium* sp.
	Brachythecium turgidum (Hartm.) Kindb.
Calliergon	*Calliergon giganteum* (Schimp.) Kindb.
	Calliergon richardsonii (Mitt.) Kindb. *in* Warnst.
	Calliergon trifarium (Web. & Mohr) Kindb.
	Orthothecium chryseum (Schwaegr. *in* Schultes) Schimp. *in* B.S.G.
	Pseudocalliergon turgescens (T.Jens.) Loeske
	Sarmenthypnum sarmentosum (Wahlenb.) Tuom. & T.Kop.
Campylium	*Campylium stellatum* (Hedw.) C.Jens
Drepanocladus complex	*Drepanocladus brevifolius* (Lindb.) Warnst.
	Hypnum cupressiforme Hedw.
	Hypnum sp.
	Leptobryum pyriforme (Hedw.) Wils.
	Limprichtia revolvens (Sw.) Loeske
	Loeskypnum badium (Hartm.) Paul
	Sanionia uncinata (Hedw.) Loeske
	Warnstorfia exannulata (Schimp. *in* B.S.G.) Loeske
Fissidens	*Fissidens* sp.
Hylocomium	*Hylocomium splendens* (Hewd.) Schimp. *in* B.S.G.
Meesia	*Meesia triquetra* (Richt.) Ångstr.
	Meesia uliginosa Hedw.
Rhytidium	*Rhytidium rugosum* (Hedw.) Kindb.
Tomenthypnum	*Tomentypnum nitens* (Hedw.) Loeske
Sphagnum moss	
Sphagnum	*Sphagnum contortum* Schultz
	Sphagnum girgensohnii Russ.
	Sphagnum sp.
	Sphagnum squarrosum Crome
	Sphagnum warnstorfii Russ.
Leafy liverwort	
Leafy liverwort	*Anastrophyllum* sp.
	Blepharostoma trichophyllum (L.) Dum.
	Cephaloziella sp.
	Chiloscyphus polyanthus (L.) Corda
	Diplophyllum sp.
	Lophozia sp.
	Tritomaria quinquedentata (Huds.) Buch
	Unidentified leafy liverwort
Ptilidium	*Ptilidium ciliare* (L.) Hampe
Scapania	*Scapania paludicola* Loeske et K.Müll.
Thalloid liverwort	
Aneura	*Aneura pinguis* (L.) Dum.
Unidentified bryophyte	
Unidentified bryophyte	Unidentified bryophyte
Fungus	
Fungus	
Mushroom	Mushroom

Table V-3. Continued.

Broad Growth Form	Narrow Growth Form	Species Grouping	Species
Lichen			
	Crustose		
		Crustose lichen	*Caloplaca* sp.
			Psoroma hypnorum (Vahl) Gray
			Rinodina sp.
			Unidentified crustose lichen
		Pertusariaceae complex	*Ochrolechia frigida* (Sw.) Lynge
			Ochrolechia sp.
			Pertusaria sp.
	Foliose		
		Cetraria complex 1	*Asahinea chrysantha* (Tuck.) Culb. & C.Culb.
			Flavocetraria cucullata (Bellardi) Kärnefelt & Thell
			Flavocetraria nivalis (L.) Kärnefelt & Thell
		Cetraria complex 2	*Cetraria islandica* (L.) Ach.
			Cetraria kamczatica Savicz
			Cetraria laevigata Rass.
			Cetrariella cf. delisei (Bory *ex* Schaerer) Känefelt & Thell
			Masonhalea richardsonii (Hook.) Kärnefelt
		Cetraria unidentified	*Cetraria* sp.
		Parmelia complex	*Hypogymnia* sp.
			Parmelia sp.
		Peltigera complex	*Lobaria linita* (Ach.) Rabenh.
			Nephroma sp.
			Peltigera aphthosa (L.) Willd.
			Peltigera canina (L.) Willd.
			Peltigera cf. leucophlebia (Nyl.) Gyeln.
			Peltigera cf. malacea (Ach.) Funck
			Peltigera cf. rufescens (Weis.) Humb.
			Peltigera cf. venosa (L.) Hoffm.
			Peltigera sp.
			Solorina crocea (L.) Ach.
	Fruticose		
		Alectoria complex	*Alectoria nigricans* (Ach.) Nyl.
			Alectoria ochroleuca (Hoffm.) A.Massal.
			Bryocaulon divergens (Ach.) Kärnefelt
		Cladonia complex	*Cladina mitis* (Sandst.) Hustich
			Cladina rangiferina (L.) Nyl. Syn.
			Cladonia amaurocraea (Floerke) Schaerer
			Cladonia cf. coccifera (L.) Hoffm.
			Cladonia cf. cornuta (L.) Hoffm.
			Cladonia cf. gracilis (L.) Willd.
			Cladonia cf. pleurota (Flörke) Schaerer
			Cladonia cf. squamosa Hoffm.
			Cladonia pyxidata (L.) Hoffm.
			Cladonia sp.
			Cladonia uncialis (L.) F.H.Wigg.
		Dactylina	*Dactylina arctica* (Richardson) Nyl.
		Siphula	*Siphula ceratites* (Wahlenb.) Fr.
		Sphaerophorus	*Sphaerophorus globosus* (Hudson) Vainio
		Stereocaulon	*Stereocaulon cf. alpinum* Laurer *ex* Funck
		Thamnolia	*Thamnolia subuliformis* (Ehrh.) Culb.
			Thamnolia vermicularis (Sw.) Ach. *ex* Schaerer
	Unidentified lichen		
		Unidentified lichen	Unidentified lichen

Table V-3. Continued.

Broad Growth Form Narrow Growth Form Species Grouping	Species
Forb	
Cushion Forb	
Draba lactea	*Draba lactea* Adams
Draba micropetala	*Draba micropetala* Hook.
Erect Forb	
Cardamine pratensis	*Cardamine pratensis* L.
Papaver hultenii	*Papaver hultenii* Knaben
Petasites frigidus	*Petasites frigidus* (L.) Franch.
Polygonum bistorta	*Polygonum bistorta* L.
Potentilla hyparctica	*Potentilla hyparctica* Malte
Ranunculus nivalis	*Ranunculus nivalis* L.
Saxifraga hirculus	*Saxifraga hirculus* L.
Saxifraga punctata	*Saxifraga punctata* L.
Senecio atropurpureus	*Senecio atropurpureus* (Ledeb.) Fedtsch.
Mat Forb	
Cerastium	*Cerastium beeringianum* Cham. & Schlecht.
	Cerastium jenisejense Hult.
Minuartia obtusiloba	*Minuartia obtusiloba* (Rydb.) House
Stellaria	*Stellaria edwardsii* R.Br.
	Stellaria humifusa Rottb.
	Stellaria laeta Richards.
Rosette Forb	
Antennaria friesiana	*Antennaria friesiana* (Trautv.) Ekman
Artemisia borealis	*Artemisia borealis* Pall.
Chrysosplenium tetrandrum	*Chrysosplenium tetrandrum* (Lund) T.Fries
Cochlearia officinalis	*Cochlearia officinalis* L.
Pedicularis kanei	*Pedicularis kanei* Durand
Pedicularis sudetica	*Pedicularis sudetica* Willd.
Saxifraga cernua	*Saxifraga cernua* L.
Saxifraga flagellaris	*Saxifraga flagellaris* Willd.
Saxifraga foliolosa	*Saxifraga foliolosa* R.Br.
Saxifraga hieracifolia	*Saxifraga hieracifolia* Waldst. & Kit.
Graminoid	
Caespitose Graminoid	
Luzula arctica	*Luzula arctica* Blytt
Luzula confusa	*Luzula confusa* Lindeb.
Luzula wahlenbergii	*Luzula wahlenbergii* Rupr.
Single Graminoid	
Alopecurus alpinus	*Alopecurus alpinus* Sm.
Arctagrostis latifolia	*Arctagrostis latifolia* (R.Br.) Griseb.
Arctophila fulva	*Arctophila fulva* (Trin.) Anderss.
Carex bigelowii	*Carex bigelowii* Torr.
Carex complex	*Carex aquatilis* Wahlenb.
	Carex rariflora (Wahlenb.) J.E.Sm.
	Carex rotundata Wahlenb.
	Carex subspathacea Wormsk.
Dupontia fisheri	*Dupontia fisheri* R.Br. [note misspelling in Hulten]

Table V-3. Continued.

Broad Growth Form	**Narrow Growth Form**	Species Grouping	Species
Graminoid			
	Single Graminoid		
		Eriophorum angustifolium	*Eriophorum angustifolium* Honck.
		Eriophorum complex	*Eriophorum russeolum* E. Fries
			Eriophorum scheuchzeri Hoppe
		Hierochloe alpina	*Hierochloe alpina* (Sw.) Roem. & Schult.
		Juncus biglumis	*Juncus biglumis* L.
		Poaceae complex	*Calamagrostis holmii* Lange
			Hierochloe pauciflora R.Br.
			Poa arctica R.Br.
			Poa malacantha Kom.
			Poa sp.
		Trisetum spicatum	*Trisetum spicatum* (L.) Richter
Woody deciduous			
	Deciduous Shrub		
		Betula nana	*Betula nana* L.
		Salix phlebophylla	*Salix phlebophylla* Anderss.
		Salix polaris	*Salix polaris* Wahlenb.
		Salix pulchra	*Salix pulchra* Cham.
		Salix rotundifolia	*Salix rotundifolia* Trautv.
Woody evergreen			
	Evergreen Shrub		
		Cassiope tetragona	*Cassiope tetragona* (L.) D.Don
		Diapensia lapponica	*Diapensia lapponica* L.
		Ledum palustre	*Ledum palustre* L.
		Vaccinium vitis-idaea	*Vaccinium vitis-idaea* L.
Other			
	Feces		
	Bare Ground		
	Research Equipment		
	Litter		

Canopy height was calculated by averaging the height of all live uppermost contacts sampled in each plot. Species richness was determined by summing the number of species recorded in each plot. This measure under estimates species richness because some species were aggregated into taxon that were identifiable in the field and only species that were recorded below a grid point were counted. The Shannon index was calculated based on the relative cover estimates of all species for each plot using the computer software *PC-ORD 4.0* (McCune and Mefford 1999).

Canopy height, strata, condition, species richness, and Shannon index data were analyzed using a single factor repeated ANOVA. The analyses were run separately for each site, and an overall analysis was run for all sites combined.

Community changes that occurred in the control plots were separated from the response to the experimental warming. The response to warming was then separated into an initial response assessed after 2 summers of warming, and a secondary response assessed after an additional 3-5 summers of warming. The method used to calculate the amount of change that occurred in the control plots and in response to warming is presented in Figure V-2. An estimation of the changes that occurred in the control plots (C) and in response to warming (W), which was further separated into the initial response (W_i) and secondary response (W_s), was calculated from the average of the control plots at sampling 1 (C1, baseline), the average of the control plots at sampling 2 (C2), the average of the warmed plots at sampling 1 (W1), and the average of the warmed plots at sampling 2 (W2). For example, if the C1 = 5.0, C2 = 7.0, W1 = 6.0, and W2 = 9.0, then: C = C2-C1 = 2.0; W_i = W1-C1 = 1.0; W_s = (W2-W1)-(C2-C1) = 1.0; and W = W_i + W_s = W1-C1 + [(W2-W1)-(C2-C1)] = W2-C2 = 2.0. By converting the data into the values C, W, W_i, and W_s changes that occurred in the control plots and the changes in response to experimental warming were clearly identified. Furthermore we could define and subsequently interpret the initial response to warming separately from the secondary response. The statistical significance of C, W, W_i, and W_s was determined by comparing the following populations in a one factor ANOVA: C, C1 vs C2; W_i, C1 vs W1; W_s, (W2-W1) vs (C2-C1); and W, C2 vs W2. The calculation of the difference used for Ws was performed on a plot-by-plot basis. When the populations being compared deviated greatly from normality a non-parametric Kruskall Wallis test was used. There were three potential problems concerning the calculation of values. First, a potential methodological problem arises for rare species when the cover in the warmed plots was near zero during both samplings and the cover in the control plots decreases. Such a situation could cause W_s to be significantly positive because it was calculated relative to the changes in the control plots. Second, W_i was only accurate if there were no differences in cover between treatments at the time of site establishment. Third, C may have been influenced by differences in level of species identification between the samplings. Where these problems were identified they were considered artifacts of the methods and not included in the summary of the analyses.

All data were analyzed by plot, thus all sample sizes were 24. The *p*-values reported and other summarized statistical tests were calculated in SAS (2000). An ordination of the vegetation was performed using a Correspondence Analysis (CA) that included all sites, treatments, and sampling times using SAS (2000). The relative cover values of all species (except algae, fungi, unidentified bryophytes, and unidentified lichens) and their condition (live or dead) were included in the ordination (this totaled to

123 variables). Correspondence Analysis was chosen because of its wide spread familiarity and known performance. The undesirable effects associated with the increased weight of rare species inherent with CA were believed to be minimal in this analysis because plots were distributed within four relatively homogeneous community types. However, interpretation between community types is limited in this and any ordination method. To address the influence of rare species the CA was run several times after removing rare species and the CA was also run separately by site.

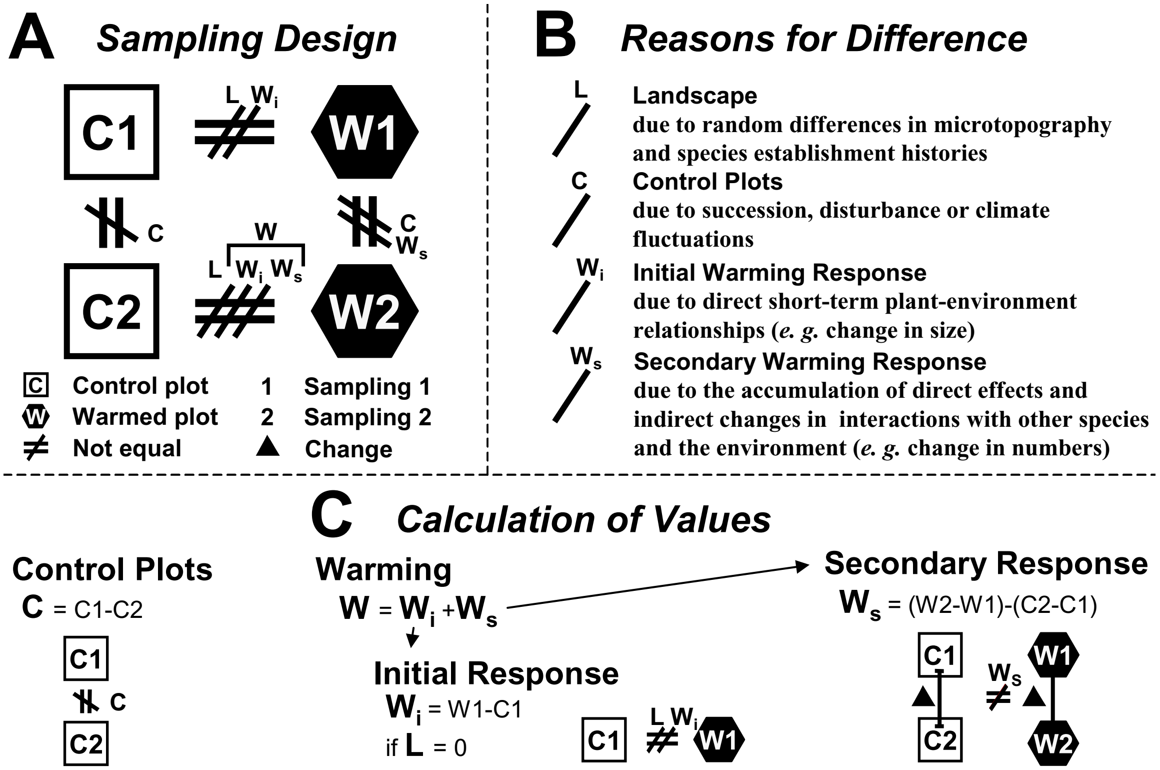

Figure V-2. Conceptual diagram of the experimental analytical design. The sampling design (***A***), theoretical reasons for differences between plots (***B***), and the formulae used to calculate differences between plots (***C***) are displayed. Mathematically the compositional change that occurred in the control plots can be estimated by calculating the difference between the control plots at sampling 2 and sampling 1 (C = C2-C1). The response to warming can be calculated as the sum of the initial and secondary responses or the difference between the warmed plots and the control plots at sampling 2 ($W = W_i + W_s = W2-C2$). The initial response to warming can be estimated by calculating the difference between the warmed plots and the control plots at sampling 1 ($W_i = W1-C1$) if it is assumed that there were no differences between the warmed and control plots prior to site establishment (L = 0). The secondary response to warming can be estimated by calculating the difference between the change in the control plots over time and the change in the warmed plots over time ($W_s = (W2-W1)-(C2-C1)$).

V.4 RESULTS

V.4.1 Species Diversity

Species area curves indicated that the sampling methods adequately characterized species assemblage at both the plots and sites level (Figure V-3). In the average plot the number of species encountered increased by less than 5 after 50 grid points were sampled, and within a site 4 or less new species were encountered after 15 plots were sampled. Species richness in the AW site decreased in the second sampling time by 5 species in the control plots and 9 species in the warmed plots relative to the control plots at the first sampling time. In the other sites species richness was within 2 species for each treatment and sampling time combination. The average species richness of each plot was lower in the warmed plots relative to the controls, and the warmed plots in the second sampling were lower than the first sampling (Figure V-4). The species richness value in the control plots was on average lower in the second sampling than the first except in the BD site. The Shannon diversity index of the warmed plots was on average lower than the control plots except in the AW site (Figure V-5). The Shannon index was also on average lower in the second sampling than the first for both treatments except in the AD site warmed plots. The species abundance curves for each site approximated a log normal distribution; the curves for the Barrow sites were longer and less steep than the Atqasuk sites (Figure V-6). The curves for the AW site were the shortest and steepest, it was also the only site where there was a large difference between treatments and sampling times (the curve for the second sampling warmed plots was shorter and steeper than the other curves).

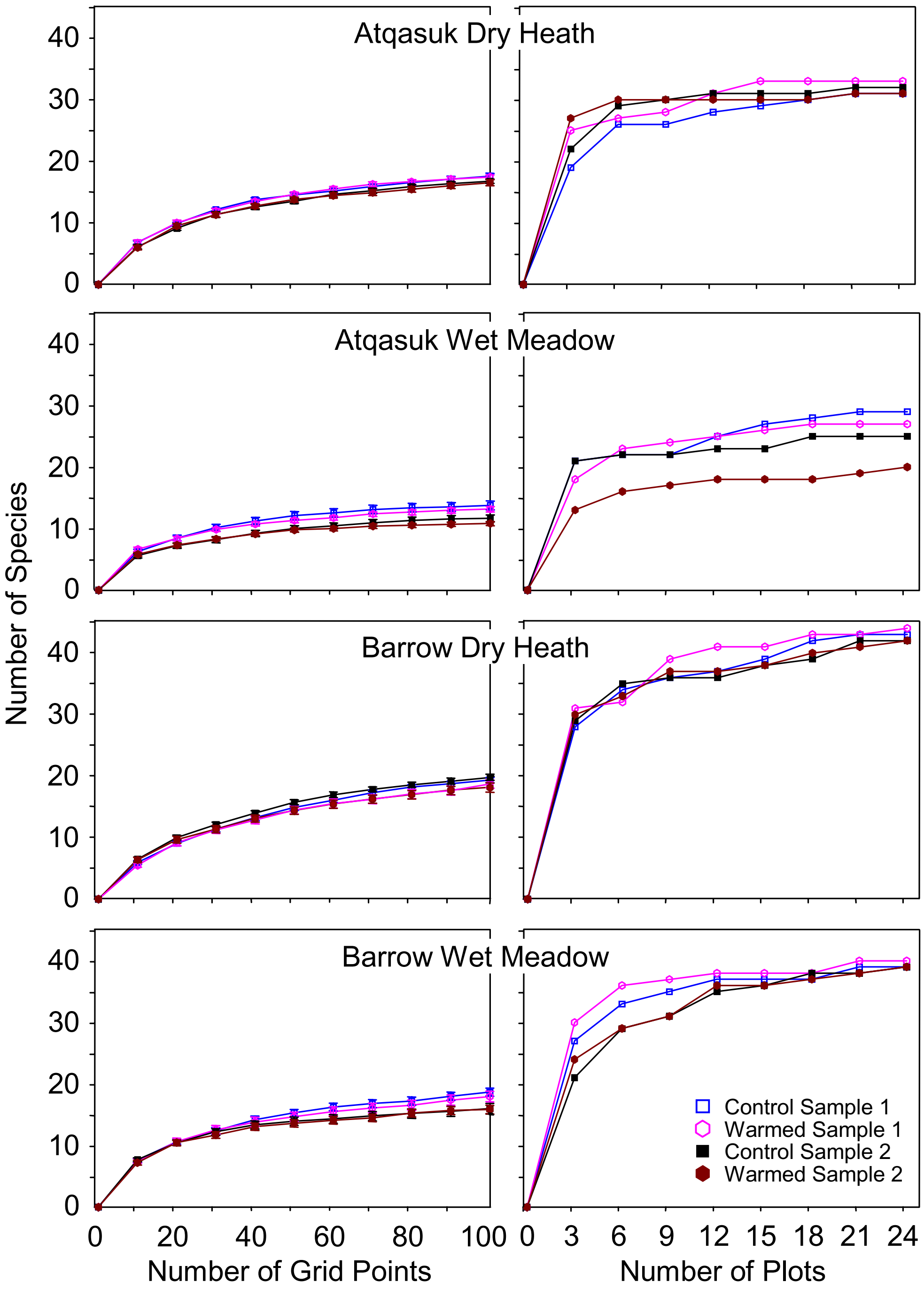

Figure V-3. Species area curves for each site. ***Left***, the cumulative number of species sampled is graphed against the number of grid points measured (error bars = ±1 SE, *n* = 24). ***Right***, the cumulative number of species encountered is graphed against the number of plots sampled.

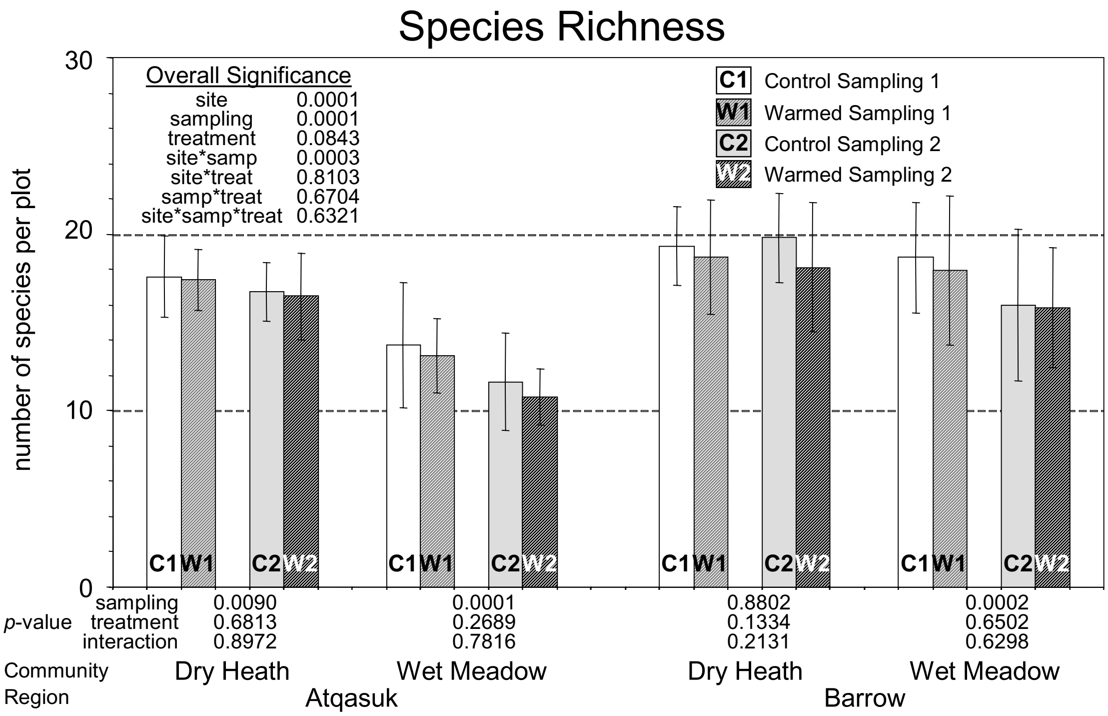

Figure V-4. Average species richness for each treatment at all sites (community and region) during both sampling times (error bars = ±1 SE, *n* = 24). Site and overall *p*-values were calculated from a two way and three way ANOVA respectively.

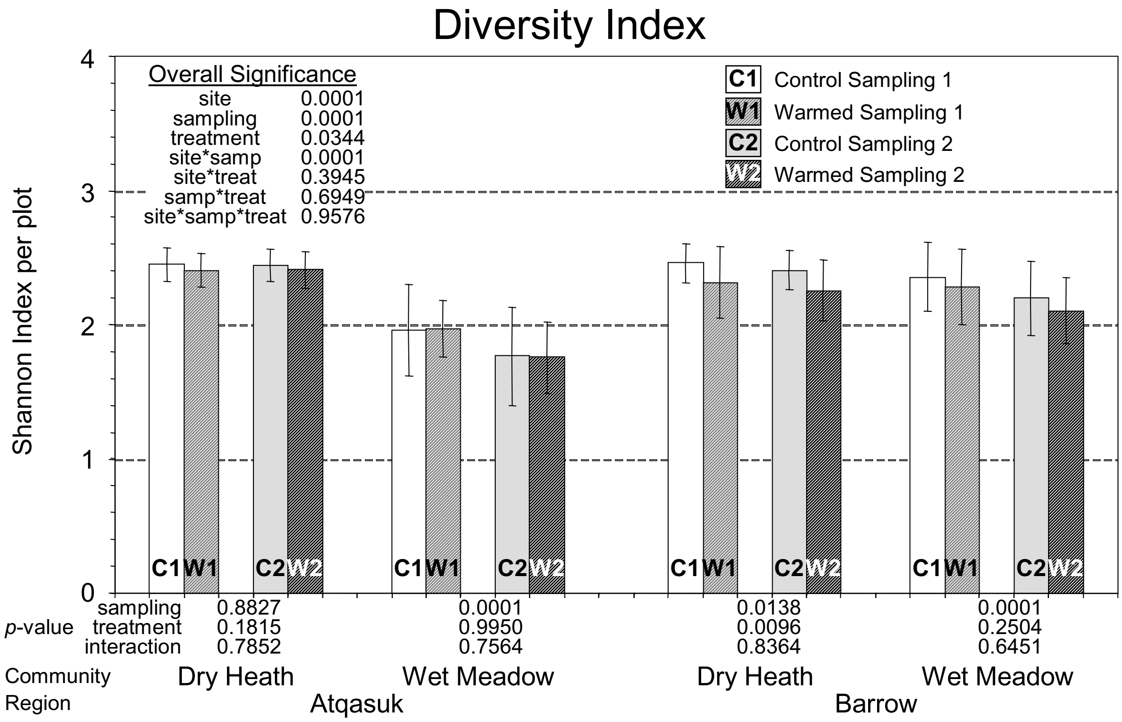

Figure V-5. Average Shannon index of diversity for each treatment at all sites (community and region) during both sampling times (error bars = ±1 SE, *n* = 24). Site and overall *p*-values were calculated from a two way and three way ANOVA respectively.

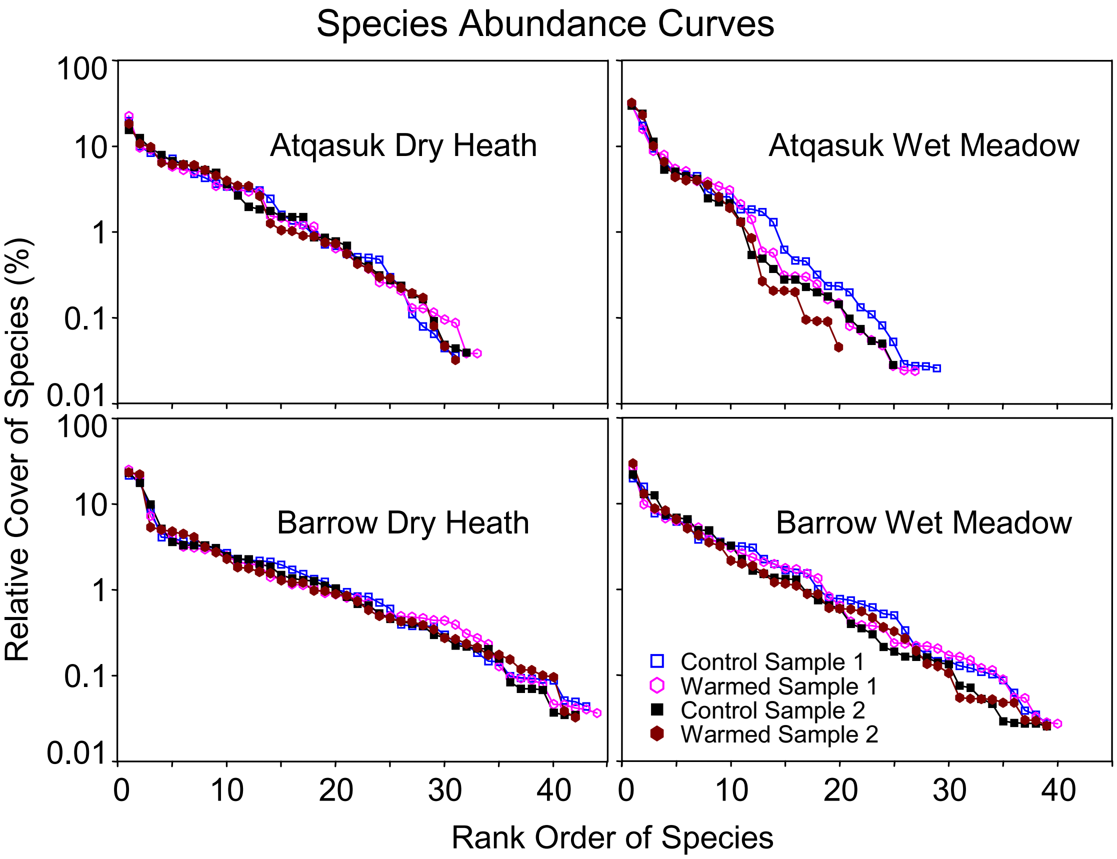

Figure V-6. Species abundance plots for each site. The relative cover of each species is graphed in sequence from highest cover to lowest cover for each treatment and sampling time.

V.4.2 Canopy Structure

Canopy height was greater in warmed plots than controls, and the warmed plots in the second sampling were on average taller than the first sampling except in the AD site (Figure V-7). There was no consistent pattern in the canopy height of control plots between samplings. All sites except for the AD site had higher relative cover of the tall stratum and lower relative cover of the ground stratum in the warmed plots and the warmed plots in the second sampling had higher relative cover of the tall stratum and lower relative cover of the ground stratum than during the first sampling (Figure V-8). There was no consistent pattern in the relative cover of the short stratum nor was there a consistent pattern in the control plots over time for any strata. There was a greater relative cover of dead contacts and lower relative cover of live contacts in the warmed plots than the control plots for all sites during both samplings (Figure V-9). There was no consistent pattern in relative cover of condition (live or dead) between sampling times. The statistical significance of treatments and sampling times for the strata (ground, short, and tall) and plant condition (live and dead) are presented in Table V-4. The count of live and dead plant matter contacts recorded during the second sampling showed that there was significantly more standing dead plant matter in the warmed plots, but there was no difference in live leaf area index between treatments (Figure V-10).

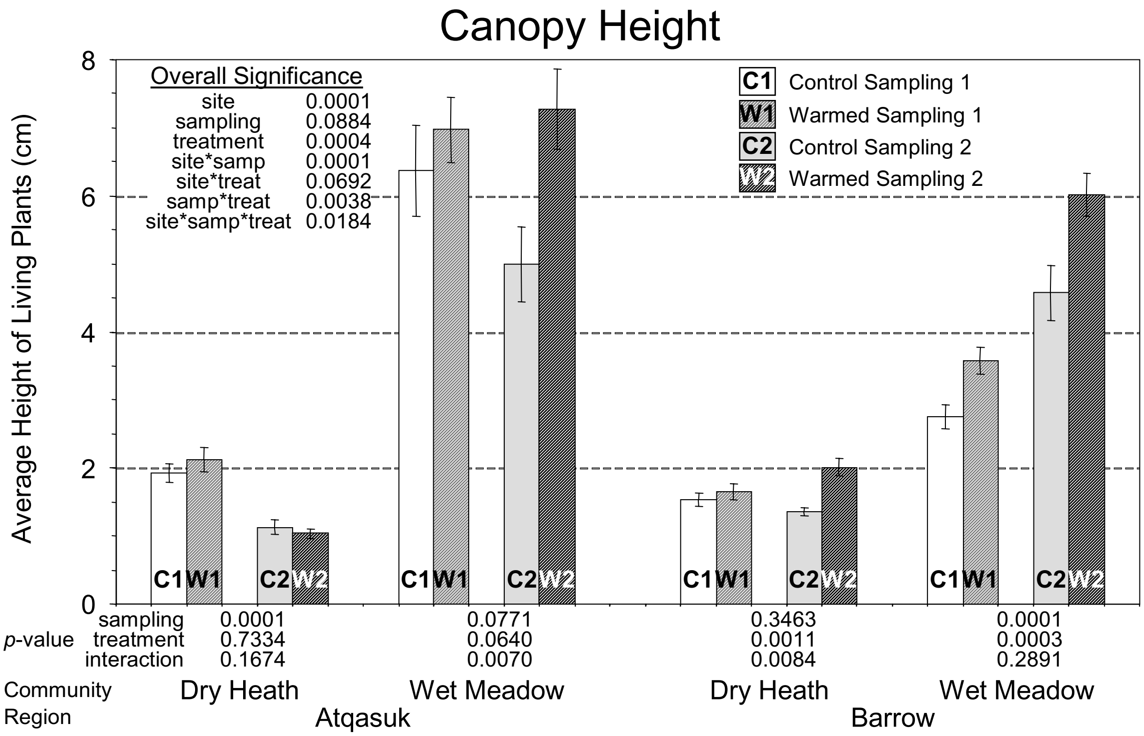

Figure V-7. Canopy height presented as the average height of all the living uppermost contacts for each treatment within all sites (community and region) during both samplings (error bars = ±1 SE, *n* = 24). Site and overall *p*-values were calculated from a two way and three way ANOVA respectively.

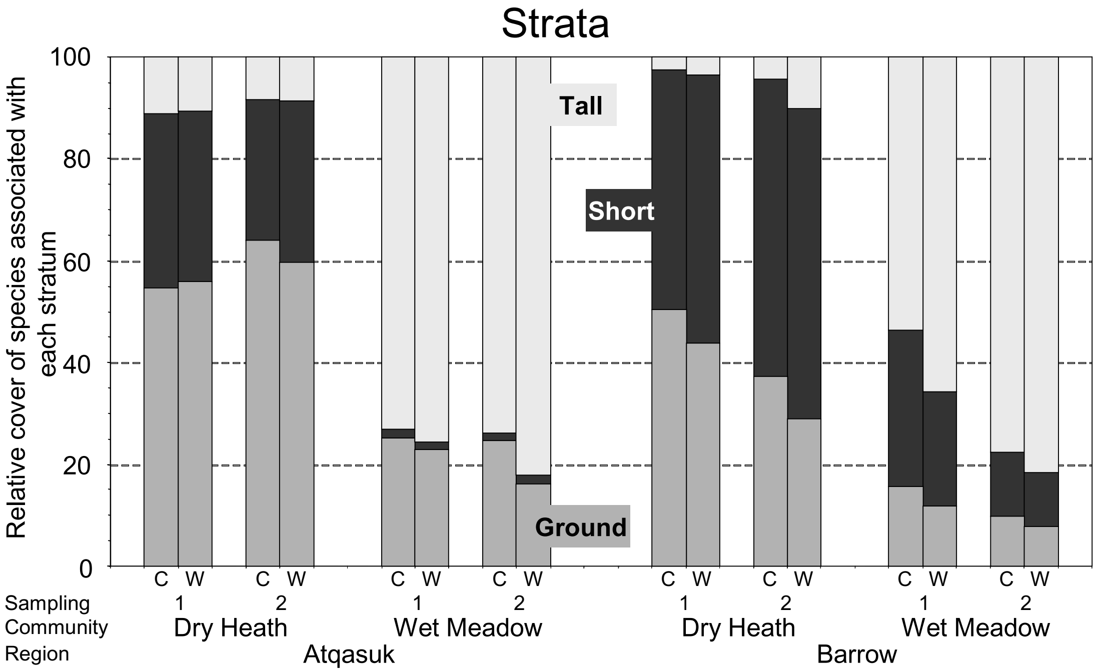

Figure V-8. Average relative cover of ground stratum (bare ground, litter, and non-vascular plants); short stratum (forbs, short graminoids, and prostrate shrubs); and tall stratum (tall graminoids and erect shrubs) for each treatment (C - control; W - warmed) within all sites (community and region) during both sampling times (*n* = 24).

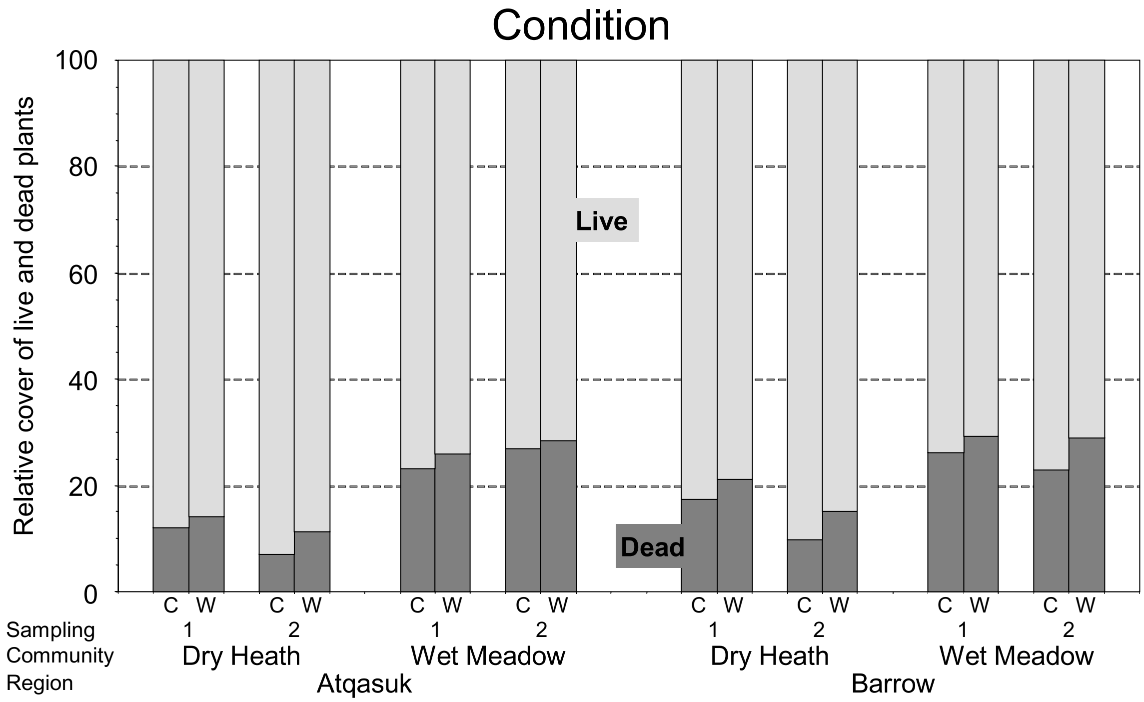

Figure V-9. Condition presented as the average relative cover of live or dead for each treatment (C - control; W - warmed) within all sites (community and region) during both sampling times (*n* = 24).

Table V-4. The significance level associated with the relative covers of strata (tall, short, and ground) and condition (live and dead). Site and overall *p*-values were calculated from two way and three way ANOVAs, respectively.

	Tall	**Short**	**Ground**	**Live/Dead**
OVERALL				
site	0.0001	0.0001	0.0001	0.0001
sampling	0.0017	0.0036	0.9355	0.0011
treatment	0.0057	0.3975	0.0038	0.0001
site*samp	0.0001	0.0001	0.0001	0.0001
site*treat	0.0657	0.0345	0.2977	0.6744
samp*treat	0.7134	0.0159	0.0466	0.3143
site*samp*treat	0.0030	0.0331	0.9645	0.7263
Atqasuk Dry Heath (AD)				
sampling	0.0064	0.0012	0.0001	0.0001
treatment	0.9830	0.3899	0.4350	0.0165
samp*treat	0.7924	0.2475	0.2754	0.2323
Atqasuk Wet Meadow (AW)				
sampling	0.0576	0.7973	0.0466	0.0001
treatment	0.2162	0.8247	0.0757	0.0666
samp*treat	0.0322	0.4881	0.0070	0.4024
Barrow Dry Heath (BD)				
sampling	0.0008	0.0001	0.0001	0.0001
treatment	0.2311	0.0580	0.0055	0.0003
samp*treat	0.0504	0.8730	0.2569	0.3708
Barrow Wet Meadow (BW)				
sampling	0.0080	0.0001	0.0008	0.4537
treatment	0.0044	0.0727	0.2755	0.0746
samp*treat	0.0529	0.0140	0.6477	0.5290

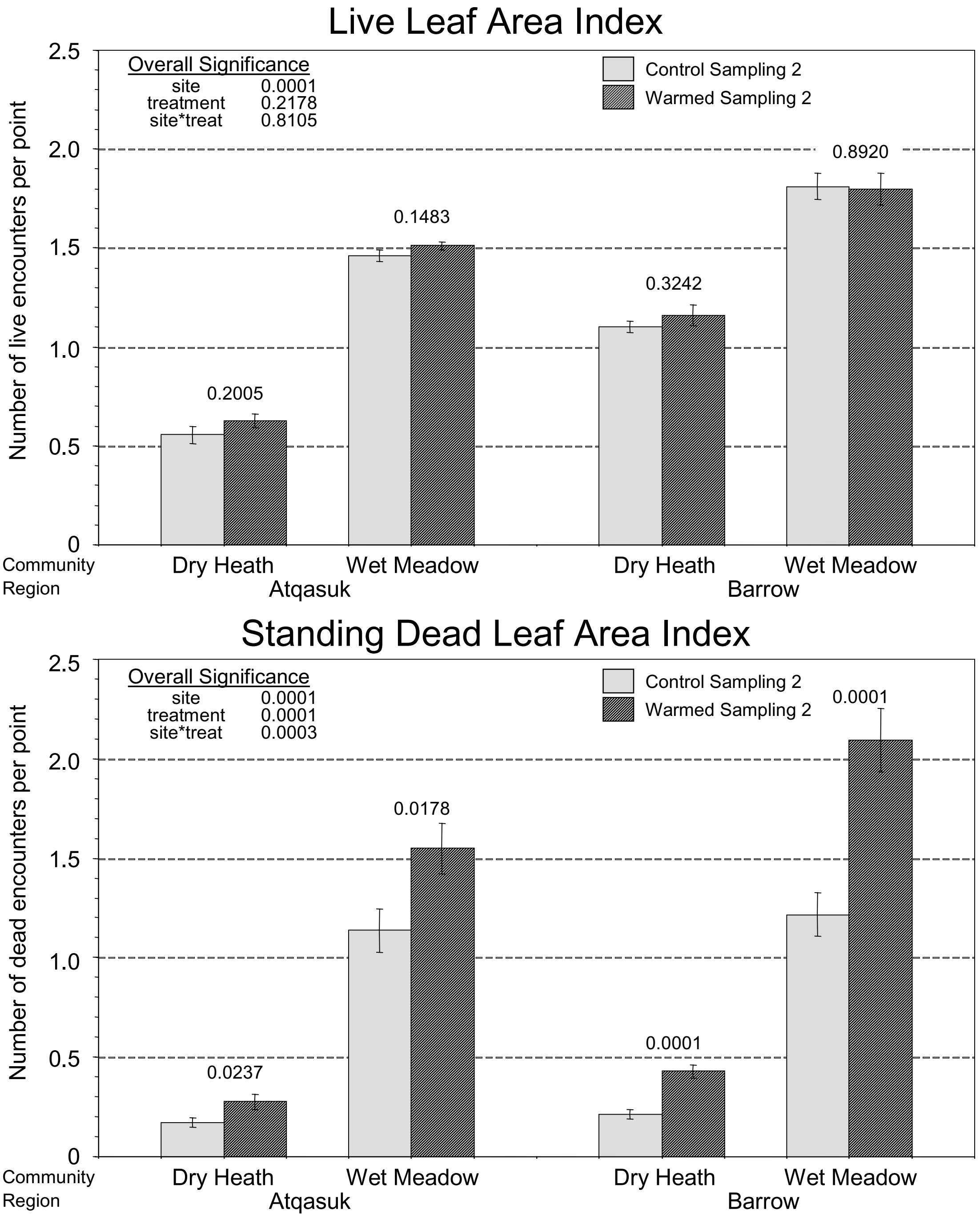

Figure V-10. Average number of live (***top***) and dead (***bottom***) contacts at each grid point (leaf area index) for each treatment within all sites (community and region) during the second sampling (error bars = ±1 SE, $n = 24$). Site and overall p-values were calculated from a one way and two way ANOVA respectively.

V.4.3 Calculated Changes in Community Attributes

The changes in community attributes that occurred in the control plots and changes in response to warming are presented in Table V-5. Significant changes are summarized in Table V-6. The most consistent change in the control plots was a trend towards decreased species diversity (¯0.5-2.7 species/plot) and these differences were significant in the wet communities; the other significant changes were site specific. The response to warming was a trend toward decreased diversity (0.1-1.7 species/plot), increased canopy height (¯0.1-2.3cm), decreased relative cover of the ground stratum (2.0-8.6%), increased relative cover of the tall stratum (0.1-8.2%), and increased standing dead plant matter (1.5-6.0%). The initial response was more consistent across sites than the secondary response; moreover, the initial response was sometimes opposite in direction to the secondary response particularly in the BW site. Caribou grazed the AD site the winter before the second sampling, which explains the decrease in canopy height and the increase in the ground stratum in the control plots, but the herbivory was generally uniform across treatments and did not alter the warming response.

V.4.4 Community Composition

The average change in relative cover of all species groupings at all four sites that occurred in control plots and in response to warming is presented in Table V-7. The significant changes are summarized in Table V-6. More change occurred in control plots than in response to warming. The initial and secondary responses to warming were often different. The change in relative cover of the broad growth forms is noted below if the they were greater than 1% regardless of their statistical significance.

Table V-5. Comparison of the magnitude of change that occurred in the ambient environment and associated with warming on species richness, Shannon index, stature, and relative cover of the groups ground stratum, short stratum, tall stratum, live and dead at the four sites (AD - Atqasuk Dry Heath, AW - Atqasuk Wet Meadow, BD - Barrow Dry Heath, BW - Barrow Wet Meadow). The values for the change that occurred in the control plots (C) and due to warming (W), separated into the initial response (W_i), and secondary response (W_s), were calculated relative to the control plots at sampling 1 (Baseline) according to the methods presented in Figure V-2. The significance values for each site were calculated from a single factor ANOVA (*p*-values: $^?$ <0.1, *<0.05, ** <0.01, *** <0.001).

Site	**Baseline** C1	**C** mean Δ	**W** mean Δ	**W_i** mean Δ	**W_s** mean Δ
		Species Richness (#species/plot)			
AD	17.6	-0.8	-0.2	-0.2	-0.1
AW	13.8	-2.1**	-0.8?	-0.6?	-0.2
BD	19.3	0.5	-1.7?	-0.6	-1.0
BW	18.7	-2.7*	-0.1	-0.7	0.6
		Shannon Index			
AD	2.5	-0.0	-0.0	-0.0	0.0
AW	2.0	-0.2?	-0.0	0.0	-0.0
BD	2.5	-0.1	-0.1**	-0.1*	-0.0
BW	2.4	-0.2*	-0.1	-0.1	-0.0
		Stature (cm)			
AD	1.9	-0.8***	-0.1	0.2	-0.3
AW	6.4	-1.4*	2.3**	0.6	1.7**
BD	1.5	-0.2	0.7***	0.1	0.5**
BW	2.7	1.8***	1.4***	0.8**	0.6
		Ground Stratum (relative cover)			
AD	54.6	9.4*	-4.4	1.3	-5.7?
AW	25.3	-0.6	-8.6**	-2.5	-6.1*
BD	50.4	-13.1***	-8.4**	-6.6*	-1.8
BW	15.7	-5.8*	-2.0	-3.9	1.9
		Short Stratum (relative cover)			
AD	34.2	-6.6*	4.3	-0.8	5.1?
AW	1.8	-0.4	0.4	-0.1	0.6
BD	47.2	11.2***	2.7	5.6?	-2.9
BW	30.7	-18.2***	-2.1	-8.2**	6.1?
		Tall Stratum (relative cover)			
AD	11.1	-2.8	0.1	-0.5	0.7
AW	73.0	1.0	8.2*	2.6	5.6*
BD	2.4	1.9	5.6	1.0	4.6
BW	53.6	24.0**	4.1	12.0**	-8.0*
		Live (relative cover)			
AD	87.9	4.9***	-4.2	-2.0	-2.2
AW	76.9	-3.8**	-1.5*	-2.7*	1.3
BD	82.5	7.7***	-5.3*	-3.6*	-1.7
BW	73.7	3.3	-6.0	-3.0	-3.0
		Dead (relative cover)			
AD	12.1	-4.9***	4.2	2.0	2.2
AW	23.1	3.8**	1.5*	2.7*	-1.3
BD	17.5	-7.7***	5.3*	3.6*	1.7
BW	26.3	-3.3	6.0	3.0	3.0

Table V-6. Summary of the significant changes that occurred in the control plots (C) and in response to warming (W), separated into the initial response (W_i) and secondary response (W_s), on community attributes (species richness, Shannon index, stature, and relative cover of the groups ground stratum, short stratum, tall stratum, live and dead) and three taxonomic levels (broad growth form, narrow growth form, and species groups) at the four study sites. An arrow in the direction of the change is presented for all statistically significant differences (*p*-value <0.05). The data are presented in Tables V-5 and V-7. The two regions are Atqasuk (A) and Barrow (B); the two community types are Dry Heath (D) and Wet Meadow (W).

Character	factor	**C**				**W**				**W_i**				**W_s**			
	region	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**
	community	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**
COMMUNITY ATTRIBUTE																	
Species Richness		–	↓	–	↓	–	–	–	–	–	–	–	–	–	–	–	–
Shannon Index		–	–	–	↓	–	–	↓	–	–	–	↓	–	–	–	–	–
Stature		↓	↓	–	↑	–	↑	↑	↑	–	–	–	↑	–	↑	↑	–
Ground Stratum		↑	–	↓	↓	–	↓	↓	–	–	–	↓	–	–	↓	–	–
Short Stratum		↓	–	↑	↓	–	–	–	–	–	–	–	↓	–	–	–	–
Tall Stratum		–	–	–	↑	–	↑	–	–	–	–	–	↑	–	↑	–	↓
Live		↑	↓	↑	–	–	↓	↓	–	–	↓	↓	–	–	–	–	–
Dead		↓	↑	↓	–	–	↑	↑	–	–	↑	↑	–	–	–	–	–
TAXON																	
Bryophytes		↑	–	–	–	–	↓	–	–	–	–	↓	–	–	↓	–	–
Acrocarpous Mosses		↑	–	↓	–	–	–	–	–	–	–	↓	–	–	–	↑	–
Bryum/Mnium complex		–	↓	–	↑	–	–	–	–	–	↓	–	–	–	–	–	–
Conostomum		↑	·	–	·	–	·	–	·	–	·	–	·	–	·	–	·
Oncophorus		·	–	–	↓	·	–	–	–	·	–	–	–	·	–	–	–
Polytrichum complex		↑	–	–	–	–	–	–	–	–	–	–	–	–	–	↑	–
Racomitrium		↑	·	–	·	–	·	–	·	–	·	–	·	–	·	–	·
Pleurocarpous Mosses		·	–	–	–	·	–	–	–	·	–	–	–	·	–	–	–
Brachythecium		·	·	·	–	·	·	·	–	·	·	·	↓	·	·	·	↑
Calliergon		·	–	·	–	·	↓	·	–	·	·	·	–	·	·	·	–
Hylocomium		·	↓	–	–	·	–	–	–	·	↓	–	–	·	–	–	–
Sphagnum Mosses		·	–	·	–	·	–	·	–	·	–	·	–	·	–	·	–
Leafy Liverworts		↑	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leafy liverwort		↑	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ptilidium		·	–	–	·	·	↓	–	·	·	·	–	·	·	·	–	·
Scapania		·	↓	·	·	·	–	·	·	·	–	·	·	·	↓	·	·
Thalloid Liverworts		·	↓	·	–	·	–	·	–	·	–	·	–	·	–	·	–
Aneura		·	↓	·	–	·	–	·	–	·	–	·	–	·	–	·	–
Lichens		–	–	–	–	–	–	↓	–	–	–	–	–	–	–	↓	–
Crustose Lichens		↑	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pertusariaceae complex		↑	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Foliose Lichens		–	–	–	–	↓	–	↓	–	↓	–	–	–	–	–	–	–
Cetraria complex 1		–	·	–	–	↓	·	↓	–	↓	·	–	–	–	·	–	–
Parmelia complex		–	·	↑	·	–	·	–	·	–	·	–	·	–	·	–	·
Peltigera complex		↓	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fruticose Lichens		–	–	–	–	–	–	↓	–	–	–	–	–	–	–	↓	–
Alectoria complex		↓	·	–	·	–	·	↓	·	–	·	–	·	↓	·	↓	·
Cladonia complex		↑	–	↑	·	–	–	–	·	–	–	–	·	–	–	–	·
Sphaerophorus		↓	–	–	·	–	–	↓	·	–	–	↓	·	–	–	–	·
Thamnolia		↓	↓	–	–	–	–	–	–	–	–	–	–	–	–	–	–

↑ significant increase
↓ significant decrease

– no change
· not present

Table V-6. Continued.

Character	factor	**C**				**W**				**W_i**				**W_s**			
	region	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**	**A**	**A**	**B**	**B**
	community	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**	**D**	**W**
TAXON																	
Wood Deciduous		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Deciduous Shrubs		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Wood Evergreen		↓	·	–	·	–	·	–	·	–	·	–	·	↑	·	–	·
Evergreen Shrubs		↓	·	–	·	–	·	–	·	–	·	–	·	↑	·	–	·
Cassiope tetragona		↓	·	–	·	–	·	–	·	–	·	–	·	–	·	–	·
Forbs		–	–	–	↓	–	–	–	–	–	–	–	–	–	–	–	–
Cushion Forbs		·	·	–	↑	·	·	–	–	·	·	–	–	·	·	–	–
Draba lactea		·	·	·	↑	·	·	·	–	·	·	·	–	·	·	·	–
Erect Forbs		–	·	–	–	–	·	–	–	–	·	–	–	–	·	–	–
Saxifraga punctata		·	·	↑	·	·	·	–	·	·	·	–	·	·	·	↓	·
Mat Forbs		–	·	–	↓	–	·	–	–	–	·	–	–	–	·	–	↑
Cerastium		·	·	·	–	·	·	·	–	·	·	·	–	·	·	·	↑
Stellaria		·	·	–	↓	·	·	–	–	·	·	–	–	·	·	–	–
Rosette Forbs		–	–	–	↓	–	–	–	–	–	–	–	–	–	–	–	–
Saxifraga cernua		·	·	–	–	·	·	–	–	·	·	–	–	·	·	↓	–
Saxifraga foliolosa		·	·	–	↓	·	·	–	–	·	·	–	–	·	·	–	↑
Graminoids		–	–	–	–	–	↑	–	↑	–	–	–	–	–	–	–	–
Caespitose Graminoids		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Single Graminoids		–	–	–	–	–	↑	↑	↑	–	–	–	–	–	–	↑	–
Alopecurus alpinus		·	·	–	–	·	·	↑	–	·	·	–	–	·	·	↑	–
Carex complex		·	–	–	–	·	–	–	–	·	–	–	↑	·	–	–	–
Carex bigelowii		–	·	·	·	–	·	·	·	–	·	·	·	–	·	·	·
Dupontia fisheri		·	–	·	↑	·	–	·	–	·	–	·	–	·	–	·	–
Eriophorum angustifolium		·	–	·	↑	·	–	·	–	·	–	·	–	·	–	·	–
Eriophorum complex		·	↓	·	↑	·	–	·	–	·	–	·	–	·	–	·	–
Juncus biglumis		·	–	–	↓	·	–	–	–	·	–	–	–	·	–	–	–
Poaceae complex		–	·	–	↓	–	·	↑	–	–	·	–	–	–	·	↑	–
Trisetum spicatum		↑	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

Table V-7. Comparison of the magnitude of change that occurred in the control plots and in response to warming on the relative cover at the four study sites. The values for the change that occurred in the control plots (C) and due to warming (W), separated into the initial response (W_i), and secondary response (W_s), were calculated relative to the control at sampling 1 (Baseline) according to the model presented in Figure V-2. The significance values for each site were calculated from a single factor ANOVA (^{ME} - significant due to a methodological error, ^{LE} - significant due to random differences in the landscape before site establishment, ^{RE} - significant due to researcher differences between sampling times (*p*-values: $^?$ <0.1, *<0.05, ** <0.01, *** <0.001). Plant growth forms are presented in bold.

Broad Growth Form					
Narrow Growth Form	**Baseline**	**C**	**W**	**W_i**	**W_s**
Species Group	C1	mean Δ	mean Δ	mean Δ	mean Δ
Atqasuk Dry Heath (AD)					
Bryophytes	**7.1**	**4.6****	**-1.4**	**-0.5**	**-1.0**
Acrocarpous Mosses	**6.3**	**3.6***	**-2.4**	**-1.1**	**-1.3**
Bryum/*Mnium* complex	0.5	0.3	-0.2	-0.3	0.1
Conostomum	0.0	0.3**	-0.1	0.0	-0.1
Dicranum complex	1.0	-0.1	0.0	-0.6?	0.6
Pogonatum	1.4	-0.5	-0.1	-0.1	0.0
Polytrichum complex	3.4	3.1*	-1.7	-0.1	-1.6
Racomitrium	0.0	0.5*	-0.2	0.0	-0.2
Leafy Liverworts	**0.7**	**0.8***	**1.2?**	**0.8**	**0.4**
Leafy liverwort	0.7	0.8*	1.2?	0.8	0.4
Unidentified Bryophytes	**0.1**	**0.1**	**-0.2**	**-0.1?**	**0.0**
Unidentified bryophyte	0.1	0.1	-0.2	-0.1?	0.0
Lichens	**45.6**	**4.7**	**-4.3**	**-0.1**	**-4.2**
Crustose Lichens	**1.3**	**5.7*****	**-0.6**	**0.0**	**-0.6**
Crustose lichen	0.0	0.0	0.0	0.0	0.1
Pertusariaceae complex	1.3	5.7***	-0.6	0.0	-0.6
Foliose Lichens	**11.2**	**-1.1**	**-3.4****	**-2.1***	**-1.4**
Cetraria complex 1	8.7	-0.4	-2.8**	-2.7**	-0.1
Cetraria complex 2	1.7	-0.1	-0.6	-0.1	-0.6
Cetraria unidentified	0.0	0.0	0.0	0.1	-0.1
Parmelia complex	0.3	-0.1	0.0	0.5	-0.5?
Peltigera complex	0.5	-0.5**	0.0	0.1	-0.1
Fruticose Lichens	**33.1**	**0.1**	**-0.2**	**2.0**	**-2.2**
Alectoria complex	20.6	-7.7***	-1.8	2.8	-4.6*
Cladonia complex	4.9	11.2***	2.9	0.4	2.6
Dactylina	0.6	0.1	-0.4?	-0.3?	-0.1
Sphaerophorus	3.4	-1.6**	-0.5	-0.3	-0.2
Stereocaulon	0.1	-0.1	0.0	0.0	0.1
Thamnolia	3.5	-2.0**	-0.5	-0.4	-0.1
Wood Deciduous	**0.5**	**-0.1**	**0.0**	**-0.4**	**0.3**
Deciduous Shrubs	**0.5**	**-0.1**	**0.0**	**-0.4**	**0.3**
Salix phlebophylla	0.5	-0.1	0.0	-0.4	0.3
Wood Evergreen	**28.1**	**-4.8***	**3.1**	**-1.7**	**4.8***
Evergreen Shrubs	**28.1**	**-4.8***	**3.1**	**-1.7**	**4.8***
Cassiope tetragona	7.6	-2.5**	1.2	-0.3	1.5?
Diapensia lapponica	3.8	-1.0	0.8	-0.2	1.1?
Ledum palustre	10.4	-0.5	0.3	-0.4	0.7
Vaccinium vitis-idaea	6.3	-0.8	0.8	-0.8	1.6?

Table V-7. Continued.

Broad Growth Form **Narrow Growth Form** Species Group	**Baseline** C1	**C** mean Δ	**W** mean Δ	**W_i** mean Δ	**W_s** mean Δ
		Atqasuk Dry Heath (AD)			
Forbs	**0.7**	**-0.3**	**0.8**	**0.4**	**0.4**
Erect Forbs	**0.7**	**-0.4**	**0.5**	**0.0**	**0.5** ?
Polygonum bistorta	0.7	-0.4	0.5	0.0	0.5 ?
Mat Forbs	**0.0**	**0.1**	**0.3**	**0.3** LE	**0.1**
Minuartia obtusiloba	0.0	0.1	0.3	0.3 LE	0.1
Rosette Forbs	**0.0**	**0.0**	**0.0**	**0.1**	**-0.2** ?
Antennaria friesiana	0.0	0.0	0.0	0.0	-0.1
Artemisia borealis	0.0	0.0	0.0	0.1	-0.1
Graminoids	**17.9**	**-4.0**	**1.8**	**2.3**	**-0.5**
Caespitose Graminoids	**7.7**	**-1.6**	**0.8**	**2.2**	**-1.4**
Luzula arctica	0.2	-0.1	0.1	0.2	-0.2
Luzula confusa	7.5	-1.5	0.8	2.0	-1.3
Single Graminoids	**10.2**	**-2.5**	**1.0**	**0.1**	**0.9**
Arctagrostis latifolia	0.1	0.0	-0.1	0.0	-0.1
Carex bigelowii	3.2	-1.3	-0.8	-2.0	1.2 ?
Hierochloe alpina	4.4	-2.4 ?	1.5	0.9	0.7
Poaceae complex	0.0	0.0	0.0	0.1	-0.1
Trisetum spicatum	2.5	1.2 *	0.4	1.0	-0.7
		Atqasuk Wet Meadow (AW)			
Bryophytes	**53.1**	**1.8** ?	**-2.6** **	**-0.3**	**-2.3** *
Acrocarpous Mosses	**19.1**	**0.1**	**-1.5**	**0.0**	**-1.5**
Aulacomnium	4.7	0.0	-0.6	1.0	-1.5 ?
Bryum/*Mnium* complex	1.8	-1.7 ***	0.0	-1.6 ***	1.6 ME
Dicranum complex	0.1	0.1	0.0	-0.1 ?	0.1
Oncophorus	9.8	2.1	-1.4	-0.6	-0.8
Polytrichum complex	2.7	-0.4	0.4	1.4	-0.9 ?
Pleurocarpous Mosses	**7.9**	**-2.1**	**1.0**	**0.8**	**0.3**
Calliergon	0.5	-0.3 ?	-0.2 *	-0.2	0.0
Drepanocladus complex	7.0	-1.3	1.3	1.4	-0.1
Hylocomium	0.5	-0.5 **	0.0	-0.4 *	0.4 ME
Tomenthypnum	0.0	0.1	-0.1	0.0	-0.1
Sphagnum Mosses	**1.9**	**0.6**	**-0.6**	**0.3**	**-0.8**
Sphagnum	1.9	0.6	-0.6	0.3	-0.8
Leafy Liverworts	**22.3**	**4.8**	**-1.5**	**-0.9**	**-0.6**
Leafy liverwort	18.2	6.9	-1.0	-1.6	0.6
Ptilidium	1.4	-0.9 ?	-0.4 *	-0.8	0.4
Scapania	2.7	-1.3 *	0.0	1.4 ?	-1.5 *
Thalloid Liverworts	**1.9**	**-1.6** **	**-0.1**	**-0.5**	**0.4**
Aneura	1.9	-1.6 **	-0.1	-0.5	0.4
Unidentified Bryophytes	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Unidentified bryophyte	0.0	0.0	0.0	0.0	0.0
Fungi	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Fungi	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Unidentified mushroom	0.0	0.0	0.0	0.0	0.0

Table V-7. Continued.

Broad Growth Form Narrow Growth Form Species Group	Baseline C1	C mean Δ	W mean Δ	W_i mean Δ	W_s mean Δ
		Atqasuk Wet Meadow (AW)			
Lichens	**0.6**	**-0.3**	**-0.2** ?	**-0.1**	**-0.1**
Crustose Lichens	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Pertusariaceae complex	0.0	0.0	0.0	0.0	0.0
Foliose Lichens	**0.2**	**-0.1**	**0.0**	**0.1**	**-0.1**
Cetraria complex 2	0.1	-0.1	0.0	0.1	-0.1
Cetraria unidentified	0.0	0.0	0.0	0.0	0.0
Peltigera complex	0.0	0.0	0.0	0.0	0.0
Fruticose Lichens	**0.5**	**-0.2**	**-0.1** ?	**-0.1**	**0.0**
Cladonia complex	0.2	-0.1	-0.1	0.0	-0.1
Siphula	0.0	0.1 ?	-0.1 ?	0.0	-0.1 ?
Sphaerophorus	0.0	0.0	0.0	0.0	0.0
Thamnolia	0.2	-0.2 *	0.0	-0.1	0.1
Wood Deciduous	**5.8**	**0.5**	**-0.8**	**-1.6**	**0.8**
Deciduous Shrubs	**5.8**	**0.5**	**-0.8**	**-1.6**	**0.8**
Betula nana	0.2	0.1	-0.4 ?	-0.2	-0.1 ME
Salix polaris	0.7	-0.1	0.3	0.0	0.4
Salix pulchra	4.9	0.5	-0.7	-1.3	0.6
Forbs	**0.3**	**0.0**	**-0.1**	**0.0**	**-0.1**
Rosette Forbs	**0.3**	**0.0**	**-0.1**	**0.0**	**-0.1**
Pedicularis sudetica	0.3	0.0	-0.1	0.0	-0.1
Graminoids	**40.2**	**-2.0**	**3.7** *	**1.9**	**1.8**
Caespitose Graminoids	**0.1**	**-0.1**	**0.0**	**0.0**	**0.0**
Luzula confusa	0.0	0.0	0.0	0.0	0.0
Luzula wahlenbergii	0.0	0.0	0.0	0.1	-0.1
Single Graminoids	**40.1**	**-1.9**	**3.7** *	**1.9**	**1.8**
Carex complex	31.8	-0.6	2.4 ?	1.3	1.1
Dupontia fisheri	0.1	0.1	0.0	0.2	-0.1
Eriophorum angustifolium	3.1	1.3	-0.6	0.1	-0.8
Eriophorum complex	5.0	-2.7 **	1.9 ?	0.3	1.5
Juncus biglumis	0.1	-0.1	0.0	-0.1	0.1
		Barrow Dry Heath (BD)			
Bryophytes	**12.5**	**-2.2**	**-1.4**	**-3.9** *	**2.5** ?
Acrocarpous Mosses	**8.5**	**-2.4** *	**0.4**	**-2.9** *	**3.3** *
Aulacomnium	0.8	0.0	0.0	-0.3	0.4
Bartramia	0.0	0.0	0.0	0.0	-0.1
Bryum/*Mnium* complex	1.0	-0.7 ?	-0.1	-0.5	0.4
Bryoerythrophyllum	0.0	0.0	0.2 ?	0.0	0.2 ?
Conostomum	0.2	0.2	-0.3 ?	-0.2	-0.1
Dicranum complex	2.2	-0.3	-0.1	-0.2	0.1
Oncophorus	0.2	0.0	0.0	-0.2	0.2
Polytrichum complex	1.8	-0.7	0.6	-0.8	1.4 *
Racomitrium	2.2	-0.9	0.0	-0.8	0.7 ?
Tortella	0.0	0.0	0.1	0.0	0.1
Pleurocarpous Mosses	**2.3**	**0.6**	**-1.0**	**-0.8**	**-0.1**
Drepanocladus complex	0.2	-0.1	0.2	-0.1	0.2
Hylocomium	2.0	0.5	-1.3	-1.2	-0.1
Rhytidium	0.0	0.0	0.0	0.0	0.0
Tomenthypnum	0.1	0.1	0.2	0.4	-0.2

Table V-7. Continued.

Broad Growth Form					
Narrow Growth Form	**Baseline**	**C**	**W**	**W_i**	**W_s**
Species Group	C1	mean Δ	mean Δ	mean Δ	mean Δ
	Barrow Dry Heath (BD)				
Leafy Liverworts	**1.4**	**0.0**	**-0.8**	**-0.3**	**-0.5**
Leafy liverwort	1.4	0.0	-0.8	-0.3	-0.5
Ptilidium	0.0	0.0	0.0	0.0	0.0
Unidentified Bryophytes	**0.4**	**-0.4** RE	**0.0**	**0.1**	**-0.1**
Unidentified bryophyte	0.4	-0.4 RE	0.0	0.1	-0.1
Lichens	**31.1**	**-3.6** ?	**-9.1** ***	**-3.5**	**-5.6** **
Crustose Lichens	**3.4**	**-1.2**	**-0.3**	**-0.3**	**0.0**
Crustose lichen	0.0	0.2 ?	-0.1	0.0	-0.1
Pertusariaceae complex	3.4	-1.4	-0.2	-0.3	0.1
Foliose Lichens	**7.2**	**-1.1**	**-1.8** *	**-0.8**	**-1.0**
Cetraria complex 1	3.2	0.2	-1.0 *	-0.4	-0.6
Cetraria complex 2	0.9	0.7	-0.6	0.0	-0.6
Cetraria unidentified	2.3	-2.2 RE	0.0	-0.1	0.1
Parmelia complex	0.1	0.6 **	-0.2 ?	-0.1	-0.1
Peltigera complex	0.7	-0.3	0.1	-0.2	0.3
Fruticose Lichens	**19.2**	**0.0**	**-7.0** ***	**-2.4**	**-4.6** ***
Alectoria complex	9.0	1.2	-4.6 **	-1.5	-3.1 **
Cladonia complex	0.1	0.5 *	-0.3	0.0	-0.2
Dactylina	3.8	-0.6	-0.3	-0.5	0.2
Sphaerophorus	1.6	-0.2	-1.1 **	-1.1 **	0.0
Stereocaulon	0.6	-0.3	-0.2	-0.2	0.0
Thamnolia	4.1	-0.4	-0.5	1.0	-1.5 ?
Unidentified Lichens	**1.3**	**-1.3** RE	**0.0**	**-0.1**	**0.1**
Unidentified lichen	1.3	-1.3 RE	0.0	-0.1	0.1
Wood Deciduous	**22.2**	**1.6**	**-1.1**	**-1.7**	**0.6**
Deciduous Shrubs	**22.2**	**1.6**	**-1.1**	**-1.7**	**0.6**
Salix rotundifolia	22.2	1.6	-1.1	-1.7	0.6
Wood Evergreen	**18.7**	**-0.1**	**5.4** LE	**7.1** LE	**-1.7**
Evergreen Shrubs	**18.7**	**-0.1**	**5.4** LE	**7.1** LE	**-1.7**
Cassiope tetragona	18.6	-0.4	5.8 LE	7.2 LE	-1.4
Vaccinium vitis-idaea	0.1	0.3	-0.4	-0.1	-0.3
Forbs	**7.1**	**0.6**	**0.4**	**0.2**	**0.2**
Cushion Forbs	**0.1**	**0.0**	**0.1**	**0.0**	**0.0**
Draba micropetala	0.1	0.0	0.1	0.0	0.0
Erect Forbs	**3.6**	**0.2**	**-0.9**	**0.2**	**-1.2**
Papaver hultenii	0.1	0.0	0.3	0.2	0.1
Potentilla hyparctica	2.8	-0.4	-1.0 ?	-0.2	-0.8
Saxifraga punctata	0.4	0.8 *	-0.4	0.3	-0.7 *
Senecio atropurpureus	0.4	-0.2	0.1	-0.1	0.2
Mat Forbs	**3.2**	**0.2**	**1.2**	**-0.1**	**1.3**
Stellaria	3.2	0.2	1.2	-0.1	1.3
Rosette Forbs	**0.3**	**0.2**	**0.1**	**0.1**	**0.0**
Pedicularis kanei	0.3	0.2	0.0	-0.1	0.1
Saxifraga cernua	0.0	0.1	-0.1	0.1 ?	-0.2 *
Saxifraga foliolosa	0.0	0.0	0.1	0.0	0.1

Table V-7. Continued.

Broad Growth Form					
Narrow Growth Form	**Baseline**	**C**	**W**	**W_i**	**W_s**
Species Group	C1	mean Δ	mean Δ	mean Δ	mean Δ
	Barrow Dry Heath (BD)				
Graminoids	**8.4**	**3.7**	**5.8**	**1.8**	**4.0** $^{?}$
Caespitose Graminoids	**4.6**	**1.4** $^{?}$	**-0.8**	**0.5**	**-1.3**
Luzula arctica	0.4	0.3	0.3	0.5	-0.2 $^{?}$
Luzula confusa	4.2	1.1	-1.1	0.0	-1.1
Single Graminoids	**3.8**	**2.2**	**6.6** *	**1.3**	**5.3** **
Alopecurus alpinus	0.2	-0.2	1.0 *	0.2	0.8 **
Arctagrostis latifolia	2.3	1.1	1.5	-0.3	1.8
Carex complex	0.1	0.1	1.4	1.0	0.4
Juncus biglumis	0.1	0.0	0.0	-0.1	0.0
Poaceae complex	1.0	1.3	2.8 ***	0.4	2.4 **
	Barrow Wet Meadow (BW)				
Algae	**0.1**	**-0.1**	**0.1**	**0.1**	**-0.1**
Algae	**0.1**	**-0.1**	**0.1**	**0.1**	**-0.1**
Nostoc	0.1	-0.1	0.1	0.1	-0.1
Bryophytes	**27.9**	**3.0**	**-4.6** $^{?}$	**-0.8**	**-3.8**
Acrocarpous Mosses	**11.3**	**2.6**	**-1.9**	**-1.1**	**-0.8**
Aulacomnium	0.0	0.0	0.0	0.2	-0.2
Bryum/Mnium complex	0.8	6.1 ***	-0.3	0.9 $^{?}$	-1.2
Dicranum complex	6.2	-1.3	-0.6	-1.0	0.4
Oncophorus	3.6	-1.9 *	-0.8 $^{?}$	-1.0	0.2
Polytrichum complex	0.7	-0.3	-0.3	-0.3	0.0
Pleurocarpous Mosses	**13.6**	**1.0**	**-2.7**	**0.5**	**-3.2**
Brachythecium	0.7	0.0	-0.2	-0.7 *	0.6 *
Calliergon	3.3	1.6	-1.3	0.6	-1.9
Campylium	3.1	-1.6	0.5	0.4	0.1
Drepanocladus complex	6.0	0.6	-1.4	0.4	-1.8
Fissidens	0.0	0.0	0.0	0.0	0.0
Hylocomium	0.0	0.0	0.0	0.0	0.0
Meesia	0.5	0.1	0.0	-0.1	0.1
Tomenthypnum	0.0	0.2 $^{?}$	-0.2 $^{?}$	0.0	-0.2 $^{?}$
Sphagnum Mosses	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Sphagnum	0.0	0.0	0.0	0.0	0.0
Leafy Liverworts	**2.3**	**0.0**	**-0.4**	**0.1**	**-0.5**
Leafy liverwort	2.3	0.0	-0.4	0.1	-0.5
Thalloid Liverworts	**0.6**	**-0.4**	**0.4**	**-0.2**	**0.6**
Aneura	0.6	-0.4	0.4	-0.2	0.6
Unidentified Bryophytes	**0.1**	**-0.1** ^{RE}	**0.0**	**0.0**	**0.0**
Unidentified bryophyte	0.1	-0.1 ^{RE}	0.0	0.0	0.0
Fungi	**0.1**	**-0.1**	**0.0**	**-0.1**	**0.1**
Fungi	**0.1**	**-0.1**	**0.0**	**-0.1**	**0.1**
Mushroom	0.1	-0.1	0.0	-0.1	0.1

Table V-7. Continued.

Broad Growth Form **Narrow Growth Form** Species Group	**Baseline** C1	**C** mean Δ	**W** mean Δ	**W_i** mean Δ	**W_s** mean Δ
	Barrow Wet Meadow (BW)				
Lichens	**1.9**	**-0.1**	**-0.8**	**-0.9**	**0.1**
Crustose Lichens	**0.0**	**0.0**	**0.1**	**0.0**	**0.1**
Pertusariaceae complex	0.0	0.0	0.1	0.0	
Foliose Lichens	**1.9**	**-0.1**	**-0.8**	**-0.9**	**0.1**
Cetraria complex 1	0.2	-0.2 ?	0.0	-0.2 ?	0.2 ME
Cetraria complex 2	0.0	0.2	-0.1	0.0	-0.1
Cetraria unidentified	0.1	0.2	-0.2	0.0	-0.3
Peltigera complex	1.6	-0.2	-0.4	-0.7	0.3
Fruticose Lichens	**0.0**	**0.0**	**0.0**	**0.1**	**-0.1**
Dactylina	0.0	0.0	0.0	0.0	0.0
Stereocaulon	0.0	0.0	0.0	0.1	-0.1
Thamnolia	0.0	0.0	0.0	0.1	-0.1
Wood Deciduous	**0.1**	**-0.1**	**0.3** ?	**0.1**	**0.2**
Deciduous Shrubs	**0.1**	**-0.1**	**0.3** ?	**0.1**	**0.2**
Salix rotundifolia	0.1	-0.1	0.3 ?	0.1	0.2
Forbs	**13.1**	**-4.4** *	**-0.1**	**-1.7**	**1.5**
Cushion Forbs	**0.0**	**0.2** *	**0.0**	**0.1** ?	**-0.1**
Draba lactea	0.0	0.2 *	0.0	0.1 ?	-0.1
Draba micropetala	0.0	0.0	0.0	0.0	0.0
Erect Forbs	**5.0**	**-0.4**	**-1.6**	**-1.2**	**-0.4**
Cardamine pratensis	1.0	-0.1	0.3	0.5 ?	-0.3
Petasites frigidus	0.1	-0.1	0.2	0.1	0.1
Ranunculus nivalis	0.0	0.0	0.0	0.0	0.0
Saxifraga hirculus	3.8	-0.3	-2.0 ?	-1.7 ?	-0.2
Mat Forbs	**5.2**	**-3.2** **	**1.3**	**-0.7**	**2.0** **
Cerastium	2.0	-1.3	0.5	-0.6	1.1 *
Stellaria	3.2	-1.9 **	0.9	-0.1	0.9
Rosette Forbs	**2.9**	**-0.9** *	**0.1**	**0.1**	**0.0**
Chrysosplenium tetrandrum	0.0	0.0	0.0	0.0	0.0
Cochlearia officinalis	0.1	0.0	0.0	0.2	-0.1
Saxifraga cernua	1.5	-0.2	-0.2	0.2	-0.4
Saxifraga foliolosa	0.5	-0.3 **	0.3	-0.2	0.4 *
Saxifraga hieracifolia	0.8	-0.4	0.0	-0.1	0.1
Graminoids	**56.8**	**1.8**	**5.1** *	**3.2**	**2.0**
Caespitose Graminoids	**0.3**	**-0.1**	**0.0**	**0.0**	**0.1**
Luzula arctica	0.2	0.0	0.0	0.0	0.0
Luzula confusa	0.1	-0.1	0.1	0.0	0.0
Single Graminoids	**56.4**	**2.0**	**5.1** *	**3.2**	**1.9**
Alopecurus alpinus	0.0	0.0	0.0	0.0	0.0
Carex complex	19.8	2.2	7.5 ?	6.7 *	0.8
Dupontia fisheri	7.2	5.4 **	-3.7 ?	-1.6	-2.2
Eriophorum angustifolium	7.8	5.2 *	0.1	-1.0	1.1
Eriophorum complex	1.7	1.6 *	-0.1	0.3	-0.3
Juncus biglumis	0.3	-0.3 *	0.0	-0.1	0.1
Poaceae complex	19.7	-12.0 ***	1.3	-1.2	2.4

Changes in the control plots were site specific. In the AD site bryophytes increased (4.6%); groups within the lichens increased (5.7-11.2%) and decreased (0.5-7.7%) resulting in a non-significant overall increase in lichens (4.7%); evergreen shrubs decreased (4.8%) – particularly *Cassiope tetragona* (2.5%); and *Trisetum spicatum* increased (1.2%) despite a non-significant overall decrease in graminoids (4.0%). In the AW site groups within the bryophytes decreased (0.5-1.7%) despite a non-significant overall increase in bryophytes (1.8%); the lichen *Thamnolia* decreased (0.2%); and *Eriophorum* complex decreased (2.7%) contributing to a non-significant overall decrease in graminoids (1.9%). In the BD site acrocarpous mosses decreased (2.4%) contributing to a non-significant overall decrease in bryophytes (2.2%); groups within the lichens increased (0.5-0.6%) despite a non-significant overall decrease in lichens (3.6%), there was a non-significant overall increase in deciduous shrubs (1.6%); the forb *Saxifraga punctata* increased (0.8%); and there was a non-significant overall increase in the graminoids (3.7%). In the BW site groups within the acrocarpous mosses increased (6.1%) and decreased (1.9%) contributing to a non-significant overall decrease in bryophytes (3.0%); forbs decreased (4.4%) – except for *Draba lactea* which increased (0.2%); and groups with the graminoids increased (1.6-5.4%) and decreased (0.3-12.0%) resulting in an overall non-significant increase in graminoids (1.8%).

The significant changes in response to warming were consistent within growth forms: if there was a change, then there was a decrease in bryophytes (1.4-4.6%) or lichens (0.2-9.1%) and an increase in evergreen shrubs (3.1-5.4%) or graminoids (1.8-5.8%). The initial response and secondary response to warming were often different. The initial responses were relatively consistent across sites; there was little change and the change that did occur was a decrease in bryophytes (0.3-3.9%) or lichens (0.1-3.5%) and an increase in graminoids (1.8-3.2%). The secondary responses were site specific. In the AD site the *Alectoria* complex decreased (4.6%) contributing to a non-significant overall decrease in lichens (4.2%); and evergreen shrubs increased (4.8%). In the AW site bryophytes decreased (2.3%); and there was a non-significant overall increase in graminoids (1.8%). In the BD site acrocarpous mosses increased (3.3%) contributing to a non-significant overall increase in bryophytes (2.5%); lichens decreased (5.6%); there was a non-significant overall decrease in evergreen shrubs (1.7%); groups within the forbs decreased (0.2-0.7%); and single graminoids increased (5.3%) contributing to a non-significant overall increase in graminoids (4.0%). In the BW site *Brachythecium* increased (0.6%) despite a non-significant overall decrease in bryophytes (3.8%); groups within the forbs increased (0.4-2.0%) contributing to a non-significant overall increase in forbs (1.5%); and there was a non-significant increase in graminoids (2.0%).

V.4.5 Correspondence Analysis (CA)

Figure V-11 summarizes the results from a CA of the vegetation by showing the 95% confidence ellipsoids around the mean dimensional value of each site, treatment, and sampling time combination. The first 4 dimensions of the CA accounted for 16.7, 9.9, 8.6, and 3.2 percent of the variation in the data; therefore only the first 3 dimensions are interpreted. Dimension 1 appears to be linked with site moisture and dimension 2 with temperature. However, this inference was true at the site level but does not hold true when examining gradients within a site. More illustrative was the comparison of treatments and sampling times within a site in relation to the other sites.

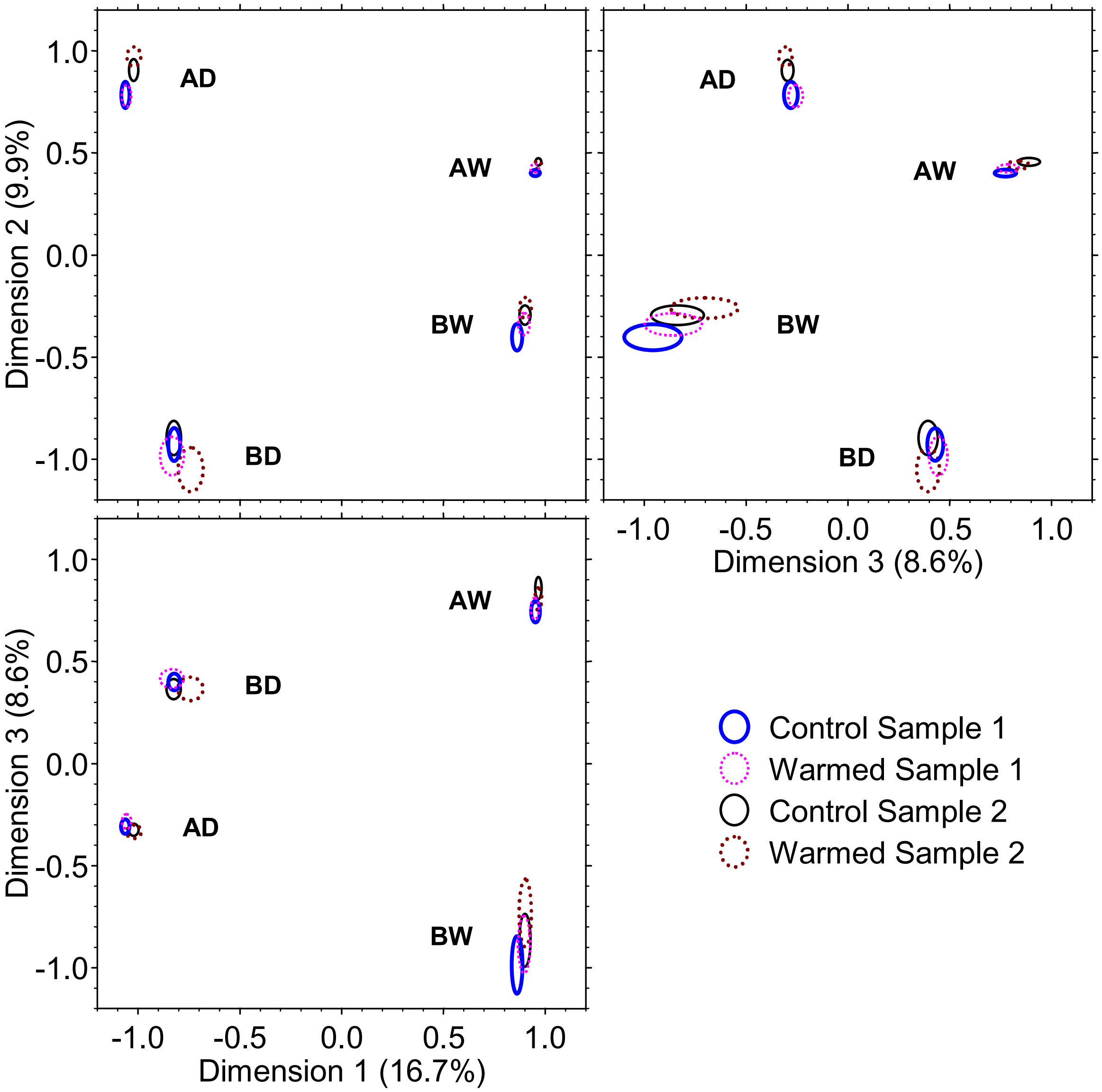

Figure V-11. Summary results from a Correspondence Analysis of all the plots measured in the study. Ellipses are 95% confidence intervals around the mean dimensional score of each site, treatment, and sampling time combination (AD - Atqasuk Dry Heath, AW - Atqasuk Wet Meadow, BD - Barrow Dry Heath, BW - Barrow Wet Meadow).

The amount of change in mean dimensional values calculated from the CA due to changes that occurred in the control plots and in response to warming are plotted as 2-dimensional vectors in Figure V-12. From the vectors it was clear that the trajectories of change representing secondary and initial responses to warming were near opposite each other except in the BD site. A comparison of vector directions across sites was less meaningful because each site had a unique assemblage of species and a different array of potential trajectories. A scalar value based on the vectors of change was calculated to represent all the compositional changes that occurred in control plots and in response to warming. This value was calculated using the Euclidean distance of mean change in the first 3 dimensions (Table V-8). The change that occurred in the control plots was only marginally greater than the change in response to warming and the amount of change that occurred in the control plots was not an indicator of change in response to warming. To adjust for differences in the duration of the experiment at the four sites the vectors representing the secondary response to warming and the changes that occurred in the control plots were linearly interpolated to estimate the change at year five of the experiment (Table V-8). When adjusted, the change that occurred in the control plots was larger at Barrow than Atqasuk and larger in the wet sites than the dry sites. The response to warming was larger in Barrow than Atqasuk. The magnitude of the secondary response was similar among sites except in the AD site (which was larger). The CA and vector calculations were run separately for each site and run several times after removing rare species to test the stability of the analysis. There were changes in configuration and the results from the CA should not be over interpreted, but the broad patterns described above held true for all the separate runs of the analysis.

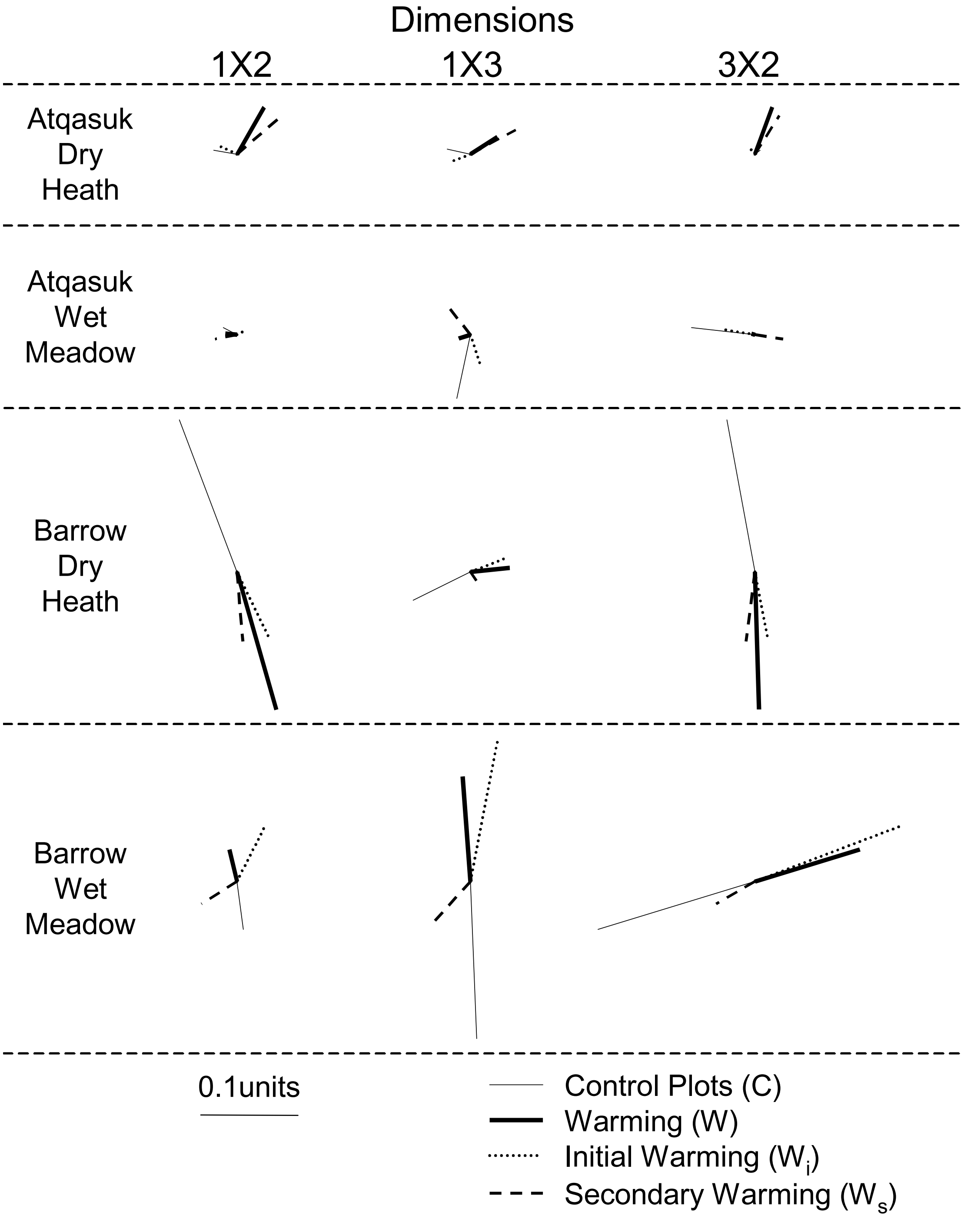

Figure V-12. The trajectories of community change that occurred in the control plots and in response to warming, separated into the initial response and secondary response, calculated from the distance between the centers of the ellipses shown in Figure V-11. The distance has been exaggerated to show small differences; the unit-less scale from the Correspondence Analysis is provided in the bottom corner for comparison with Figure V-11.

Table V-8. The amount of community change that occurred in the control plots (C) and in response to warming (W), separated into the initial response (W_i) and secondary response (W_s), derived from the 3 dimensional distances between the centers of the ellipses shown in Figure V-10 for each study site. The adjusted values have been linearly interpolated to 5 years of warming for all sites; the original data had unequal durations of time between samplings. Scalar values were categorized as follows: zero <0.04; small 0.04-0.12; medium 0.13-0.21; large >0.21.

Site	C		W		W_i		W_s	
Original data								
Atqasuk Dry Heath	zero	0.02	small	0.06	zero	0.02	small	0.07
Atqasuk Wet Meadow	small	0.07	zero	0.01	zero	0.04	zero	0.04
Barrow Dry Heath	large	0.17	medium	0.15	small	0.08	small	0.07
Barrow Wet Meadow	large	0.17	medium	0.11	large	0.16	small	0.06
Adjusted to 5 years								
Atqasuk Dry Heath	zero	0.02	small	0.06	zero	0.02	small	0.07
Atqasuk Wet Meadow	small	0.07	zero	0.01	zero	0.04	zero	0.04
Barrow Dry Heath	medium	0.10	medium	0.12	small	0.08	zero	0.04
Barrow Wet Meadow	medium	0.14	medium	0.12	large	0.16	small	0.05

V.5 DISCUSSION

There were detectable community level changes in response to short-term (2-7yrs) of moderate canopy warming. The response to warming was separated into an initial response assessed after 2 summers of warming, and a secondary response assessed after an additional 3-5 summers of warming, according to the procedures presented in Figure V-2. There were clear differences between the initial and secondary response to warming. The initial response to warming was considered to be a result of changes in growth and biomass allocation of previously established individuals. Observed initial responses were probably due to immediate changes in the plant-environment relationship that were conceptually constrained by the physiology of the preexisting species. The secondary response may have been a result of changes in numbers of individuals and was not limited to changes in growth and biomass allocation. Observed secondary responses were considered to be due to an accumulation of initial effects and indirect changes in species interactions with other species and the environment that were conceptually only constrained by the resource limits of the ecosystem. Future changes in species composition are more likely to reflect the secondary response to warming. Yet even these changes are unlikely to accurately predict long-term (>20yrs) change because change in species composition generally involve non-linear and threshold changes. Thus, the secondary response to warming is considered to be the most accurate mid-term (10-20yrs) predictor of future change.

V.5.1 Species Diversity

The trend towards lower diversity in the warmed plots was not generally statistically significant but does suggest that the communities were changing. Several field studies have shown a similar decline in diversity with warming (Chapin *et al.* 1995, Molau and Alatalo 1998, Walker *et al*. in prep). Generally, when a perturbation occurs species are first lost and subsequently new species invade (Forbes *et al*. 2001) and it may be more appropriate to view the decline in diversity as a perturbation response rather than exclusively a warming response. The secondary response to warming was generally less of a decline or an increase in diversity relative to the initial response. This finding suggests that a decline in diversity is only short-term. Huntley (1997) predicted that the warm range limit of species would respond fastest and that the cool range limits would respond more slowly in the Arctic. Yurtsev (1997) predicted an initial decrease in biodiversity in the Arctic due to warming because plant immigrations are not expected to occur as rapidly as local extinctions. The ultimate future diversity of these tundra communities will more likely increase with long-term warming (Walker 1995). The general decline in diversity in the control plots suggests that the region is in a state of change. Similarly long-term vegetation studies in the region have shown a decline in species diversity at the plot level and suggest that this is a response to regional warming (Tweedie *et al*. in prep). The findings reported here are counter to the conventional paradigms that suggest an increase in diversity with warming based on latitudinal trends, but these findings are short-term and emphasize the importance of separating short-term changes from long-term trends.

V.5.2 Canopy Structure

The increase in canopy height in the warmed plots was commensurate with the classical understanding of the relationship between plants and micro-climate in tundra systems (*e. g*. Sørensen 1941, Bliss 1956, Wielgolaski 1966, Warren Wilson 1966). Increased plant growth due to warming has also been shown to occur within a single growing season based on measures of individual plants in both experimental warming and comparisons with warm years (Walker *et al*. 1995, Henry and Molau 1997, Arft *et al*. 1999, Chapter IV). Many of the species, particularly tall graminoids, grew taller and consequently increased the maximum canopy height. As these plants grew larger they overtopped species occupying the ground stratum. Due to the general long lived perennial growth strategy, slowly expanding colonial growth, and limited seedling establishment of tundra communities, it was unlikely that at the first sampling there were actual changes in the numbers of individuals in the warmed plots. Studies of plant morphology at theses sites have shown a consistent increase in growth and stature due to warming each year (Walker 1997, Hollister 1998, Chapter IV); therefore, the continued increase in canopy height in the warmed plots was likely due to an increase in the abundance of individuals of short or tall stratum. The net result of warming was an increase in canopy height and canopy closure due to an increase in size of individual plants (initial response) and a shift in composition from non-vascular to vascular species (secondary response). This change in structure towards a taller, less open canopy could alter the energy balance and within canopy light regime of the tundra system (McFadden *et al*. 1998) and habitat quality for birds and small mammals.

V.5.3 Standing Dead Plant Matter

The accumulation of standing dead plant matter in response to warming may be explained as a combination of several factors. First, there was a measurable increase in growth due to warming for many species during the study (Chapter IV). Leaves of these plants die and may take several years to fall and decompose (Heal and French 1974, Flanagan and Bunnell 1980); thus, even a small increase in biomass each year may incrementally accumulate. Second, in the warmed plots there was a shift in abundance towards large graminoids that generally maintain standing dead longer than most other species. Third, the presence of a chamber that blocks the wind reduces the compaction and removal of standing dead plant matter. However, the chambers were removed during the winter when much of the compaction and removal of standing dead occurs, and changes in standing dead plant matter also occurred in the control plots. Therefore, the increase in standing dead plant matter may have been overestimated by the presence of a chamber but is a probable response to warming for many tundra communities.

V.5.4 Community Composition

The lack of similarity between changes in the control plots and those due to warming suggest that the changes occurring in the control plots were due to non-temperature factors. The significant changes in relative cover in response to warming were consistent within growth forms: bryophytes and lichens decreased while graminoids increased; similar findings have been reported by Chapin *et al.* (1995), Molau and Alatalo (1998), Robinson *et al.* (1998), and Cornelissen *et al.* (2001). These changes do not necessarily reflect the long-term effect of warming because they were heavily influenced by the initial response to warming. Because the initial response to warming was most likely a biomass response it was constrained by the growth morphology of the preexisting species. The few significant initial responses to warming were a decrease in bryophytes and lichens and an increase in graminoids. Presumably graminoids increased because they have the ability to grow larger in a single growing season, while lichens and bryophytes decreased because they cannot. A decrease in relative cover does not necessarily imply that the species declined in absolute cover. Furthermore, the ability of a species to grow larger in a warmer environment does not necessarily mean that the species will be a better long-term competitor in that environment. Therefore, these results should be interpreted with caution.

The trends for long-term change suggested by the secondary response to warming were site specific, but there were some commonalities. In both dry sites lichens decreased. In the BD site the lichen decrease was associated with an increase in graminoids and acrocarpous mosses, while in the AD site the lichen decrease was associated with an increase in evergreen shrubs. In both wet sites bryophytes decreased. In the AW site the bryophyte decrease was associated with an increase in graminoids and deciduous shrubs, while in the BW site the bryophyte decrease was associated with an increase in forbs and graminoids. Presumably species occupying the ground stratum such as bryophytes and lichens have declined due to light competition with tall vascular plants, particularly graminoids.

The CA has the ability to show the net result of a large number of very small changes; therefore, the interpretation of the vectors of change calculated from the CA was considered informative despite the limitations of the method. The scalar distance calculated from each 3-dimensional vector is a synthetic method of representing whole community change. The finding that change in the control plots was larger at Barrow than Atqasuk and larger in the wet sites than dry sites was consistent with other ongoing research in the region (Tweedie *et al*. in prep). The response to warming was not a simple summation of the scalar initial and secondary responses because they were not in the same direction. The response to warming in the Barrow sites was larger than in the Atqasuk sites after 5 years due to the greater initial response in Barrow. However, the secondary response to warming was larger at Atqasuk than Barrow and if the secondary response is linearly extrapolated, then within 16 years the warming response would be larger in Atqasuk. This finding may help explain an apparent contradiction in the literature where recent studies have found community change to be larger in lower arctic sites despite generally larger documented increases in growth and reproductive effort in higher arctic sites (*cf*. Wookey *et al*. 1993, Henry and Molau 1997, Jonasson *et al*. 1999, Walker *et al*. in prep).

V.5.5 Summary and Conclusions

There were significant community level changes detected after 2-7 years in the control plots and in response to 0.6-2.2 ^{o}C of growing season warming. The only consistent change that occurred in the control plots was a trend towards lower diversity of up to 2.7 species per plot, which was significant in the two wet sites; other changes were site specific. The overall change that occurred in the control plots (measured by the CA) was larger at Barrow than Atqasuk and larger in the wet sites than dry sites. The response to warming was site specific, but some generalization was possible. There was a trend toward lower diversity (0.1-1.7 species/plot), an increase in canopy height (¯0.1-2.3 cm), an increase in standing dead plant matter (1.5-6.0%), an increase in graminoids (1.8-5.8%), a decrease in lichens (0.2-9.1%), and a decrease in bryophytes (¯1.4-4.6%). The secondary response to warming was considered to be the best predictor of future changes. The secondary response on species composition was site specific. These responses were as follows: in the AD site there was a shift from lichens (-4.2%) to evergreen shrubs (4.8%); in the AW site there was a shift from bryophytes (-2.3%) to graminoids (1.8%); in the BD site there was a shift from lichens (-5.6%) and evergreen shrubs (-1.7%) to graminoids (4.0%) and bryophytes (2.5%); and in the BW site there was a shift from bryophytes (-3.8%) to graminoids (2.0%) and forbs (1.5%). The initial response to warming (measured by the CA) was larger at Barrow than Atqasuk presumably due to increase in growth of previously existing species, however the secondary response was larger at Atqasuk presumably due to gradual changes in species composition.

In many instances the initial and secondary responses to warming were opposite in direction to each other. This caused the overall change due to warming to be smaller than the initial or secondary response. The initial responses to warming are dominated by changes in growth and biomass allocation of the preexisting species, these changes occurred within two growing seasons and probably do not have the ability to continue to change. The secondary response may involve changes in the numbers of individuals and was constrained by the generally less immediate limits of the ecosystem. Therefore, forecasts projected from the secondary response are more likely to be accurate, at least for the mid-term (10-20yrs), while forecasts based on the overall changes due to warming will be biased towards the initial response.

The response of each community to warming was unique despite useful generalizations regarding changes in community attributes or growth forms. The different mixtures of species in each community lead to unique changes in species composition due to warming. Predictions about the community structure are likely to be correct and short-term (<10yrs) changes in species composition are reasonable, but long-term (>20yrs) changes in species composition are influenced by indirect changes in the plant-environment and complex species interactions that are beyond our current ability to predict.

V.6 ACKNOWLEDGEMENTS

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Chapter VI

CONCLUDING REMARKS

VI.1 TOWARD FORECASTING TUNDRA VEGETATION CHANGE

One rationale for examining the response of traits of many plant species to warming is based on the assumption that plant responses (phenological development, growth, and reproduction) will modify the competitive balances between species and ultimately lead to changes in community composition (Figure VI-1). The long-lived nature of arctic vegetation and the natural variability of arctic environments suggest that tundra communities will be slow to respond to warming. Therefore, changes in the response of species may be early indicators of future community change. Several difficulties with this reductionistic approach include: determining which traits are most important for each species, determining the correct lag times for traits where the warming response was subordinate to other factors, and accounting for species interactions. The value of this approach for tundra communities needs addressing. From a practical perspective tundra communities are generally less complex in terms of the number of species and the number of interactions between species and the environment (Section I.4.1); therefore, they could be easier to model. From a theoretical perspective the connection between positive and negative responders is likely to scale less directly in tundra communities due to the reduced prevalence of competition and sexual reproduction in tundra communities (Section I.4.1).

Nevertheless, useful insights into the role of temperature on vegetation have been obtained from this reductionistic approach (Section VI.2). The next step is to integrate this work with process studies addressing the mechanisms driving the observed response.

Yet, even with a thorough understanding of the processes involved, it is unlikely that this approach can be used to accurately predict changes in species composition. Community change acts through successional processes. These changes are generally non-linear and often involve thresholds and chance events that are not easily predicted. Changes in temperature may change the competitive environment of the plant community, but community composition is ultimately the result of complex species interactions (Figure VI-2).

The direct measurements of community change represent a more holistic approach to forecasting change. Extrapolations based on the amount of change measured in the warming experiments can be used to assist in forecasts of vegetation change. Still there are many uncertainties associated with using short-term empirical information to predict longer-term change. This work has suggested that different mechanisms may be involved in the initial and secondary community responses to warming. In particular, the initial response is probably due to a change in size of previously existing individuals, while secondary changes may involve changes in the abundance of species. Change in species interactions and feedbacks with the environment are expected to cause indirect effects of warming. For example, a feedback between plant response and nutrient cycling has been speculated due to changes in soil temperatures, species composition, and litter quality. Therefore, it is important to compare changes in plant phenological development, growth, and reproduction with changes in plant cover in an attempt to identify similarities and differences in results obtained from each approach.

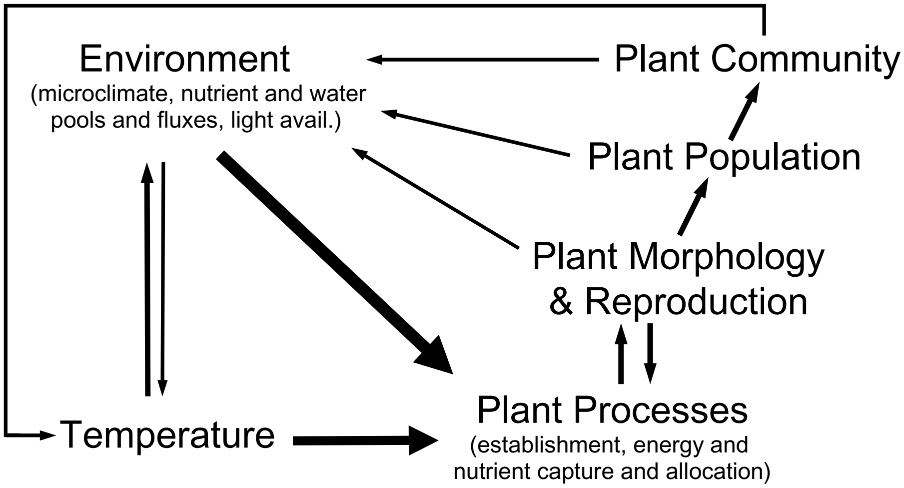


Figure VI-1. Conceptual model of the paths of influence of temperature and the environment on plants. Temperature is a component of the environment but is separated here to emphasize its importance. The examples provided for environment and internal processes are a small subset of many possibilities. Arrows represent a pathway of influence. The data presented in this dissertation show that the influence of the non-temperature environment is often larger than the influence of temperature; therefore the arrow thickness is drawn accordingly. Changes in plant morphology and reproduction may be a useful indicator of future population and community change.

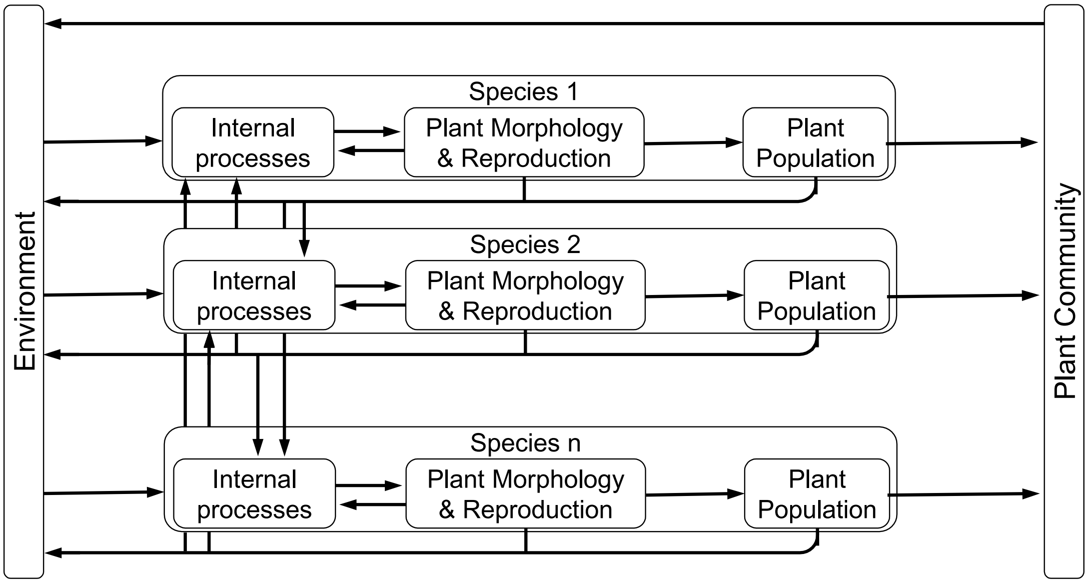


Figure VI-2. Conceptual model of the paths of influence of the environment on a plant community emphasizing the influence of species interactions. Arrows represent a pathway of influence. The long-term effects of a changing environment on the plant community may be difficult to predict due to the many interactions between species.

The results presented here show few parallels between the response of plant traits and community composition (Table VI-1). The most likely reason for the lack of correspondence between the two approaches is the importance of different mechanisms acting at the two levels. Plant phenological development, growth, and reproduction are believed to be affected more directly by temperature, whereas changes in cover are believed to be less directly affected by temperature and more the result of interactions with other species. Understanding the linkage between the responses of species traits with changes in cover is essential to understanding the dynamics of vegetation change. As of now much research is still necessary to bridge this gap.

Physiological modeling is a common method used to predict vegetation change (Section I.3.2). Prediction of some community attributes is probably reasonable with the current understanding of the relationship of temperature on tundra vegetation. For example, documented increases in stature due to a shift in composition from species of the ground stratum (primarily bryophytes and lichens) toward species of the taller stratum (primarily shrubs, graminoids, and erect forbs) are a probable response of many tundra communities to warming (Figure IV-3). Yet, accurate prediction of the changes in composition at the species level is unrealistic. These findings suggest the response of tundra plant species to warming is complex and varies greatly by species and habitat type. Therefore, it is likely that in the near future the most accurate forecasts of changes in tundra vegetation at the regional and species level will be derived from *in situ* experimental manipulations rather than predictions based on physiological models.

Table VI-1. Response of species traits to temperature and changes in cover in the control plots and due to warming (initial and secondary response) at the four study sites.

Trait Type	Phenological			Growth		Reproductive		Cover			
Trait	Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flower Emergence	Leaf Length	Change in Size	No. Inflorescences / plot	Inflorescence Length	Change in the Control Plots	Warming (W)	Initial Response (W_i)	Secondary Response (W_s)
Species & Growth Forms by Site											
Atqasuk Dry Heath											
Woody Evergreen	●	●	●	●	●	●	●	↓	↗	↘	↑
Cassiope tetragona	•	•	•	n	P	n	•	↓	↗	–	↗
Diapensia lapponica	–	i	–	p	•	N	–	↘	–	–	↗
Ledum palustre	–	–	–	•	•	–	•	–	–	–	–
Vaccinium vitis-idaea	–	–	–	–	P	n	•	–	–	–	↗
Forb	●	●	●	●	●	●	●	–	–	–	–
Polygonum bistorta	–	•	•	P	–	–	P	–	–	–	–
Graminoid	●	●	●	●	●	●	●	↘	↗	↗	–
Carex bigelowii	–	–	•	–	N	•	•	↘	–	↘	↗
Hierochloe alpina	–	–	p	P	–	p	p	↘	↗	–	–
Luzula arctica	–	•	–	–	–	i	–	–	–	–	–
Luzula confusa	i	p	p	–	–	i	n	↘	–	↗	↘
Atqasuk Wet Meadow											
Forb	●	●	●	●	●	●	●	–	–	–	–
Pedicularis sudetica	–	•	•	p	•	–	•	–	–	–	–
Graminoid	●	●	●	●	●	●	●	↘	↑	↗	↗
Carex aquatilis	–	i	p	p	•	i	p	–	↗	↗	↗
Dupontia fisheri/psilosantha	n	•	•	–	–	–	–	–	–	–	–
Eriophorum angustifolium	–	•	•	P	–	–	i	↗	–	–	–
Eriophorum russeolum	–	•	•	P	N	–	p	↓	↑	–	↗
Luzula wahlenbergii	i	•	•	P	•	•	•	–	–	–	–

note: "Change in Size" was generally the change in the number of ramets (graminoids and most forbs), number of branches (shrubs), or average diameter of rosette (some forbs) between years.

P positive dominant response
p positive subordinate response
N Negative dominant response
n negative subordinate response
i inconsistent response
– unresponsive response
● not enough information to determine

↑ significant increase
↗ increasing trend
↓ significant decrease
↘ decreasing trend
– no change

Table VI-1. Continued.

Trait Type		Phenological			Growth		Reproductive		Cover			
Trait		Day of Leaf Emergence	Day of Inflorescence Emergence	Day of Flower Emergence	Leaf Length	Change in Size	No. Inflorescences / plot	Inflorescence Length	Change in the Control Plots	Warming (W)	Initial Response (W_i)	Secondary Response (W_s)
Species & Growth Forms by Site												
Barrow Dry Heath												
Woody Deciduous		•	•	•	•	•	•	•	↗	↘	↘	—
Salix rotundifolia	female	p	p	p	p	•	i	p	↗	↘	↘	–
	male	–	–	p	p	•	i	•	↗	↘	↘	–
Woody Evergreen		•	•	•	•	•	•	•	—	—	—	↘
Cassiope tetragona		–	p	p	i	–	p	•	–	–	–	↘
Forb		•	•	•	•	•	•	•	—	—	—	—
Draba lactea		i	•	–	–	•	–	–	–	–	–	–
Draba micropetala		–	p	–	–	–	p	p	–	–	–	–
Papaver hultenii		p	i	p	•	–	–	P	–	–	–	–
Potentilla hyparctica		p	p	p	•	–	–	P	–	–	–	–
Saxifraga foliolosa		–	•	•	–	•	•	–	–	–	–	–
Saxifraga punctata		p	–	p	p	–	–	P	↑	–	–	↓
Senecio atropurpureus		–	–	p	–	–	i	–	–	–	–	–
Stellaria laeta		p	p	p	•	–	P	•	–	↗	–	↗
Graminoid		•	•	•	•	•	•	•	↗	↗	↗	↗
Arctagrostis latifolia		–	p	•	–	p	–	p	↗	↗	–	↗
Luzula arctica		–	–	–	–	i	–	p	–	–	–	–
Luzula confusa		p	p	p	p	–	–	p	↗	↘	–	↘
Poa arctica		–	p	–	p	–	–	p	↗	↑	–	↑
Barrow Wet Meadow												
Forb		•	•	•	•	•	•	•	↓	—	↘	↗
Cardamine pratensis		P	p	p	P	•	P	P	–	–	–	–
Draba lactea		–	–	–	–	–	–	P	↑	–	–	–
Saxifraga cernua		–	–	–	i	•	–	P	–	–	–	–
Saxifraga foliolosa		p	–	P	–	–	–	P	↓	–	–	↑
Saxifraga hieracifolia		U	–	p	P	–	–	P	–	–	–	–
Saxifraga hirculus		n	–	p	•	•	–	P	–	↘	↘	–
Stellaria laeta		–	–	–	•	–	P	•	↓	–	–	–
Graminoid		•	•	•	•	•	•	•	↗	↑	↗	↗
Carex aquatilis/stans		–	p	p	p	i	–	P	↗	↗	↑	↗
Dupontia fisheri		n	–	P	–	p	i	P	↑	↘	↘	↘
Eriophorum angustifolium/triste		–	P	p	–	–	–	p	↑	–	–	↗
Eriophorum russeolum		–	–	p	p	–	–	P	↑	–	–	–
Hierochloe pauciflora		–	p	p	P	•	n	i	↓	↗	↘	↗
Juncus biglumis		–	–	–	–	–	–	P	–	–	–	–
Luzula arctica		–	p	p	–	–	–	P	–	–	–	–
Luzula confusa		–	–	–	–	–	–	P	–	–	–	–
Poa arctica		i	–	•	–	•	–	P	↓	↗	↘	↗

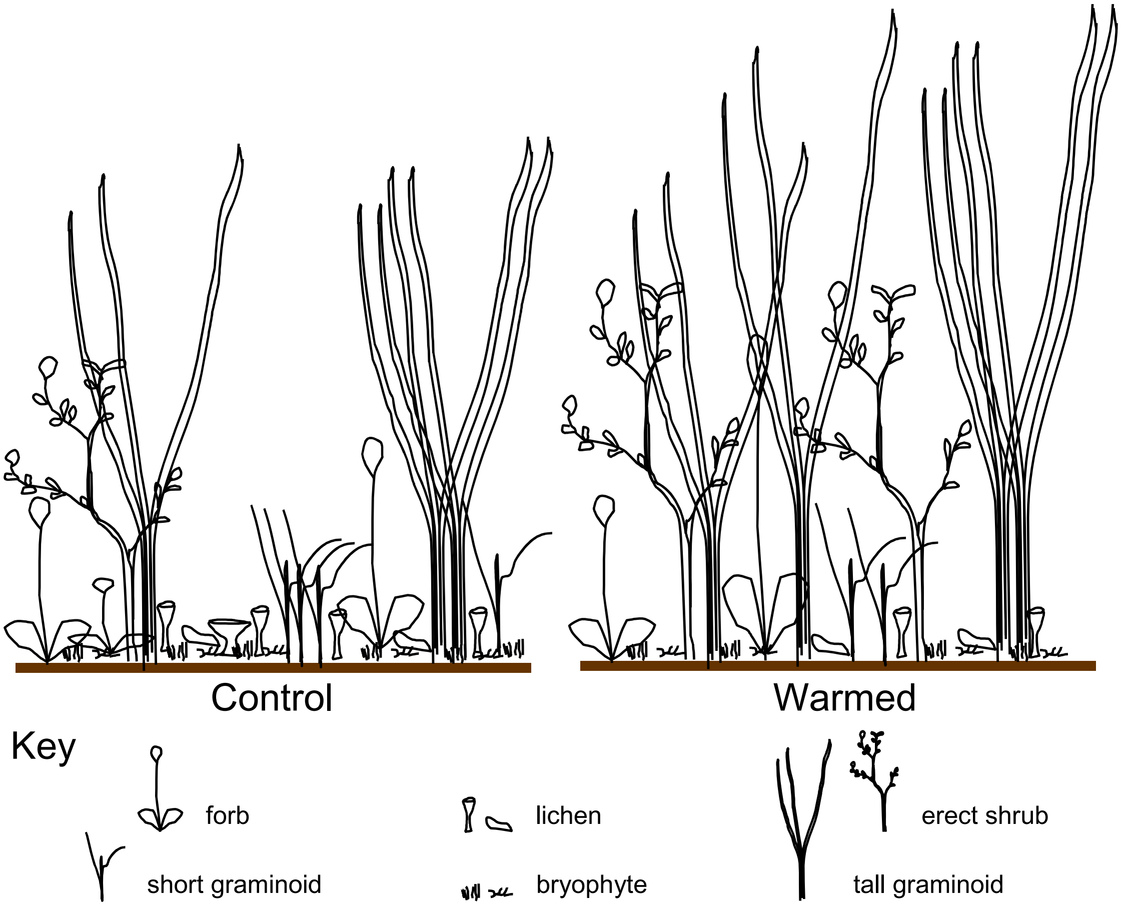


Figure VI-3. Summary diagram of the response of tundra vegetation to warming. There is a general increase in canopy height due to both an expansion of previously existing plant species and an increase in the abundance of plant species occupying the tall stratum. The plant species diversity within a plot generally declined due to a loss of species occupying the ground stratum especially lichens.

VI.2 SUMMARY OF THE DISSERTATION

Researchers increasingly rely on results from observation based on experimentation as vegetation models shift from a more correlational approach of matching plant life-form distribution with climate toward a more mechanistic approach aimed at understanding the physiology associated with individual species characteristic of a climatic regime. This study has provided the detailed observations necessary to parameterize species based models, test model output, and explore underlying mechanisms.

This study uniquely integrates the results from natural variation in temperature between four field sites, interannual variability, and experimental warming to characterize the relationship between plants and temperature. It goes beyond previous tundra warming studies presented in Table I-5 by examining many species at four sites over seven years with the same experimental design and methods. This allowed a characterization of the effect of temperature on plant species traits that is believed to be valid and may be useful for predicting community change due to warming over the next decade (Section IV.5.1).

This study is one of the few where the usefulness of the open-top chambers has been thoroughly scrutinized and validated with biotic data. Chapters II-IV address chamber attributes and provide clear evidence through comparisons with interannual variability and natural temperature gradients that the response observed in the warmed plots is due to temperature.

This study has greatly expanded the evidence that temperature effects the phenological development, growth, reproductive effort, and relative cover of tundra plants (Chapters IV and V). It re-affirms that plant species respond individualistically to temperature and showed that the same species may respond differently within its natural distribution. It found no clear groups of common species response when examining multiple traits. Even when examining a single trait there were no characteristic responses within growth forms or phylogenic group, however there was at least one ecological group that showed a similar response (i.e., the inflorescence length of nearly all the monitored species of varying growth forms in the Barrow Wet Meadow responded positively to temperature) (Section IV.5.2). This is one of the few studies that have compared the warming response with other fluctuating factors in the natural environment (Section IV.5.2). It found, while temperature was the most important single factor in many cases, its influence was generally subordinate to the influence of other factors (i.e., measured differences of plant responses were often larger between years than treatments).

The study examined community attributes such as diversity and structure and found that not only were there clear changes due to warming but that the control plots were also changing (Chapter V). The changes that occurred in the control plots were site specific and related to non-temperature causes. The general response to warming was a trend toward lower diversity, an increase in canopy height, an increase in standing dead plant matter, and a decrease in lichens. Other changes due to warming were site specific (i.e., in the AD site there was a shift from lichens to evergreen shrubs; in the AW site there was a shift from bryophytes to graminoids; in the BD site there was a shift from lichens and evergreen shrubs to graminoids and bryophytes; and in the BW site there was a shift from bryophytes to graminoids and forbs). Although often hypothesized, this is one of the few studies to show clear differences between the short-term initial community response to warming and the longer-term secondary response. It also showed that the size of the initial response was larger at cooler Barrow and the size of the secondary response was larger at warmer Atqasuk (Section V.5.4).

Finally, this may be the most detailed study to address the feasibility of accurately forecasting tundra vegetation change due to warming (Sections II.5.3, III.5.1, IV.5.3, IV.5.4, V.5.5, and VI.1). This study found few similarities between the response of plant traits and the response of community attributes (Section VI.1). It concluded that the use of physiological models that predict the outcome of community attributes is reasonable, however physiological models can not accurately predict species compositional change and in the near future the most accurate forecasts of the future state of regional tundra vegetation will be derived from *in situ* long-term experimental manipulations.

A more detailed description of the principal discoveries presented in each of the first five chapters of the dissertation is presented below.

Chapter I, “The Study System,” provides an in-depth review of the important literature associated with tundra plants and vegetation change due to warming. While the chapter primarily provides the foundation for the study by presenting the major relevant concepts in Polar Ecology, it also provides a thorough review of the warming experiments used in tundra environments. The latter is the most complete to date and will be useful for the ITEX network (Section I.2.3).

Chapter II, “The Microenvironments of Four Experimentally Warmed Arctic Tundra Communities,” provides a detailed description of the microenvironments of the four field sites and describes the performance of the warming device (open-top chamber) in considerable detail. It provides a description of microenvironments based on longer recording times than is generally reported in the literature and provides comparisons between communities. It contributes to the physical descriptive work primarily done in the 70's and 80's in a way that focuses on aspects relevant to plants. It also provides the most detailed description of the performance of this design of open-top chambers in multiple locations. Several other studies have reported on the performance of different chamber types in different environments, but those studies could not distinguish between differences in chamber performance due to chamber style or site characteristics. This study clearly showed that the performance of the chambers used here was different in the different sites and that these differences were large enough to make it imperative for other studies to document the chamber performance in order to interpret the response of vegetation to the manipulation.

Chapter III, "Biotic Validation of Small Open-Top Chambers in a Tundra Ecosystem," provides a unique comparison of plant response to the same amount of seasonal warmth in the warmed plots of a cool year with the control plots of a warm year. The chapter provides biotic validation that the open-top chambers used in the Barrow Wet Meadow site stimulated a response similar to the response observed in a warmer year, this finding led to the conclusion that the open-top chambers are a reasonable analog of regional climate warming. The chapter justifies the use of findings from the warming experiment toward prediction of vegetation change due to climate warming.

Chapter IV, "Plant Response to Temperature in Northernmost Alaska: Implications for Predicting Vegetation Change," provides a concise description of the response of plant species traits to temperature. The chapter integrates results from experimental warming, interannual variability, and natural temperature gradients to independently validate the results obtained from each method so that response can be assigned to temperature. The most common response to warming was earlier phenological development and increased growth and reproductive effort. Nevertheless, the individuality of species is demonstrated by the great variety in response among species and for several species the response varied among sites. The chapter also emphasizes the importance of integrating the response derived from warming experiments with interannual variability in order to characterize the temperature response in relation to other important fluctuating factors in a given location. The chapter provides evidence that most warming responses do not override other naturally fluctuating factors in a given location. This led to the conclusion that warming experiments may lead to an over estimation of the importance of temperature on the rate of vegetation change.

Chapter V, “Detection of Community Change due to Moderate Warming of Tundra Vegetation: Separation of Initial and Secondary Response,” provides a detailed account of the changes that occurred in the four sites as a result of natural variation in the control plots and that due to warming. The study showed that warming does cause detectable community change even when measured at short time scales. It also showed that the control plots were changing as a result of non-temperature related factors. It further separated the response to warming into an initial response and a secondary response. The study showed that in many cases the initial and secondary responses to warming were not in the same direction and argued that future change will more likely resemble the secondary response. It showed that the initial response was larger at Barrow and the secondary response was larger at Atqasuk and concluded that the long-term response to warming will be larger at Atqasuk despite the larger response measured at

Barrow in the first 5 years. It concluded that the most likely reason for the difference was a larger increase in growth of previously existing species at Barrow and a gradual change in species composition at Atqasuk. The analytical method used to separate changes occurring in the control plots from changes due to warming where the initial response was teased apart from the secondary response was novel and could have wide applicability to many fields.

VI.3 FUTURE RESEARCH

The results presented in this dissertation are part of an ongoing research project. It is hoped that the experimental manipulations will stay in place for many years. At present the level of monitoring of the sites has been reduced to measurements of the microenvironment provided in Chapter II. The author of this dissertation intends to sample community change in the plots at approximately five-year intervals. By continuing to collect this information a test of the hypothesis that future change will closer resemble the secondary response to warming can be performed (Section V.5.5). Of equal importance, the continued monitoring of the control plots could provide information on the effects of documented warming trends on vegetation in the region (Section I.4.3-1). Other scientists using a variety of techniques to test a variety of hypotheses may also be able to capitalize on the long-term nature of the permanently marked plots.

Among the many future analyses that could be done with the existing data presented in this dissertation, the ones that have the highest priority are listed below:

- Perform a more comprehensive integration of the results from the community analysis and the response of individual plants.
- Perform data "mining" on the response of individual traits to identify patterns of response of whole species.
- Perform a detailed analysis of the warming response of a few key species.
- Examine the genome size of the plant species to test its relationship with the growth response to warming (Section I.4.2).

This project has several ongoing collaborations including:

- Comparisons of the change documented in the studied plots with changes recorded over the last 20 or more years in plots associated with the International Biological Programme in Barrow (Section I.5.1-2), and Research on Arctic Tundra Environments in Atqasuk (Section I.5.1-3).
- Documentation of changes in plot-level CO_2 exchange in each study site.
- Documentation of the seasonal progression of light reflectance from the studied plots. Changes in wavelength frequencies reflect attributes of the vegetation such as chlorophyll content.

New research on the effects of warming on tundra should focus on mechanistic studies that address issues related to scaling from plant phenological development, growth, and reproduction to changes in cover. It should also address changes in long-term responses to indirect affects of warming on the environment and complex species interactions.

Appendix A

PLOT MAPS

The following figures contain maps of the plot locations within the four study sites associated with the research presented in this dissertation.

The maps included are:

Figure A-1. Map of the plot locations within the Atqasuk Dry Heath (AD) site.

Figure A-2. Map of the plot locations within the Atqasuk Wet Meadow (AW) site.

Figure A-3. Map of the plot locations within the Barrow Dry Heath (BD) site.

Figure A-4. Map of the plot locations within the Barrow Wet Meadow (BW) site.

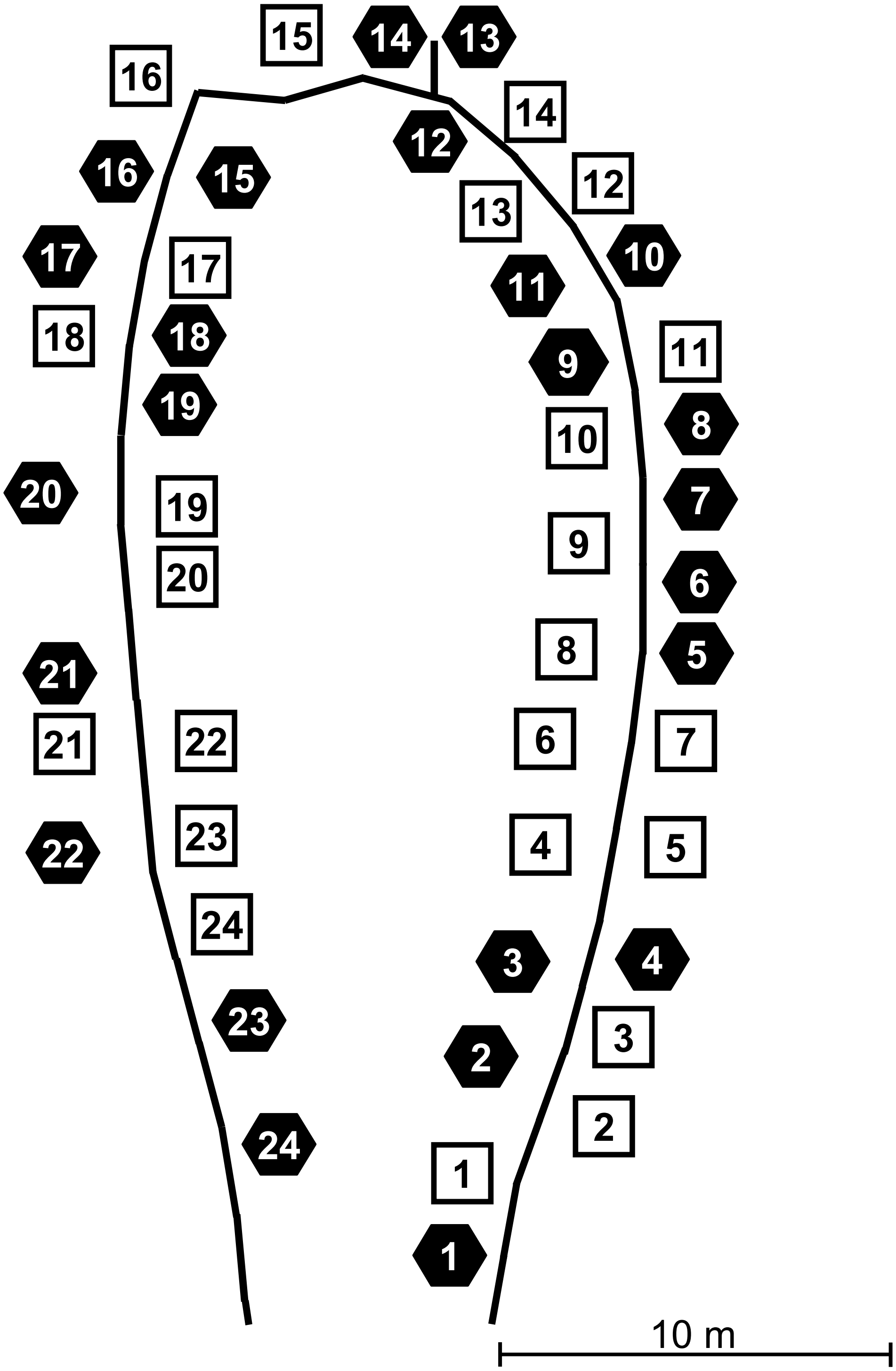


Figure A-1. Map of the plot locations within the Atqasuk Dry Heath (AD) site. The closed hexagon symbol represents an open-top chamber (OTC), the open square symbol represents a control plot, and the line represents the boardwalk.

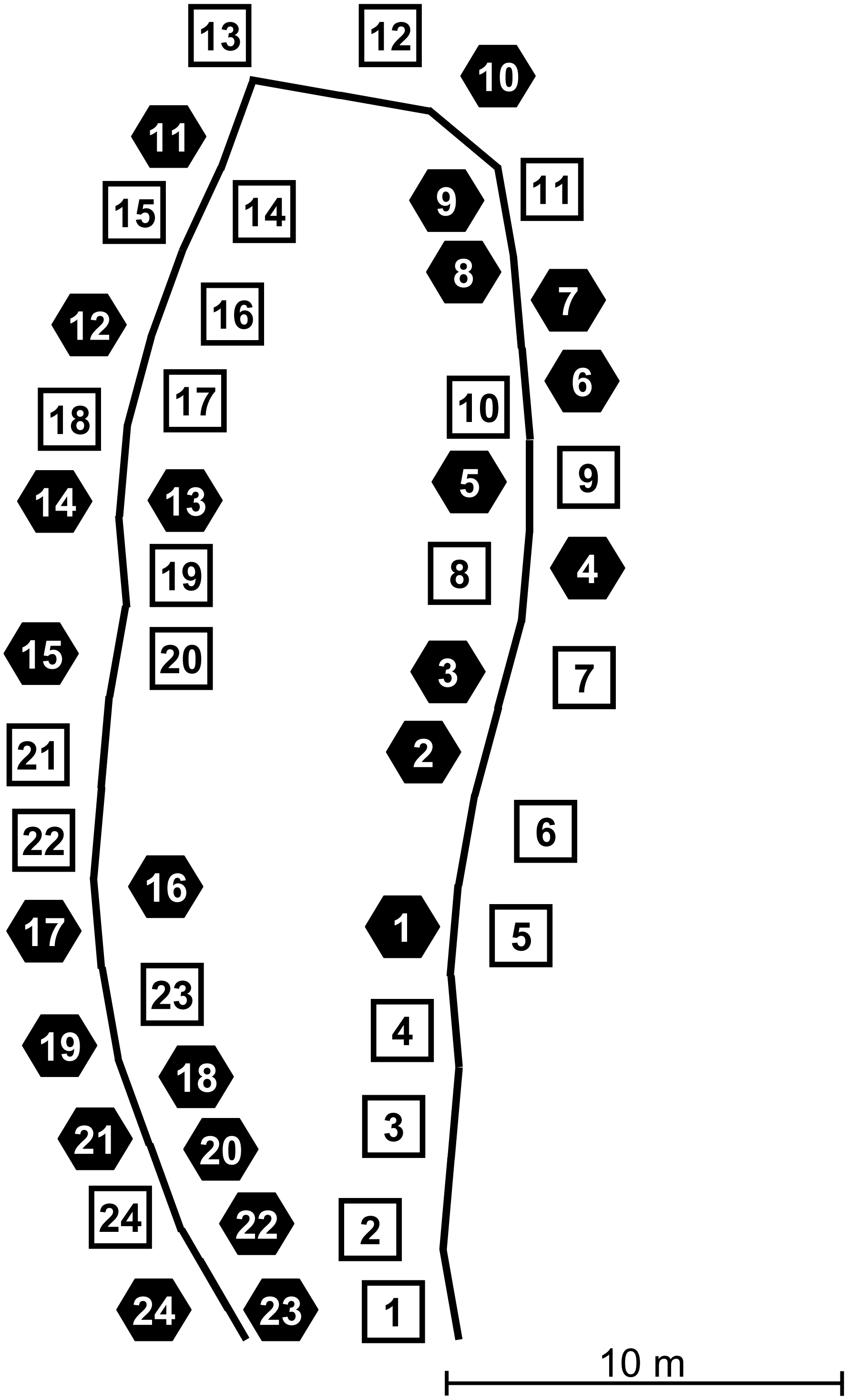


Figure A-2. Map of the plot locations within the Atqasuk Wet Meadow (AW) site. The closed hexagon symbol represents an open-top chamber (OTC), the open square symbol represents a control plot, and the line represents the boardwalk.

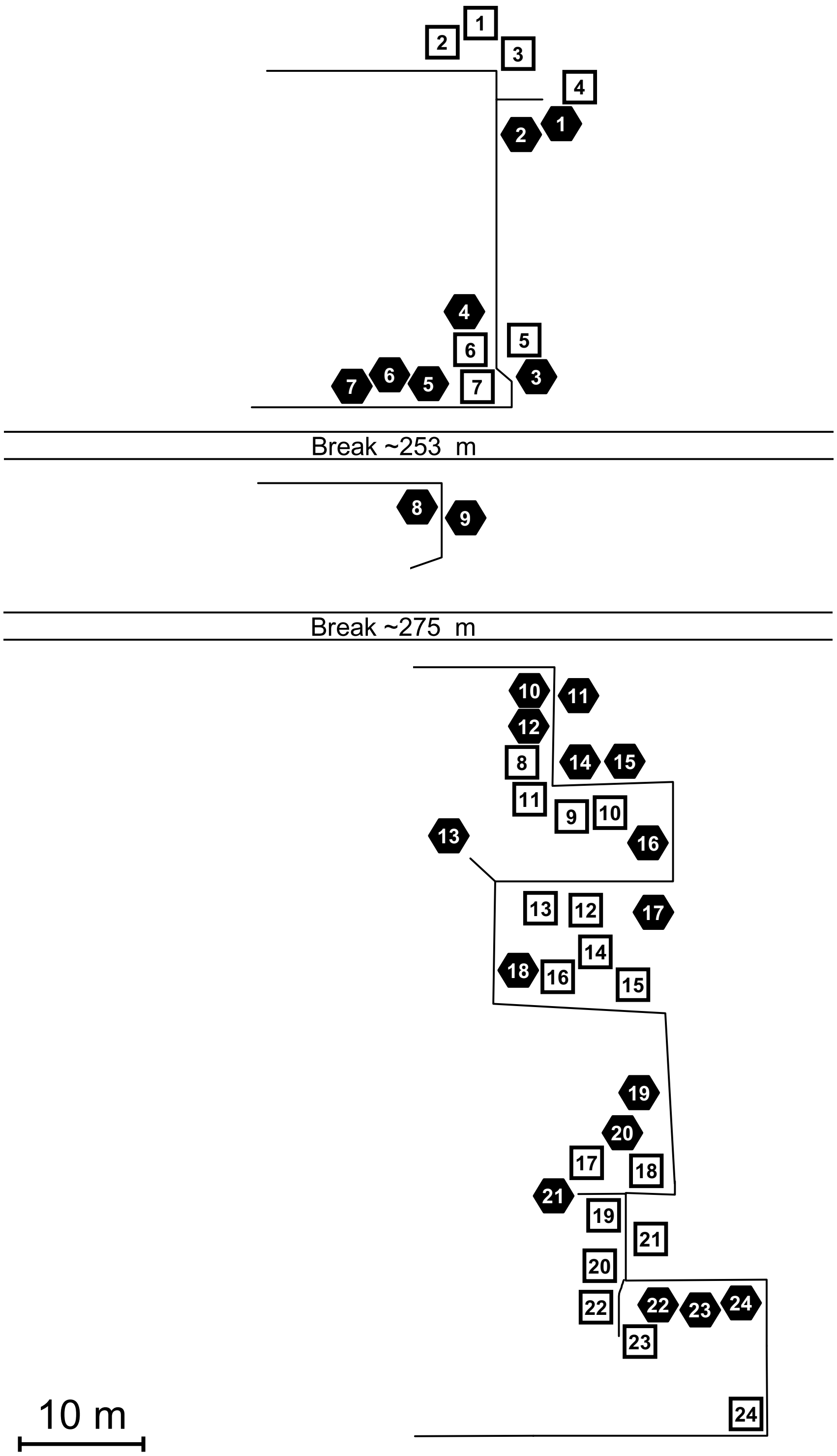


Figure A-3. Map of the plot locations within the Barrow Dry Heath (BD) site. The closed hexagon symbol represents an open-top chamber (OTC), the open square symbol represents a control plot, and the line represents the boardwalk.

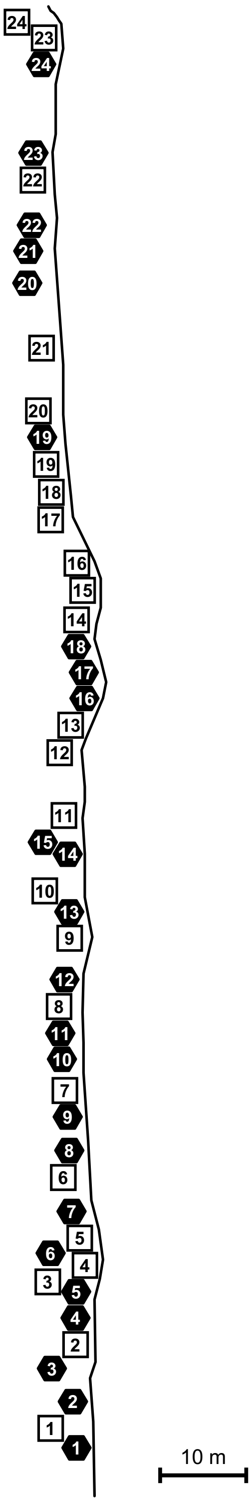


Figure A-4. Map of the plot locations within the Barrow Wet Meadow (BW) site. The closed hexagon symbol represents an open-top chamber (OTC), the open square symbol represents a control plot, and the line represents the boardwalk.

Appendix B

METADATA OF THE ARCHIVED DATASETS

A summary of the metadata for the datasets collected and archived in association with the project associated with the research presented in this dissertation are listed below. These data sets are available through the National Snow and Ice Data Center (449 UCB, University of Colorado Boulder, CO 80309-0449).

The metadata files include:

B.1 Macroclimate Metadata

B.2 Plot Microclimate Metadata

B.3 Detailed Plot Microclimate Metadata

B.4 Thaw Metadata

B.5 Plant Metadata

B.6 Community Metadata

B.1 MACROCLIMATE METADATA

This file contains meta-data for file <1998-2001 Barrow Atqasuk Site Climate v1.txt>

File <1998-2001 Barrow Atqasuk Site Climate v1.txt> contains data representing the climate of the study sites in Barrow and Atqasuk in a text tab delimited format.

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J. (MSU)/Hollister, Robert D
DATA COVERAGE = START: 1998081908; STOP: 2001082507 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Campbell CR10X (Model 107 Temperature Probe, TE525 Tipping Bucket Rain Gage, 03001 Wind Sentry), Onset StowAway Light Intensity Logger
DATA VERSION = 1.0 (15 October 2001)

DATA COLLECTION

Model 107 Temperature Probe, TE525 Tipping Bucket Rain Gage, and 03001 Wind Sentry were recorded on a CR10X Datalogger. Readings were taken every 15 minutes averaged and recorded every hour except for Rain measures which were summed. Light intensity recorded with the StowAway Light Intensity Loggers was recorded every 16 minutes and averaged each hour. Information on the equipment is provided below.

CR10X,
Model 107 Temperature Probe,
TE525 Tipping Bucket Rain Gage, and
03001 Wind Sentry
Produced by Campbell Scientific Inc.
815 W. 1800 N.
Logan, UT 84321-1784, USA

StowAway Light Intensity Logger
Produced by Onset Computer Corporation
PO Box 3450
Pocasset, MA 02559-3450, USA

B.2 PLOT MICROCLIMATE METADATA

This file contains meta-data for file <1995-2001 Barrow Atqasuk ITEX Plot Microclimate v1.txt>

File <1995-2001 Barrow Atqasuk ITEX Plot Microclimate v1.txt> contains data representing the microclimate of ITEX plots in Barrow and Atqasuk in a text tab delimited format. The data presented are hourly plant canopy temperature and relative humidity of up to 48 plots (24 experiment open-top chamber plots and 24 control plots) at four sites (Atqasuk Wet Meadow, Atqasuk Dry Heath, Barrow Wet Meadow, and Barrow Dry Heath). Generally the number of plots per site per treatment that data is available for is between 5 and 10 plots.

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J (MSU)/Hollister, Robert D
FUNDING SOURCE AWARD # = NSF OPP 9714103
DATA COVERAGE = START: 1995062008; STOP: 2001081607 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Onset Computer Corporations StowAway Temperature
Loggers, StowAway Relative Humidity Loggers, and
Hobo Temperature Loggers.
DATA VERSION = 1.0 (12 December 2001)

DATA COLLECTION

Temperature and Relative Humidity was recorded between every 10-72 minutes and averaged by the hour. When no data was recorded within an hour (for recording intervals of greater than 1 hour) or if the data was considered erroneous, the average of the hour before and the hour after is presented. Data collection was during the summer only and begun when the site was established (usually within 2 days of snowmelt) and ends on August 15th. Information on the equipment is provided below.

HOBO Temperature Logger,
StowAway Temperature Logger,
StowAway XTI Temperature Logger, and
StowAway Relative Humidity Logger
Produced by Onset Computer Corporation
PO Box 3450
Pocasset, MA 02559-3450, USA

B.3 DETAILED PLOT MICROCLIMATE METADATA

This file contains meta-data for file <1998-2001 Barrow Atqasuk Detailed Plot Microclimate v1.txt>

File <1998-2001 Barrow Atqasuk Detailed Plot Microclimate v1.txt> contains data representing the detailed microclimate of ITEX plots in Barrow and Atqasuk in a text tab delimited format. The data presented are hourly plant canopy temperature, soil temperature, soil moisture, and soil salinity of four plots (two experiment open-top chamber plots and two control plots) at four sites (Atqasuk Wet Meadow, Atqasuk Dry Heath, Barrow Wet Meadow, and Barrow Dry Heath).

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J. (MSU)/Hollister, Robert D
FUNDING SOURCE AWARD # = NSF OPP 9714103
DATA COVERAGE = START: 1998081908; STOP: 2001082507 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Campbell CR10X (MRC TP101M Temperature Probes,
Vitel HMD-10-A), Onset HOBO H8Pro
DATA VERSION = 1.0 (12 December 2001)

DATA COLLECTION

MRC Temperature Probes and Vitel Hydra Probes were recorded on a CR10X Datalogger. Temperatures were taken every 15 minutes averaged and recorded every hour. Vitel Voltages were recorded every hour and were converted to water fraction by volume (WFV) and Salinity with the Vitel Program <HDFILE.EXE>. Temperatures recorded with the HOBO Pro were recorded every 10-18 minutes and were averaged each hour. Details of the precision and accuracy of each recording device can be obtained from the manufacture. Information on the equipment is provided below.

CR10X
Produced by Campbell Scientific Inc.
815 W. 1800 N.
Logan, UT 84321-1784, USA

MRC TP101M Temperature Probes
Special produced TP101M Temperature Probes 45cm length with total of six thermistor data points at: 1, 5, 10, 15, 30, 45cm. Produced by Measurement Research Corporation
4126 4th Street NW
Gig Harbor, WA 98335, USA

Vitel HD-10-A
Hydra Probe Produced by Stevens Vitel Hydrological & Meteorological Systems.
14100 Parke Long Court
Chantilly, VA 20151, USA

HOBO H8 Pro
Produced by Onset Computer Corporation
PO Box 3450
Pocasset, MA 02559-3450, USA

B.4 THAW METADATA

This file contains meta-data for file <1995-2001 Barrow Atqasuk ITEX Thaw v1.txt>

File <1995-2001 Barrow Atqasuk ITEX Thaw v1.txt> contains data representing the thaw depths of ITEX plots in Barrow and Atqasuk in a text tab delimited format. The data presented are daily to seasonal thaw depths of 48 plots (24 experiment open-top chamber plots and 24 control plots) at four sites (Atqasuk Wet Meadow, Atqasuk Dry Heath, Barrow Wet Meadow, and Barrow Dry Heath).

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J. (MSU)/Hollister, Robert D
FUNDING SOURCE AWARD # = NSF OPP 9714103
DATA COVERAGE = START: 19950621; STOP: 20010816 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Metal rod graduated by centimeters
DATA VERSION = 1.0 (12 December 2001)

DATA COLLECTION

Thaw depths were measured to the nearest cm by inserting a graduated metal rod into the ground until the frozen surface was reached. For control plots 2-4 of the corners were measured and the average is presented. For experimental open-top chamber plots only the center of the plot was measured and thus presented.

B.5 PLANT METADATA

This file contains meta-data for file <1994-2000 Barrow Atqasuk ITEX Plant v1.txt>

File <1994-2000 Barrow Atqasuk ITEX Plant v1.txt> contains data representing the periodic plant measures of all species within each plot in a text tab delimited format. The data presented are phenological development (date of leaf bud burst, inflorescence emergence, flower bud, flower opening, flower withering, seed development, seed dispersal, and senescence), seasonal growth (length of leaf, and length of inflorescence), seasonal flowering (number of inflorescences in flower within a plot), occurrence of events (yes or no for leaf, inflorescence, bud, flower, and seed), and annual growth and reproductive effort (number of leaves, diameter of rosette, number of branches, maximum leaf length, number of inflorescences, maximum inflorescence length, number of buds, number of flowers, and number of seeds) collected weekly or yearly for all plant species during the summers of 1994-2000 for 48 plots (24 experiment open-top chamber plots and 24 control plots) at four sites (Atqasuk Wet Meadow, Atqasuk Dry Heath, Barrow Wet Meadow, and Barrow Dry Heath).

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J (MSU)/Hollister, Robert D
FUNDING SOURCE AWARD # = NSF OPP 9714103
DATA COVERAGE = START: 1994; STOP: 2000 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Point Frame with 100 points
DATA VERSION = 1.0 (12 December 2001)

DATA COLLECTION

Plant development was followed throughout the entire summer. Plant measures were determined based on species morphology and ease of information collection. Within each plot three permanently marked individuals were monitored for each species if possible. Due to the low percentage of flowering, data on reproductive traits required the measurement of non-tagged plants. Four different data types were collected. They were: 1) 1-3 permanently marked individual plants of each species within a plot; 2) total plot measures of a species, such as the number of flowers per plot or the first occurrence of a phenophase; 3) the 1-3 largest reproductive individual plants of a species within a plot; and 4) the 1-3 largest vegetative individual plants of a species within a plot.

For species such as graminoids that do not form distinct individuals unit areas were established to monitor change over years. The size of unit areas of *Carex aquatilis* subspecies *stans* in the Barrow Wet Meadow site and all the species in the Atqasuk Wet Meadow site was 10 by 10 cm. All other unit areas were 5 by 5 cm in size.

B.6 COMMUNITY METADATA

This file contains meta-data for file <1995-2000 Barrow Atqasuk ITEX Community v1.txt>.

File <1995-2000 Barrow Atqasuk ITEX Community v1.txt> contains data representing the community composition and structure of ITEX plots in Barrow and Atqasuk in a text tab delimited format. The data presented were collected on the second summer of the experiment and then again during the summer of 2001 for 48 plots (24 experiment open-top chamber plots and 24 control plots) at four sites (Atqasuk Wet Meadow, Atqasuk Dry Heath, Barrow Wet Meadow, and Barrow Dry Heath).

GENERAL INFORMATION

PI/DATA CONTACT = Webber, Patrick J. (MSU)/Hollister, Robert D
FUNDING SOURCE AWARD # = NSF OPP 9714103
DATA COVERAGE = START: 19950701; STOP: 20000812 UTC
PLATFORM/SITE = Barrow, Alaska (71°19'N 156°37'W);
Atqasuk, Alaska (70°29'N 157°25'W)
INSTRUMENT = Point Frame with 100 points
DATA VERSION = 1.0 (12 December 2001)

DATA COLLECTION

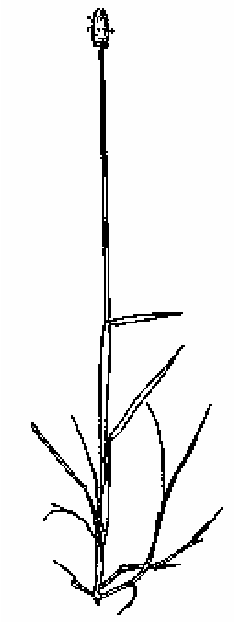
The data were gathered by placing a Point Frame over each plot and recording the top and bottom species at each location. The height of the top species was recorded relative to the ground at that location. The grids were spaced 7 cm apart and started at 3.5 cm from the edge of the square 70 cm frame. The top species was recorded at each location and the species at the ground surface was recorded if it was different from the top species. Occasionally it was difficult to distinguish which species was on the ground because there were several intertwined individuals, therefore preference was given to vascular plants, then lichens, and then mosses. Due to the limitations of field identification many species were lumped into larger taxa.

Appendix C

COLLECTION METHODS OF EACH SPECIES

The following pages provide a description of each species present in the study sites and the ideal data collection methods used for the species. In many instances measures listed were not collected in some years or some sites due to time constraints. Occasionally methods were modified over the duration of the experiment, the methods listed are the methods used in the later years of the experiment.

Genus species: *Alopecurus alpinus*
Common name: Alpine foxtail
Family: Poaceae


E. Hultén 1968

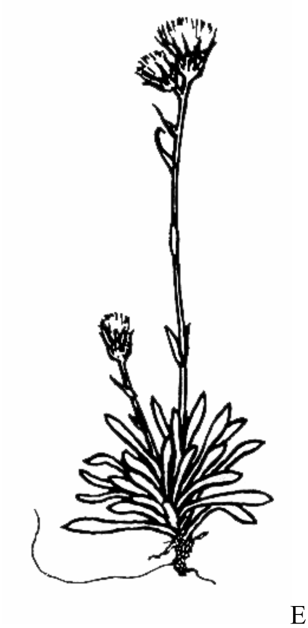
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large and flat similar to *Arctagrostis latifolia*, but with narrower blades.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is spike-like. The spikelets have a single floret and are densely wooly.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Antennaria friesiana*
Common name: Fries' pussytoes
Family: Asteraceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are wooly, white-pubescent, simple, entire, and emerge from a caespitosa rosette.
Inflorescence	The composite head is first visible. The head resembles a bud.
Flower	The head is open and white strand-like petals are visible.
Seed Dispersal	The first seeds are released from the head.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the petiole at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes in the cluster or within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences in the cluster or within the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of heads that produced seeds in the unit area.
Flowers	The number of heads that reached flowering in the unit area.
Buds	The number of heads in the unit area.
Eaten	The number of heads eaten in the unit area.

Genus species: *Arctagrostis latifolia*
Common name: Polar grass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large and flat and generally bluish. When they first emerge they look like a sword coming out of the ground.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is contracted. The spikelets have a single floret.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Arctophila fulva*
Common name: Pendant grass
Family: Poaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, often reddish, and distinctly alternate.
Inflorescence	The first inflorescence has emerged from the culm. The inflorescence is open, similar to *Poa*, but larger.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Artemisia borealis*
Common name: Field sagewort
Family: Asteraceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are deeply lobed and pubescent.
Inflorescence	The stem is first visible.
Bud	The composite head is first visible. The head resembles a bud.
Flower	A head has opened and yellow anthers are visible.
Flower Wither	All the yellow anthers have turned brown on one head.
Seed Dispersal	The first seeds are released from the head.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the leaf base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves on the individual with the longest inflorescence or the longest leaf.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of heads that produced seeds in the unit area.
Flowers	The number of heads that reached flowering in the unit area.
Buds	The number of heads in the unit area.
Eaten	The number of heads eaten in the unit area.

Genus species: *Betula nana*
Common name: Dwarf birch
Family: Betulaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are circular and unroll as they emerge similar to Salix leaves. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll.
Inflorescence	The first red colored catkin has emerged from the stem. The catkin is small and consists of many flowers.
Bud	The first buds are visible on the catkin. The buds are very small.
Flower	The first yellow colored anthers are visible on the catkin.
Flower Wither	On one catkin all the anthers have turned a dull rust color or the catkin has fallen off the stem.
Seed	The pistils on the catkin have enlarged.
Seed Dispersal	The pistils on the catkin have opened and begun to dehisce.
Senescence	At least half of the leaves have turned yellow to brown or fallen off the stem.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from either the base at the petiole to the leaf blade tip or from side to side.
Leaves	The number of leaves produced on the stem from the tag outward.
Brown Tipped Leaves	The length of the longest branch on the stem from the tag outward measured from the axis to the branch tip. Note this measure has no relevance to brown tipped leaves but fits within this column.
Individuals	The number of branches on the stem from the tag outward.
Inflorescence Length	The length of the longest inflorescence measured from the stem to the inflorescence tip.
Inflorescences	The number of catkins on the stem from the tag outward.
Seeds	The number of catkins that produced seeds on the stem from the tag outward.
Flowers	The number of catkins that flowered on the stem from the tag outward.
Eaten	The number of catkins that were eaten or fell off the stem from the tag outward.

Genus species: *Calamagrostis holmii*
Common name: Holm's reedgrass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small and grayish green. They are difficult to distinguish from *Hierochloe pauciflora* and *Poa arctica*.
Inflorescence	The first inflorescence has emerged from the culm. The spikelets have a single floret. The feather-like panicle is often purplish-black and has many spikelets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Calamagrostis* sp.
Common name: Reed bentgrass
Family: Poaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged.
Inflorescence	The first inflorescence has emerged from the culm. The spikelets have a single floret. The feather-like panicle is often purplish-black and has many florets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Cardamine pratensis*
Common name: Cuckoo flower
Family: Brassicaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	A leaf has re-greened from a yellow to brownish green to a true green or the first new leaf has emerged. The leaves are semi-evergreen and oddly pinnate. The plant forms a loose rosette.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The small, grayish green buds form in the axis of the leaves at the apex of the stem shortly after the stem emerges.
Flower	The first opening of a flower. The petals are pink.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded.
Seed Dispersal	A silique has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of the petiole at the stem or ground surface to the end of the tip of the axial leaflet.
Leaves	The number of leaves on the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of siliques produced on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Carex aquatilis*
Common name: Water sedge
Family: Cyperaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, yellowish green, and sword-like. New leaves generally emerge between two leaves from the pervious season and can be quite large.
Inflorescence	The first brown-black spike has emerged from the culm. There are generally 3-7 spikes/spikelets per inflorescence. Generally the ultimate and penultimate spikes are male.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell and is clearly larger than the scale protecting it.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty scales.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 10 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 10 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Carex aquatilis/stans*
Common name: Water sedge
Family: Cyperaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, yellowish green, and sword-like. New leaves generally emerge between two leaves from the pervious season and can be quite large.
Inflorescence	The first brown-black spike has emerged from the culm. There are generally 3-7 spikes/spikelets per inflorescence. Generally the ultimate spike is male. *Carex stans* is similar in appearance to *Carex aquatilis* but is smaller and has only one male spike.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell and is clearly larger than the scale protecting it.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty scales.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 10 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 10 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Carex bigelowii*
Common name: Bigelow's sedge
Family: Cyperaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, yellowish green, and sword-like. New leaves generally emerge between two leaves from the pervious season and can be quite large.
Inflorescence	The first brown-black spike has emerged from the culm. There are generally 3-7 spikes/spikelets per inflorescence. *Carex bigelowii* is very similar in appearance to *C. aquatilis* but lives in dry soils and the lowest bract does not extend beyond the axial spike as in *C. aquatilis*.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell and is clearly larger than the scale protecting it.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty scales.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Carex rariflora*
Common name: Loose flower alpine sedge
Family: Cyperaceae


E. Hultén 1968

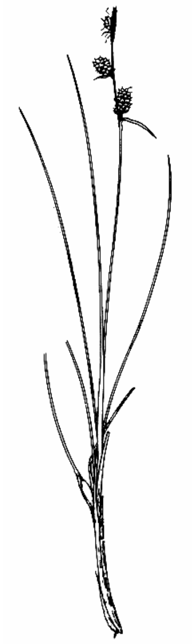
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small, bluish green, and sword-like. New leaves generally emerge between two leaves from the pervious season.
Inflorescence	The first brown-black spike has emerged from the culm. There are generally 3-5 spikes/spikelets per inflorescence. The spikes are terminal. The uppermost spike is male and the lower spikes are pendant and female.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell and is clearly larger than the scale protecting it.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty scales.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 10 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 10 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Carex rotundata*
Common name: Round sedge
Family: Cyperaceae



E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, olive green, and U-shaped in cross-section.
Inflorescence	The first spike has emerged from the culm. There are generally 3-5 spikes/spikelets per inflorescence. The spikes are spherical and green.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty spaces.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 10 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 10 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Carex subspathacea*
Common name: Hoppner's sedge
Family: Cyperaceae


E. Hultén 1968

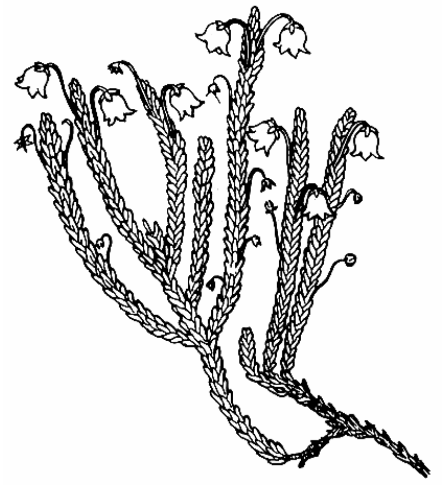
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small, yellowish green, and sword-like. New leaves generally emerge between two leaves from the pervious season. The plant is smaller than *Carex stans*.
Inflorescence	The first brown-black spike has emerged from the culm. There are generally 3-7 spikes/spikelets per inflorescence. Generally the ultimate spike is male. *Carex subspathacea* in the site appears to be a hybrid with *C. stans* and many intermediates exist.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The perigynia have enlarged and begun to swell and is clearly larger than the scale protecting it.
Seed Dispersal	The perigynia have begun to fall off the spike leaving empty scales.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.
Male Spikelets	The number of male spikes produced on the longest inflorescence.
Female Spikelets	The number of female spikes produced on the longest inflorescence.

Genus species: *Cassiope tetragona*
Common name: White arctic heather (Pilġaurat)
Family: Ericaceae


E. Hultén 1968

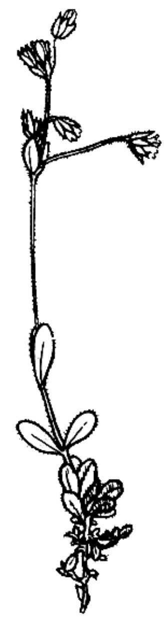
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have re-greened.
Bud	The first yellowish white buds have emerged. The bud should displace the leaves by at least 75 degrees.
Flower	The first opening of a flower.
Flower Wither	The corolla of a flower has dropped.
Seed	The red ovary has expanded so that the top of the capsule appears completely red.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the annual growth increment.
Leaves	The number of live (green) branches from the tag outward.
Brown Tipped Leaves	The number of dead (brown) branches from the tag outward.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences (should not exceed one).
Seeds	The number of capsules produced from the tag outward.
Flowers	The number of flowers produced from the tag outward.
Buds	The number of buds produced from the tag outward.

Genus species: *Cerastium beeringianum*
Common name: Bering chickweed
Family: Caryophyllaceae


E. Hultén 1968

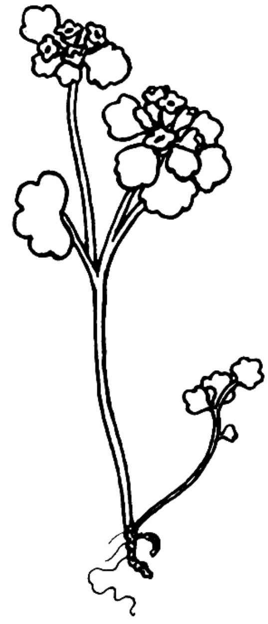
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll. The leaves are more rounded than *Stellaria laeta* and are pubescent.
Bud	The first flower bud has emerged. The buds form at the end of the stem and should show some white.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf measured from the base of the petiole at the stem to the tip of the leaf blade.
Leaves	The number of live (green) branches in the 5 cm^2 unit area.
Brown Tipped Leaves	The number of dead (brown) branches in the 5 cm^2 unit area.
Inflorescence Length	The height of the tallest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed one).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Chrysosplenium tetrandrum*
Common name: Northern golden saxifrage
Family: Saxifragaceae


E. Hultén 1968

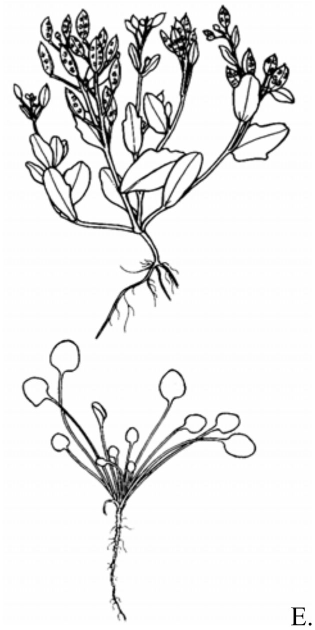
Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are round and crenate. The plant is small and could be confused with *Saxifraga cernua* or *Ranunculus pygmaeus*.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The petals have opened and form cups that hold small round to kidney shaped, reddish brown seeds.
Seed Dispersal	The seeds have begun to disperse from the cup-like calyx.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from either the base at the petiole to the leaf blade tip or from side to side.
Leaves	The number of leaves.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Cochlearia officinalis*
Common name: Scurvy grass
Family: Brassicaceae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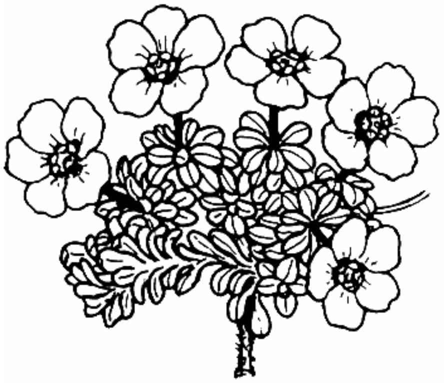
Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are round to deltoid and form a distinct rosette. A single leaf looks very similar to the axial leaflet of *Cardamine pratensis*.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The buds appear as gray spheres in the center of the rosette.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A silique has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of siliques produced on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Diapensia lapponica*
Common name: Pincushion plant
Family: Diapensiaceae



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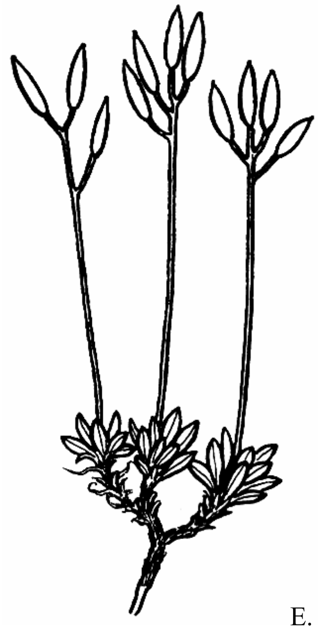
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have re-greened.
Bud	The first buds have emerged. The buds are generally red and emerge from the center of the rosette.
Flower	The first opening of a flower. The petals are white or occasionally pink.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The red ovary has expanded so that the top of the capsule appears completely red.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.
Eaten	The number of flowers eaten in the unit area.

Genus species: *Draba lactea*
Common name: Milky draba
Family: Brassicaceae



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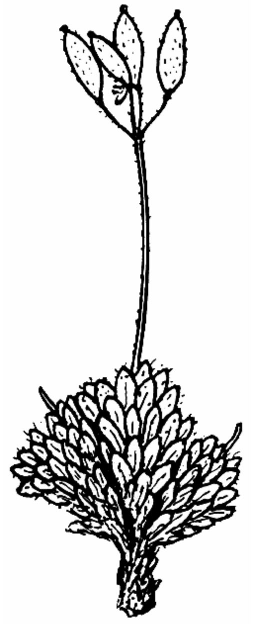
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are glabrous and form a distinct rosette.
Bud	The first buds have emerged. The buds are gray and emerge from the center of the rosette.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A silique has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length the longest leaf measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of siliques produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Draba micropetala*
Common name: Small petaled draba
Family: Brassicaceae



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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are pubescent and form a distinct rosette.
Bud	The first buds have emerged. The buds are gray and emerge from the center of the rosette.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A silique has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length the longest leaf measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of siliques produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Dupontia fisheri*
Common name: Tundra grass
Family: Poaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large and canoe-like in shape. Often the leaves are purplish.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is contracted. The spikelets have two florets and are awnless.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Dupontia fisheri/psilosantha*
Common name: Tundra grass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large and canoe-like in shape. Often the leaves are purplish.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is open. The spikelets have two florets and are awnless.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Eriophorum angustifolium*
Common name: Tall cottongrass
Family: Cyperaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, wide, olive green and U-shaped to flat in cross-section. The leaves are distinctly in 3s and generally lie close to the ground.
Inflorescence	The first brown-black spike has emerged from the center of the tiller. Often the inflorescence will emerge from a location with no apparent previous leaves. The inflorescence generally has multiple spikes.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The bristles originating from the perianth have emerged and are numerous giving the plant the characteristic cotton head appearance.
Seed Dispersal	The bristles and their associated seeds have begun to disperse.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.

Genus species: *Eriophorum angustifolium/triste*

Common name: Tall cottongrass

Family: Cyperaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, wide, olive green and nearly flat. The leaves are distinctly in 3s and generally lie close to the ground.
Inflorescence	The first brown-black spike has emerged from the center of the tiller. Often the inflorescence will emerge from a location with no apparent previous leaves. The inflorescence generally has multiple spikes.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The bristles originating from the perianth have emerged and are numerous giving the plant the characteristic cotton head appearance.
Seed Dispersal	The bristles and their associated seeds have begun to disperse.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence.

Genus species: *Eriophorum russeolum*
Common name: Red cottongrass
Family: Cyperaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small, thin, olive green and nearly flat. The leaves are distinctly in 3s and generally lie close to the ground.
Inflorescence	The first brown-black spike has emerged from the center of the tiller. Often the inflorescence will emerge from a location with no apparent previous leaves. The inflorescence has one spike only.
Bud	Not recorded.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The bristles originating from the perianth have emerged and are numerous giving the plant the characteristic cotton head appearance.
Seed Dispersal	The bristles and their associated seeds have begun to disperse.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence (should never be greater than 1).

Genus species: *Eriophorum scheuchzeri*
Common name: White cottongrass
Family: Cyperaceae


E. Hultén 1968

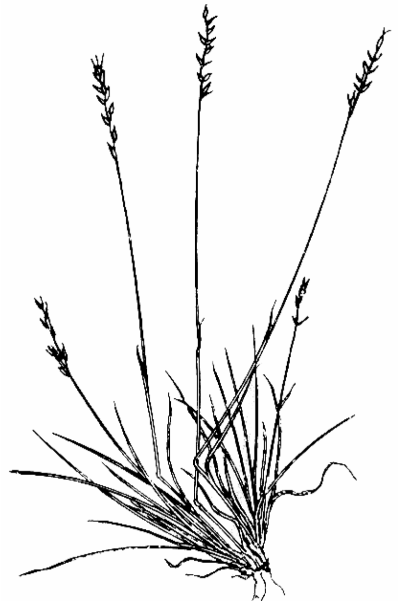
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small, and generally round.
Inflorescence	The first brown-black spike has emerged from the center of the tiller. Often the inflorescence will emerge from a location with no apparent previous leaves. The inflorescence has one spike only.
Stigma	The first white colored stigmata have emerged from beneath scales on a spike.
Flower	The first yellow colored anthers have emerged from beneath scales on a spike.
Flower Wither	On one spike all the anthers have turned a dull rust color or fallen off the spike.
Seed	The bristles originating from the perianth have emerged and are numerous giving the plant the characteristic cotton head appearance.
Seed Dispersal	The bristles and their associated seeds have begun to disperse.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the unit area (should not exceed the number of tillers).
Spikelets	The total number of spikes produced on the longest inflorescence (should never be greater than 1).

Genus species: *Festuca brachyphylla*
Common name: Alpine fescue
Family: Poaceae



E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small and grays. The plant is densely tufted.
Inflorescence	The first gray to purple colored inflorescence has emerged. The spikelets have multiple awned florets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Hierochloe alpina*
Common name: Alpine sweetgrass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large yellowish and rounded.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The spikelets have 3-florets all at the same level. The second lemma is awned.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Hierochloe pauciflora*
Common name: Arctic sweetgrass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small and bluish green. They are easily confused with *Poa arctica* and *Calamagrostis holmii*.
Inflorescence	The first gray to purple colored inflorescence has emerged. The spikelets have all the florets on one side. Generally the inflorescence will emerge from a location with no apparent prior leaves. The inflorescence resembles a sword as it first emerges from the ground.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).
Spikelets	The number of florets on the longest inflorescence.

Genus species: *Juncus biglumis*
Common name: Two flowered rush
Family: Juncaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are dark green, round and cylindrical.
Inflorescence	The first black flower emerged from the culm. *J. biglumis* has two flowers that look like two clumps of dirt on the side of the leaf near the apex.
Stigma	The first white colored stigmata have emerged from the flower.
Flower	The first yellow colored anthers have emerged from the flower.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the flower.
Seed	The black nutlet has expanded larger than the tepals surrounding it.
Seed Dispersal	The nutlet has opened and seeds have begun dispersing.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area. Generally a tiller consists of only one leaf.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Ledum palustre*
Common name: Marsh labrador tea
Family: Ericaceae

E. Hultén 1968

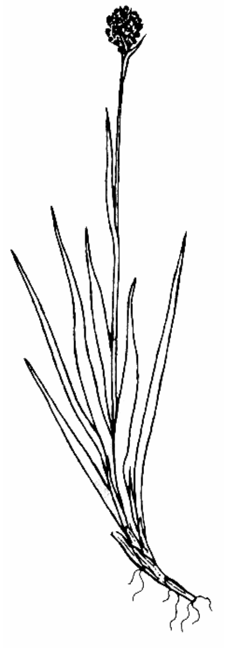
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are cylindrical and emerge from buds.
Inflorescence	The first red colored buds have emerged from the terminal end of a branch.
Bud	The red colored buds are distinctly visible and show some white.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of live (green) branches in the 5 cm^2 unit area.
Brown Tipped Leaves	The number of dead (brown) branches in the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences or flower clumps within the 5 cm^2 unit area.
Seeds	The number of capsules produced on the inflorescence with the most flowers.
Flowers	The number of flowers produced on the inflorescence with the most flowers.
Buds	The number of buds produced on the inflorescence with the most flowers.
Eaten	The number of inflorescences that were eaten or fell off the stem in the unit area.

Genus species: *Luzula arctica*
Common name: Arctic woodrush
Family: Juncaceae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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are short, wide and glabrous. The plant is densely caespitosa.
Inflorescence	The first brown-black spike has emerged from the center of the plant.
Stigma	The first white colored stigmata have emerged from the flower.
Flower	The first yellow colored anthers have emerged from the flower.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the flower.
Seed	The black nutlet has expanded larger than the tepals surrounding it.
Seed Dispersal	The nutlet has opened and seeds have begun dispersing.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Luzula confusa*
Common name: Northern woodrush
Family: Juncaceae


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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are long and have small hairs on the leaf margins.
Inflorescence	The first brown-black spike has emerged from the center of the plant.
Stigma	The first white colored stigmata have emerged from the flower.
Flower	The first yellow colored anthers have emerged from the flower.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the flower.
Seed	The black nutlet has expanded larger than the tepals surrounding it.
Seed Dispersal	The nutlet has opened and seeds have begun dispersing.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Luzula wahlenbergii*
Common name: Wahlenberg's woodrush
Family: Juncaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are short, wide and glabrous. The plant is densely caespitosa.
Inflorescence	The first brown-black spike has emerged from the center of the plant. The inflorescence is open compared with other *Luzula* species in the region.
Stigma	The first white colored stigmata have emerged from the flower.
Flower	The first yellow colored anthers have emerged from the flower.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the flower.
Seed	The black nutlet has expanded larger than the tepals surrounding it.
Seed Dispersal	The nutlet has opened and seeds have begun dispersing.
Senescence	At least half of one tiller has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Brown Tipped Leaves	The number of leaves produced in previous years that remain photosynthetic (usually more than half brown) on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Melandrium apetalum*
Common name: Apetalous catchfly
Family: Caryophyllaceae

E. Hultén 1968

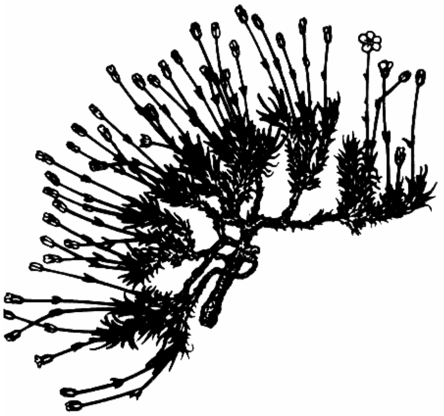
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves form a rosette.
Bud	The first buds have emerged.
Flower	The first appearance of a flower. The flowers are purple.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovary has expanded.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the leaf base at the center of the rosette to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Minuartia obtusiloba*
Common name: Twinflower sandwort
Family: Caryophyllaceae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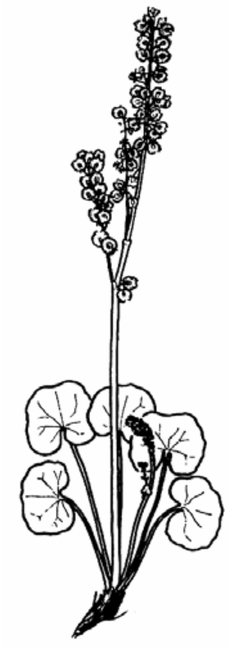
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are glabrous and form a mat.
Bud	The first buds have emerged. The buds are small and purple to gray colored.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the stem to the leaf blade tip.
Leaves	The average diameter of the mat.
Brown Tipped Leaves	Not recorded.
Individuals	The number of mats within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Oxyria digyna*
Common name: Mountain sorrel (Qunuliq)
Family: Polygonaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are round, reddish green, long-petiolated, and form a rosette.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The buds are small and form on the stem.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded.
Seed Dispersal	Seeds have begun to disperse.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from either the base at the petiole to the leaf blade tip or from side to side.
Leaves	The number of leaves on the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).

Genus species: *Papaver hultenii*
Common name: Hulten's poppy
Family: Papaveraceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged. The leaves are pubescent and form a distinct rosette.
Bud	The first buds have emerged. The buds are large with many black hairs and emerge from the center of the rosette.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the center of the rosette or ground surface to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Brown Tipped Leaves	Not recorded.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Papaver lapponicum*
Common name: Lapland poppy
Family: Papaveraceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged. The leaves are pubescent and form a distinct rosette. The plant is larger than *Papaver hultenii*.
Bud	The first buds have emerged. The buds are large with many black hairs and emerge from the center of the rosette.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the center of the rosette or ground surface to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Pedicularis kanei*
Common name: Woolly lousewort (Itkiliaġruk)
Family: Scrophulariaceae


E. Hultén 1968

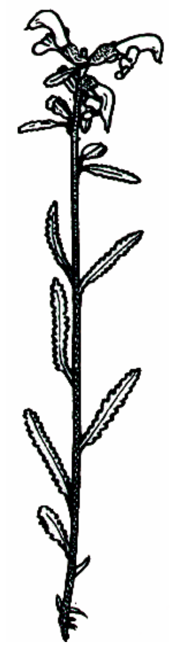
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged. The leaves are fern-like in appearance and form a distinct rosette.
Inflorescence	The first inflorescence has emerged. The inflorescence is large, white and wooly.
Bud	The first buds have emerged. The buds are pink and can be seen beneath the wooly hairs surround the inflorescence.
Flower	The first opening of a flower. The petals are pink to purple.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the center of the rosette or ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the rosette with the longest inflorescence or the longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Pedicularis lapponica*
Common name: Lapland lousewort
Family: Scrophulariaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged. The leaves are fern-like in appearance and form a distinct rosette.
Inflorescence	The appearance of a stem.
Bud	The first buds have emerged.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the center of the rosette or ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the rosette with the longest inflorescence or the longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Pedicularis sudetica*
Common name: Sudetic lousewort
Family: Scrophulariaceae


E. Hultén 1968

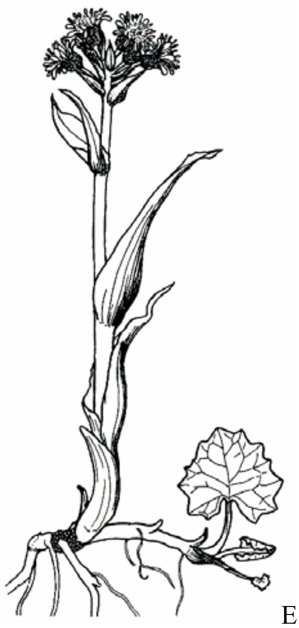
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged. The leaves are fern-like in appearance and form a distinct rosette.
Inflorescence	The appearance of a stem.
Bud	The first buds have emerged.
Flower	The first opening of a flower. The petals are pink to purple.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the center of the rosette or ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the rosette with the longest inflorescence or the longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Petasites frigidus*
Common name: Coltsfoot (Mapkutitaaġruaq)
Family: Asteraceae



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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large glabrous and somewhat resemble a maple leaf.
Inflorescence	The stem is first visible. The stem often emerges separate from previous leaves. As the stem emerges from the ground it is generally a red color and covered in pubescence.
Bud	The composite head is first visible. The head resembles a bud on the stem.
Flower	The first head is open and the petals of white ray flowers are visible.
Flower Wither	The first head has all the yellow anthers turn brown or the petals have withered.
Seed	Long white bristles have emerged from the head. The bristles are attached to seed and aid in dispersal.
Seed Dispersal	The first seeds are released from the head.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the leaf base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves produced in clump or the unit area.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of heads that produced seeds in the unit area.
Flowers	The number of heads that reached flowering in the unit area.
Buds	The number of heads in the unit area.
Eaten	The number of heads eaten in the unit area.

Genus species: *Poa arctica*
Common name: Arctic bluegrass
Family: Poaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small and canoe-like similar to *Dupontia*, but smaller.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is open. The spikelets have a multiple florets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Poa malacantha*
Common name: Bluegrass
Family: Poaceae


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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are small and canoe-like similar to *Dupontia*, but smaller. *Poa malacantha* is larger than *Poa arctica*.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is open. The spikelets have a multiple florets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Polygonum bistorta*
Common name: Meadow bistort
Family: Polygonaceae


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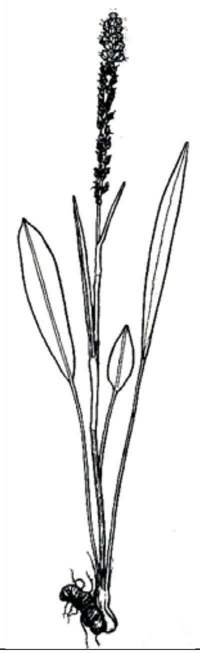
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are oval, reddish green, and glabrous.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The buds form on the stem.
Flower	The first opening of a flower. The petals are pink.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded and appear as spherical seeds often beneath withered petals.
Seed Dispersal	The seeds have begun to disperse.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves on the individual with the longest inflorescence or the longest leaf.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds on the individual with the longest inflorescence.
Flowers	The number of flowers on the individual with the longest inflorescence.
Buds	The number of buds on the individual with the longest inflorescence.

Genus species: *Polygonum viviparum*
Common name: Alpine bistort (Ippiq)
Family: Polygonaceae



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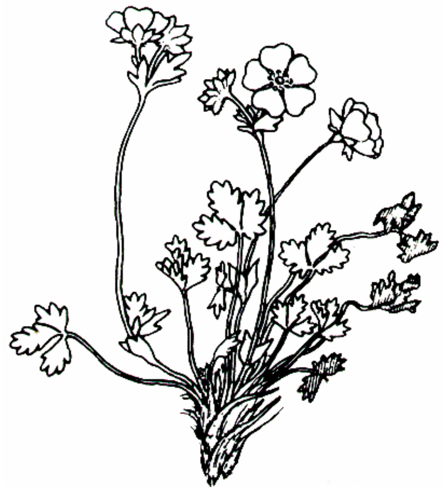
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are oval, reddish green, and glabrous.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The buds form on the stem.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded and appear as spherical seeds often beneath withered petals.
Bulbil	The first appearance of small plants emerging from the seeds while on the stem.
Seed Dispersal	The seeds have begun to disperse.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves on the individual with the longest inflorescence or the longest leaf.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds on the individual with the longest inflorescence.
Flowers	The number of flowers on the individual with the longest inflorescence.
Buds	The number of buds on the individual with the longest inflorescence.

Genus species: *Potentilla hyparctica*
Common name: Tundra rose
Family: Rosaceae



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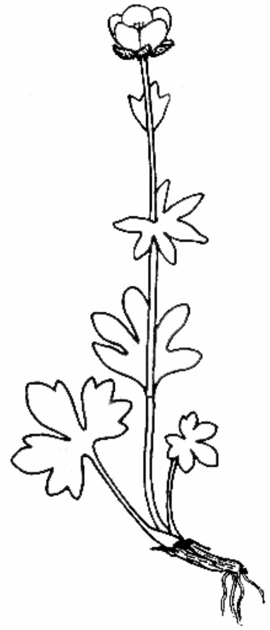
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have begun to open as they emerge. The leaves are pubescent.
Bud	The first buds have emerged. The buds are the same color as leaves except for a red tinge on the sepals.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The average diameter of the individual with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Ranunculus nivalis*
Common name: Snow buttercup
Family: Ranunculaceae



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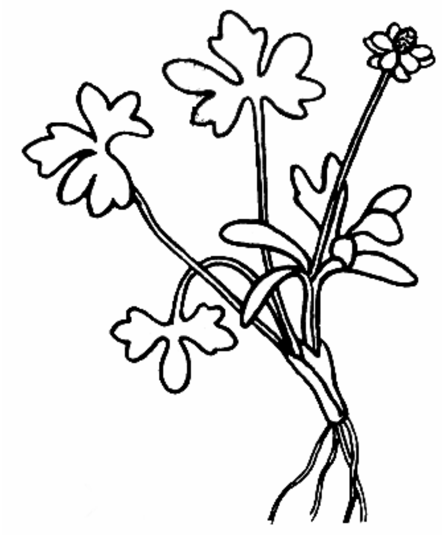
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are dark green and deeply lobed.
Bud	The first appearance of a bud. The buds occasional will emerge from a location with no apparent prior leaves.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have ripened and appear as many spherical seeds often beneath the withered petals.
Seed Dispersal	The seeds have begun to disperse.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves on the individual with the longest inflorescence or the longest leaf.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Ranunculus pygmaeus*
Common name: Pygmy buttercup
Family: Ranunculaceae



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Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are dark green and deeply lobed, and form a mat. The leaves are much smaller than *Ranunculus nivalis*. The leaves can closely resemble *Saxifraga cernua* and *Chrysosplenium tetrandrum*.
Bud	The first appearance of a bud.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have ripened and appear as many spherical seeds often beneath the withered petals.
Seed Dispersal	The seeds have begun to disperse.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The average diameter of the mat.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The height of the tallest inflorescence measured from the ground surface to the inflorescence top.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Salix phlebophylla*
Common name: Skeletonleaf willow
Family: Salicaceae

E. Hultén 1968

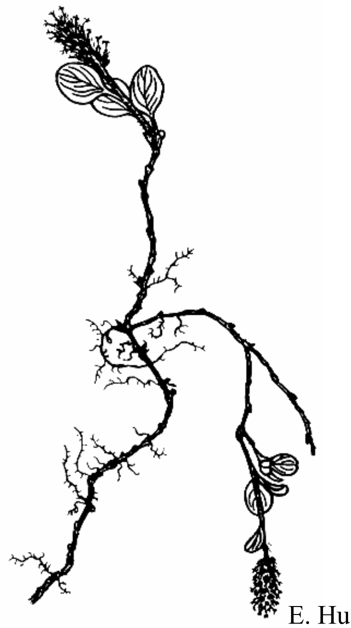
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are circular and unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll.
Inflorescence	The first red colored catkin has emerged from the stem. The catkin consists of many flowers.
Flower	The first yellow colored anthers are visible on the catkin for males. The stigmas are receptive to pollen.
Flower Wither	On one catkin all the anthers have turned a dull rust color or the catkin has fallen off the stem for males. On one catkin all the stigmas have withered for females.
Seed	The pistils on the catkin have enlarged.
Seed Dispersal	The pistils on the catkin have opened and begun to dehisce.
Senescence	At least half of the leaves have turned yellow to brown or fallen off the stem.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of leaves produced in the unit area.
Inflorescence Length	The length of the longest inflorescence measured from the stem to the inflorescence tip.
Inflorescences	The number of catkins in the unit area.
Seeds	The number of ripened pistils on the longest catkin.
Flowers	The number of pistils produced on the longest catkin.
Eaten	The number of catkins that were eaten or fell off the stem.

Genus species: *Salix polaris*
Common name: Polar willow
Family: Salicaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are circular and unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll. The stem is often yellowish. *Salix polaris* is much smaller than *S. pulchra* in Atqasuk.
Inflorescence	The first red colored catkin has emerged from the stem. The catkin consists of many flowers.
Flower	The first yellow colored anthers are visible on the catkin for males. The stigmas are receptive to pollen.
Flower Wither	On one catkin all the anthers have turned a dull rust color or the catkin has fallen off the stem for males. On one catkin all the stigmas have withered for females.
Seed	The pistils on the catkin have enlarged.
Seed Dispersal	The pistils on the catkin have opened and begun to dehisce.
Senescence	At least half of the leaves have turned yellow to brown or fallen off the stem.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of leaves produced in the unit area.
Inflorescence Length	The length of the longest inflorescence measured from the stem to the inflorescence tip.
Inflorescences	The number of catkins in the unit area.
Seeds	The number of ripened pistils on the longest catkin.
Flowers	The number of pistils produced on the longest catkin.
Eaten	The number of catkins that were eaten or fell off the stem.

Genus species: *Salix pulchra*
Common name: Tealeaf willow
Family: Salicaceae

E. Hultén 1968

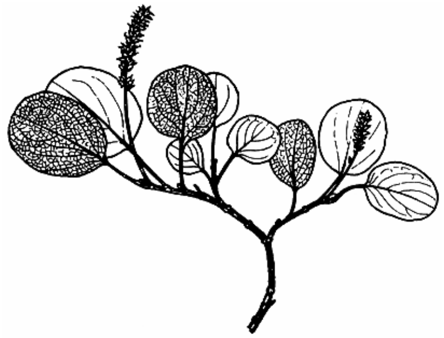
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are circular and unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll.
Inflorescence	The first red colored catkin has emerged from the stem. The catkin consists of many flowers.
Flower	The first yellow colored anthers are visible on the catkin for males. The stigmas are receptive to pollen.
Flower Wither	On one catkin all the anthers have turned a dull rust color or the catkin has fallen off the stem for males. On one catkin all the stigmas have withered for females.
Seed	The pistils on the catkin have enlarged.
Seed Dispersal	The pistils on the catkin have opened and begun to dehisce.
Senescence	At least half of the leaves have turned yellow to brown or fallen off the stem.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of leaves produced from the tag outward.
Brown Tipped Leaves	The length of the longest branch measured from the axis to the branch tip. Note this measure has nothing to do with brown tipped leaves but fits within this column.
Individuals	The number of branches on the stem from the tag outward.
Inflorescence Length	The length of the longest inflorescence measured from the stem to the inflorescence tip.
Inflorescences	The number of catkins on the stem from the tag outward.
Seeds	The number of ripened pistils on the longest catkin.
Flowers	The number of pistils produced on the longest catkin.
Eaten	The number of catkins that were eaten or fell off the stem.

Genus species: *Salix rotundifolia*
Common name: Least willow (Uqpik)
Family: Salicaceae



E. Hultén 1968

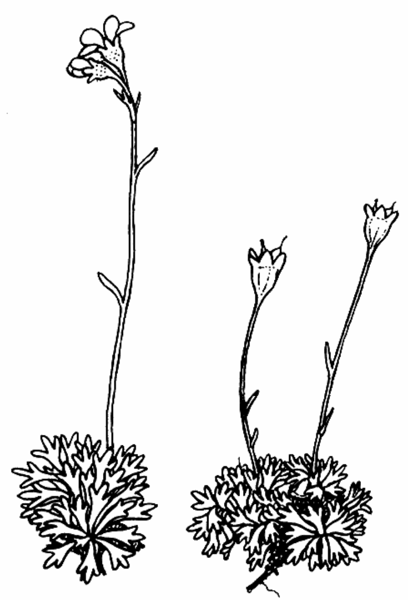
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are circular and unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll.
Inflorescence	The first red colored catkin has emerged from the stem. The catkin consists of many flowers.
Flower	The first yellow colored anthers are visible on the catkin for males. The stigmas are receptive to pollen.
Flower Wither	On one catkin all the anthers have turned a dull rust color or the catkin has fallen off the stem for males. On one catkin all the stigmas have withered for females.
Seed	The pistils on the catkin have enlarged.
Seed Dispersal	The pistils on the catkin have opened and begun to dehisce.
Senescence	At least half of the leaves have turned yellow to brown or fallen off the stem.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of leaves produced in the unit area.
Inflorescence Length	The length of the longest inflorescence measured from the stem to the inflorescence tip.
Inflorescences	The number of catkins in the unit area.
Seeds	The number of ripened pistils in the unit area.
Flowers	The number of pistils produced in the unit area.
Eaten	The number of catkins that were eaten or fell off the stem.

Genus species: *Saxifraga caespitosa*
Common name: Tufted alpine saxifrage
Family: Saxifragaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are small and form distinct rosettes.
Bud	The first buds have emerged. The buds are gray and emerge from the center of a rosette.
Stigma	Not recorded
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga cernua*
Common name: Nodding saxifrage
Family: Saxifragaceae


E. Hultén 1968

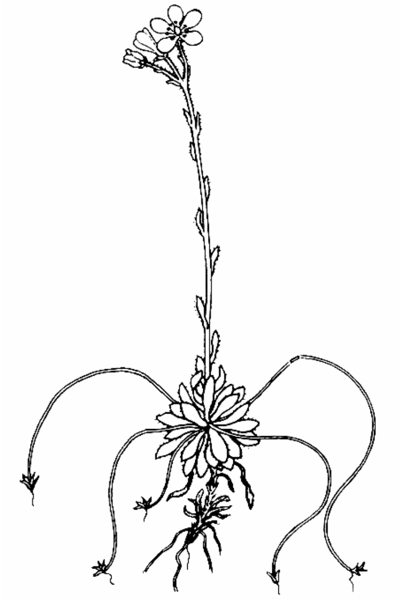
Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are round and crenate with a long petiole.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The bud forms at the apex of the stem and should show a white tinge.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Bulbil	The first red colored bulbil has emerged on the stem. The bulbil is a vegetative form of reproduction.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from either the base at the petiole to the leaf blade tip or from side to side.
Leaves	The number of non-bract leaves in the unit area.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga flagellaris*
Common name: Spiderplant
Family: Saxifragaceae



E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are small and for distinct rosettes.
Bud	The first buds have emerged. The buds are gray and emerge from the center of a rosette.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Bulbil	The runners are clearly visible.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga foliolosa*
Common name: Leafystem saxifrage
Family: Saxifragaceae

E. Hultén 1968

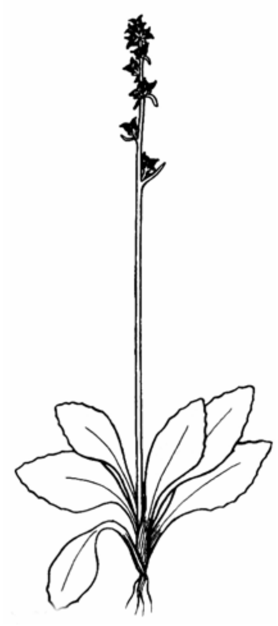
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are small and spatulate and for distinct rosettes.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The bud forms at the apex of the stem and should show a white tinge.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Bulbil	The first red colored bulbil has emerged on the stem. The bulbil is a vegetative form of reproduction.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of rosettes).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga hieracifolia*
Common name: Stiffstem saxifrage
Family: Saxifragaceae


E. Hultén 1968

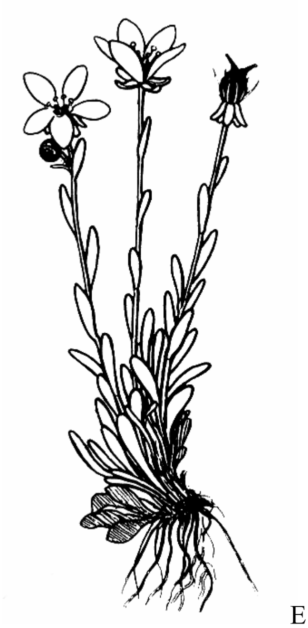
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Recorded.
Inflorescence Length	Recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are large and form distinct rosettes.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The bud forms along the stem.
Flower	The first opening of a flower. The petals are reddish green and reduced.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The number of non-bract leaves on the rosette with the longest inflorescence or longest leaf.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced capsules on the longest inflorescence.
Flowers	The number of flowers produced on the longest inflorescence.
Buds	The number of buds produced on the longest inflorescence.

Genus species: *Saxifraga hirculus*
Common name: Yellow marsh saxifrage
Family: Saxifragaceae



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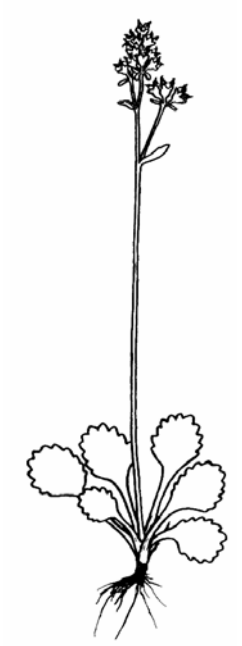
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves emerge form buds.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The bud forms at the apex of the stem.
Flower	The first opening of a flower. The petals are yellow.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base to the leaf blade tip.
Leaves	The number of non-bract leaves on the individual with the longest inflorescence or longest leaf.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced capsules in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga nivalis*
Common name: Snow saxifrage
Family: Saxifragaceae



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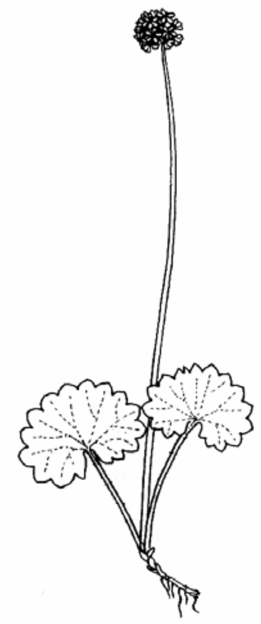
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first leaves have emerged or re-greened. The leaves are rounded and dentate and for distinct rosettes.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud. The bud forms at the apex of the stem and should show a white tinge.
Flower	The first opening of a flower. The petals are white.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from the base at the center of the rosette to the leaf blade tip.
Leaves	The average diameter of the rosette.
Individuals	The number of rosettes within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the center of the rosette or ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Saxifraga punctata*
Common name: Heartleaf saxifrage
Family: Saxifragaceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Not recorded.
Anthesis	Not recorded.
Post-anthesis	Not recorded.
Eaten/Missing/Dead	Not recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large, round and crenate with a long petiole.
Inflorescence	The first appearance of a stem.
Bud	The first appearance of a bud.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The ovaries have expanded to be larger than the original petals.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length or width of the longest leaf blade measured from either the base at the petiole to the leaf blade tip or from side to side.
Leaves	The number of non-bract leaves in the unit area.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of flowers that produced seeds in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Senecio atropurpureus*
Common name: Arctic groundsel
Family: Asteraceae


E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are glabrous and resemble a stone plant.
Inflorescence	The stem is first visible. The stem often emerges separate from previous leaves. As the stem emerges from the ground it is generally a red color and covered in pubescence.
Bud	The composite head is first visible. The head resembles a bud on the stem.
Flower	The first head is open and the petals of white ray flowers are visible.
Flower Wither	The first head has all the yellow anthers turn brown or the petals have withered.
Seed	Long white bristles have emerged from the head. The bristles are attached to seed and aid in dispersal.
Seed Dispersal	The first seeds are released from the head.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the leaf base at the petiole to the leaf blade tip.
Leaves	The number of non-bract leaves produced in clump or the unit area.
Individuals	The number of individuals within the clump or the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the clump or the 5 cm^2 unit area (should not exceed the number of individuals).
Seeds	The number of heads that produced seeds in the unit area.
Flowers	The number of heads that reached flowering in the unit area.
Buds	The number of heads in the unit area.
Eaten	The number of heads eaten in the unit area.

Genus species: *Stellaria humifusa*
Common name: Saltmarsh starwort
Family: Caryophyllaceae

E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll. The leaves are much smaller and much more rounded than the leaves of *Stellaria laeta* and *Cerastium beeringianum*.
Bud	The first flower bud has emerged. The buds form at the end of the stem and should show some white.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The petals have fallen off and the ovaries have expanded.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf measured from the base of the petiole at the stem to the tip of the leaf blade.
Leaves	The number of live (green) branches in the 5 cm^2 unit area.
Brown Tipped Leaves	The number of dead (brown) branches in the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed one).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Stellaria laeta*
Common name: Starwort
Family: Caryophyllaceae


E. Hultén 1968

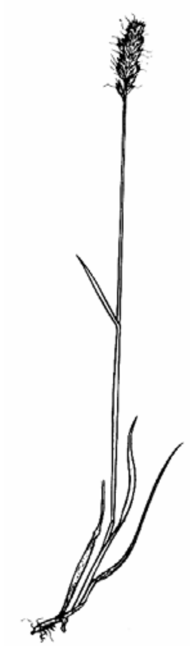
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves unroll as they emerge. The leaf and flower buds can be confused. First leaf should not be designated until at least one leaf has begun to unroll.
Bud	The first flower bud has emerged. The buds form at the end of the stem and should show some white.
Flower	The first opening of a flower.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	The petals have fallen off and the ovaries have expanded.
Seed Dispersal	A capsule has begun to dehisce.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf measured from the base of the petiole at the stem to the tip of the leaf blade.
Leaves	The number of live (green) branches in the 5 cm^2 unit area.
Brown Tipped Leaves	The number of dead (brown) branches in the 5 cm^2 unit area.
Individuals	Not recorded.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed one).
Seeds	The number of capsules produced in the unit area.
Flowers	The number of flowers produced in the unit area.
Buds	The number of buds produced in the unit area.

Genus species: *Trisetum spicatum*
Common name: Spike trisetum
Family: Poaceae


E. Hultén 1968

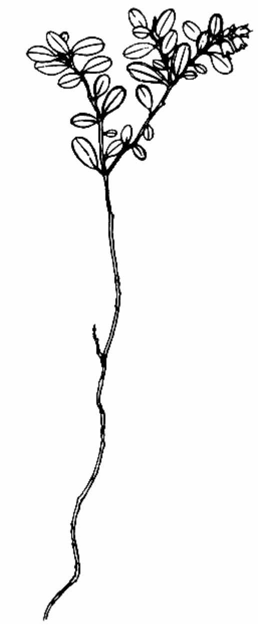
Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are large.
Inflorescence	The first gray to purple colored inflorescence has emerged from the culm. The panicle is spike-like. The spikelets have multiple florets.
Stigma	The first white colored stigmata have emerged from the floret.
Flower	The first yellow colored anthers have emerged from the floret.
Flower Wither	On one inflorescence all the anthers have turned a dull rust color or fallen off the floret.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest non-bract leaf measured from the base of culm at the ground surface to the leaf blade tip.
Leaves	The number of non-bract leaves produced this year on the tiller with the longest inflorescence or the longest leaf.
Individuals	The number of tillers within the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the base of the culm at the ground surface to the inflorescence tip.
Inflorescences	The number of inflorescences within the 5 cm^2 unit area (should not exceed the number of tillers).

Genus species: *Vaccinium vitis-idaea*
Common name: Lingonberry
Family: Ericaceae



E. Hultén 1968

Weekly Inflorescence Counts	
Pre-anthesis	Recorded.
Anthesis	Recorded.
Post-anthesis	Recorded.
Eaten/Missing/Dead	Recorded.

Weekly Growth Measures	
Leaf Length	Not recorded.
Inflorescence Length	Not recorded.

Phenological Development	
Leaf	The first new leaf has emerged. The leaves are cylindrical and emerge from buds.
Inflorescence	The first red colored buds have emerged from the terminal end of a branch.
Bud	The red colored buds are distinctly visible and show some pink.
Flower	The first opening of a flower. The petals are pink.
Flower Wither	The petals of a flower have withered or fallen off.
Seed	A berry has formed and ripened.
Seed Dispersal	A berry has dispersed.
Senescence	At least half of the plant has turned yellow to brown.
Location	A-E represents North to South; 1-7 East to West.
Comment	Any relevant field notes.
Eaten	1 represents damage due to herbivory; -1 not damaged; 0 not recorded.
Health	1 represents healthy; -1 not healthy; 0 not recorded.
Terminated	1 represents death; -1 living; 0 not recorded.

Annual Growth & Reproductive Allocation	
Leaf Length	The length of the longest leaf blade measured from the base at the petiole to the leaf blade tip.
Leaves	The number of live (green) branches in the 5 cm^2 unit area.
Brown Tipped Leaves	The number of dead (brown) branches in the 5 cm^2 unit area.
Inflorescence Length	The length of the longest inflorescence measured from the ground to the inflorescence top.
Inflorescences	The number of inflorescences or flower clumps within the 5 cm^2 unit area.
Seeds	The number of berries produced on the inflorescence with the most flowers.
Flowers	The number of flowers produced on the inflorescence with the most flowers.
Buds	The number of buds produced on the inflorescence with the most flowers.
Eaten	The number of inflorescences that were eaten or fell off the stem.

Appendix D

ESTIMATION OF MISSING TEMPERATURE DATA

This appendix contains an explanation of the linear models used to estimate missing temperature data. The two types of missing data were: A) screen height (2 m) temperatures for years before the installation of the automated weather stations at the dry heath sites in Barrow and Atqasuk; and B) canopy height (13 cm) temperatures from snowmelt until site establishment for times when site establishment was delayed.

To fill in the type A missing data screen height temperature was estimated based on a correlation between the National Ocean and Atmospheric Association (NOAA) Climate Monitoring and Diagnostics Laboratory (CMDL) in Barrow and the Barrow Dry Heath and Atqasuk Dry Heath Screen height temperatures for the years that the automated weather station was in operation (1999-2001). The correlation was performed at the hourly time scale and was run separately for each month and four times during the day. The four times were morning, day, evening, and night. Day was the six hours of a 24-hour cycle that was on average the warmest; conversely night was the coolest six hours. The separation of day into four times was considered necessary because the daily range of temperatures increases with distance from the Arctic Coast; therefore, the average daily range is greater at Atqasuk than Barrow. The resulting equations and r^2 coefficients from the correlations are presented in Table D-1. These equations were then used to model (calculate) the best possible estimation of any missing screen height temperature data.

To fill in type B missing data canopy height temperature was estimated based on a correlation between the Barrow and Atqasuk Dry Heath screen height temperature and the canopy height temperature for the controls in the dry heath and wet meadow sites in Barrow and Atqasuk form June 4 to July 15 for the times when there was data for both (1999-2001). The correlation was performed at the hourly time scale and was run separately for times during the day. The four times were morning, day, evening, and night. Day was the 6 hours of the 24-hour cycle that were had on average the most intense solar radiation; conversely night was the least intense six hours. The separation of day into four times was considered necessary because solar radiation has a major influence on climate near the ground; therefore, canopy height temperatures during the day are expected to be significantly higher than screen height temperatures and during the night the difference is often less pronounced. The resulting equations and r^2 coefficients from the correlations are presented in Table D-2. These equations were then used to model (calculate) the best possible estimation of any missing canopy height temperature data. Note for missing data before 1999 the canopy height temperature was calculated from estimated screen height data. The type B estimated data was used to more accurately estimate accumulated thawing degree-days from the time of snowmelt until the sites were established.

Table D-1. Equation coefficients and r^2 values form the linear model used to predict the temperature at screen height (2 m) over the Barrow Dry Heath (BD) and Atqasuk Dry Heath (AD) sites from the temperature data recorded at the National Ocean and Atmospheric Association (NOAA) Climate Monitoring and Diagnostics Laboratory (CMDL) in Barrow. The model coefficients were calculated from the correlation between the temperatures at the two locations between the years 1999 and 2001 at the hourly time scale. The correlation was run for each month and time of the day. The four times during the day were morning (TM: 07:00-12:00), day (TD: 13:00-18:00), evening (TE: 19:00-00:00), and night (TN: 01:00-06:00). The number of data points used in the regression (n) varied due to the recording interval (May 15 – August 15) and missing data.

Month	Time of Day	n	Equation	r^2
		Predicting BD (y) from NOAA CMDL (x)		
May	TD	304	y = 0.7201x + -0.0552	0.71
May	TE	306	y = 0.9333x + -0.2689	0.81
May	TM	302	y = 0.8225x + -1.3718	0.70
May	TN	306	y = 1.0733x + -1.6401	0.73
June	TD	531	y = 0.7090x + 1.5844	0.52
June	TE	534	y = 0.7132x + 0.1799	0.57
June	TM	528	y = 1.0654x + 1.1780	0.59
June	TN	530	y = 0.8667x + -0.8160	0.67
July	TD	558	y = 0.9153x + 2.4114	0.51
July	TE	558	y = 0.6080x + 0.6197	0.50
July	TM	558	y = 0.8721x + 1.7516	0.55
July	TN	558	y = 0.6779x + -0.2315	0.56
August	TD	270	y = 0.6523x + 3.1565	0.29
August	TE	270	y = 0.6595x + 0.8579	0.52
August	TM	270	y = 0.6548x + 2.7406	0.29
August	TN	270	y = 0.5091x + 1.0451	0.42
		Predicting AD (y) from NOAA CMDL (x)		
May	TD	304	y = 0.7735x + 1.2477	0.63
May	TE	306	y = 1.0550x + 1.5086	0.76
May	TM	302	y = 0.8524x + -0.6294	0.65
May	TN	306	y = 1.2159x + 0.0167	0.75
June	TD	531	y = 1.0994x + 7.1477	0.40
June	TE	534	y = 1.0352x + 4.2269	0.41
June	TM	528	y = 1.1738x + 4.3289	0.37
June	TN	530	y = 0.9888x + 1.3588	0.49
July	TD	558	y = 1.1274x + 8.3540	0.42
July	TE	558	y = 0.7509x + 5.9134	0.36
July	TM	558	y = 1.0298x + 5.5631	0.38
July	TN	558	y = 0.8533x + 2.6884	0.52
August	TD	270	y = 0.7446x + 7.1408	0.19
August	TE	270	y = 0.7499x + 4.4550	0.32
August	TM	270	y = 0.7700x + 5.1700	0.25
August	TN	270	y = 0.6444x + 3.1969	0.40

Table D-2. Equation coefficients and r^2 values form the linear model used to predict the temperature at canopy height (13 cm) at the four sites (AD – Atqasuk Dry Heath, AW – Atqasuk Wet Meadow, BD – Barrow Dry Heath, BW – Barrow Wet Meadow) from temperatures recorded at screen height (2 m) over the BD and AD sites. The model coefficients were calculated from the correlation between the temperatures at the two locations between the years 1999 and 2001 at the hourly time scale. The correlation was run for four different times of the day from June 4 – July 15. The four times during the day were morning (SM: 05:00-10:00), day (SD: 11:00-16:00), evening (SE: 17:00-22:00), and night (SN: 23:00-04:00). The number of data points used in the regression (n) varied due to the duration of canopy level temperature recording.

Time of Day	n	Equation	r^2
Predicting BD canopy (y) from BD screen (x)			
SD	612	y = 0.9489x + 2.3554	0.92
SE	612	y = 0.9866x + 1.3588	0.91
SM	612	y = 0.9743x + 0.7866	0.94
SN	612	y = 0.9582x + -0.0224	0.98
Predicting BW canopy (y) from BD screen (x)			
SD	450	y = 0.9451x + 2.2753	0.93
SE	450	y = 0.9911x + 1.3733	0.94
SM	450	y = 0.9741x + 0.8471	0.95
SN	450	y = 0.9594x + 0.1746	0.98
Predicting AD canopy (y) from AD screen (x)			
SD	714	y = 0.8550x + 3.1787	0.70
SE	714	y = 0.8828x + 2.0947	0.75
SM	714	y = 0.8778x + 1.2109	0.75
SN	714	y = 0.8814x + 0.5032	0.82
Predicting AW canopy (y) from AD screen (x)			
SD	606	y = 0.8708x + 2.6636	0.73
SE	606	y = 0.8728x + 2.1558	0.77
SM	606	y = 0.8881x + 1.1732	0.79
SN	606	y = 0.8628x + 0.8580	0.81

Appendix E

PHENOLOGICAL DEVELOPMENT, GROWTH, AND REPRODUCTIVE TABLES

The appendix contains summaries of the phenological development, growth, and reproductive data analyzed in Chapter IV. The average date that a phenologic event occurred is presented in Table E-1. The average annual growth and reproductive data is presented in Table E-2. The methods for the data collection are presented in Sections I.5.4-4 and IV.3. The only data not explicitly described in Section IV.3 is the average date when flowers withered and seeds became visible, the number of leaves, and the percentage of individuals flowering. All the above data were collected similarly to the methods described in Section IV.3 except the percentage of individuals flowering. Flowering percentages were calculated from all the marked plants of the species within a site; if the marked plant flowered or not it was scored as a 1 or a 0 respectively.

Table E-1. Phenological development of the plant species within the four study sites for each year and treatment (C - control plots, W - warmed plots). The data presented are the average Julian day that the specified organ or event first became visible within a plot. Letters represent the statistical difference between the populations calculated with a Tukey's studentized range test (HSD, *p* -value <0.05); if two populations do not have the same letter then they are significantly different.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
					Atqasuk Dry Heath						
Carex bigelowii	1998	156.1 b	156.4 b	·	·	·	·	·	·	·	·
	1999	165.4 a	165.4 a	·	·	·	·	·	·	·	·
	2000	166.0 a	166.0 a	·	·	·	·	·	·	·	·
Cassiope tetragona	1998	155.3 b	155.5 b	157.9 b	160.1 b	172.8 b	172.9 b	178.9 b	178.8 b	188.9 b	190.2 b
	1999	161.4 a	161.9 a	172.1 a	173.0 a	178.8 a	179.3 a	187.6 a	188.7 a	191.0 b	194.1 a
Diapensia lapponica	1998	155.7 b	155.3 b	158.0 d	161.1 c	173.0 b	173.5 b	177.9 b	178.9 b	·	·
	1999	164.7 a	164.4 a	174.0 a	173.3 a	179.2 a	178.6 a	187.3 a	186.5 a	192.5 ab	193.7 a
	2000	164.9 a	164.8 a	170.1 b	168.9 b	174.7 b	173.8 b	178.5 b	178.3 b	190.1 bc	189.1 c
Hierochloe alpina	1998	155.3 b	155.8 b	168.4 b	163.8 c	179.6 c	174.9 d	184.5 b	182.3 b	·	·
	1999	163.7 a	163.9 a	175.5 a	174.2 a	187.4 a	182.6 b	190.6 a	188.8 a	·	·
	2000	164.7 a	164.1 a	168.6 b	166.7 bc	178.0 c	177.0 cd	183.3 b	182.2 b	·	·
Ledum palustre	1998	155.8 b	155.9 b	172.6 c	173.3 c	178.7 cd	177.9 d	185.8 c	184.7 c	194.5 b	194.0 b
	1999	163.1 a	163.4 a	179.6 a	179.1 a	184.4 a	183.3 ab	190.3 b	189.7 b	197.3 b	193.9 b
	2000	164.3 a	164.2 a	175.6 b	175.5 b	181.3 bc	181.4 bc	200.0 a	197.9 a	208.3 a	205.5 a
Luzula arctica	1998	155.1 b	155.7 b	·	·	165.2 c	164.3 c	173.2 c	173.9 bc	187.7 a	188.4 a
	1999	161.4 a	161.9 a	164.6 b	167.8 ab	172.4 ab	174.1 a	178.8 a	179.1 a	190.0 a	189.1 a
	2000	162.4 a	163.4 a	171.0 a	170.6 a	171.8 ab	171.1 b	176.5 ab	176.9 a	188.0 a	189.6 a
Luzula confusa	1998	157.0 c	156.3 c	171.2 bc	167.8 c	177.1 cd	174.6 d	183.2 b	181.3 b	188.4 c	188.4 c
	1999	164.8 b	167.0 a	177.1 a	176.9 a	183.3 a	183.4 a	190.0 a	190.4 a	194.4 b	193.5 b
	2000	166.1 ab	166.0 ab	174.2 ab	173.2 b	180.2 b	179.3 bc	189.8 a	187.7 a	200.5 a	196.1 b

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
Atqasuk Dry Heath continued											
Polygonum bistorta	1998	158.2 bc	157.1 c	173.7 ab	172.0 b	183.4 b	183.8 b	194.1 b	198.2 ab	·	·
	1999	166.5 a	164.0 ab	180.6 a	178.8 ab	190.7 a	189.0 a	202.3 ab	208.0 a	·	·
	2000	164.8 a	165.4 a	·	·	·	·	·	·	·	·
Salix phlebophylla Female	1998	159.3 b	156.3 b	·	·	·	·	·	·	·	·
	1999	167.3 a	167.0 a	·	·	·	·	·	·	·	·
Male	1998	159.3 b	157.0 b	·	·	·	·	·	·	·	·
	1999	167.3 a	167.0 a	·	·	·	·	·	·	·	·
Trisetum spicatum	1998	158.8 b	158.6 b	·	·	·	·	·	·	·	·
	1999	165.9 a	168.0 a	·	·	·	·	·	·	·	·
	2000	167.4 a	167.7 a	·	·	·	·	·	·	·	·
Vaccinium vitis-idaea	1998	155.0 b	155.0 b	182.1 a	182.3 a	186.3 c	187.9 bc	197.3 c	198.5 c	·	·
	1999	160.1 a	160.4 a	180.1 ab	181.0 ab	191.0 b	190.6 b	205.1 b	204.7 b	·	·
	2000	160.4 a	161.0 a	178.8 b	178.9 b	195.1 a	195.8 a	213.3 a	216.4 a	·	·
Atqasuk Wet Meadow											
Carex aquatilis	1998	160.9 c	161.3 c	176.5 c	176.1 c	180.3 c	180.1 c	184.0 d	182.0 d	188.5 d	188.2 d
	1999	164.3 bc	165.3 b	182.9 ab	184.8 ab	186.0 b	186.1 b	190.2 c	190.3 c	193.2 bc	192.6 c
	2000	169.7 a	172.1 a	185.9 a	181.2 b	192.6 a	187.9 b	197.0 a	192.8 b	201.3 a	195.2 b
Dupontia fisheri/psilosantha	1998	162.4 c	162.9 c	·	·	·	·	198.5 a	200.0 a	·	·
	1999	172.3 ab	178.2 a	·	·	·	·	202.2 a	201.0 a	·	·
	2000	169.5 b	174.2 ab	·	·	·	·	·	·	·	·
Eriophorum angustifolium	1998	160.5 c	160.1 c	·	·	175.6 a	176.2 a	179.0 a	179.2 a	·	·
	1999	162.6 b	163.1 b	·	·	178.3 a	178.6 a	180.7 a	181.7 a	·	·
	2000	166.1 a	166.8 a	·	·	·	·	·	·	·	·

Table E-1. Continued.

Species	Year	Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
		C	W	C	W	C	W	C	W	C	W
				Atqasuk Wet Meadow continued							
Eriophorum russeolum	1998	158.2 b	159.6 b	163.8 bc	162.9 c	175.1 a	175.9 a	179.6 a	180.9 a	·	·
	1999	164.3 a	164.2 a	170.3 a	169.1 ab	178.8 a	176.6 a	183.8 a	181.4 a	·	·
	2000	165.8 a	166.6 a	·	·	·	·	·	·	·	·
Luzula wahlenbergii	1998	166.1 a	164.7 a	·	·	·	·	·	·	·	·
	1999	164.6 a	167.1 a	·	·	·	·	·	·	·	·
	2000	166.0 a	166.9 a	·	·	·	·	·	·	·	·
Pedicularis sudetica	1998	165.8 ab	161.9 b	·	·	·	·	·	·	·	·
	1999	170.1 a	168.1 a	·	·	·	·	·	·	·	·
	2000	170.8 a	169.9 a	·	·	·	·	·	·	·	·
Polygonum viviparum	1999	175.7 a	173.8 a	·	·	·	·	·	·	·	·
	2000	170.3 a	173.3 a	·	·	·	·	·	·	·	·
					Barrow Dry Heath						
Arctagrostis latifolia	1994	178.6 a	178.1 a	·	·	·	·	·	·	·	·
	1995	168.1 bcd	167.8 bcd	206.0 a	196.3 abcd	·	·	·	·	·	·
	1996	159.4 e	158.6 e	·	·	·	·	·	·	·	·
	1997	165.4 d	166.5 cd	·	·	209.3 a	202.3 ab	·	·	·	·
	1998	159.7 e	159.7 e	187.2 de	185.1 e	195.6 b	199.4 ab	·	·	·	·
	1999	171.3 b	169.9 bc	194.4 bcde	190.7 cde	·	·	·	·	·	·
	2000	167.0 bcd	168.3 bcd	204.0 ab	197.9 abc	·	·	·	·	·	·
Cassiope tetragona	1994	·	·	186.7 a	184.2 a	204.1 a	195.3 b	215.5 a	207.8 b	·	·
	1995	·	·	187.4 a	176.8 b	206.2 a	193.4 b	·	·	·	·
	1996	·	·	·	·	181.5 cd	175.5 e	192.5 d	187.2 e	·	·
	1997	168.7 a	166.5 ab	177.3 b	170.1 c	192.3 b	184.7 c	204.0 bc	199.5 c	·	·
	1998	157.8 c	157.6 c	170.2 c	170.4 c	180.8 cde	176.1 de	191.1 de	189.2 de	·	·
	2000	163.1 b	162.9 b	173.9 bc	171.5 c	194.9 b	185.7 c	205.4 b	199.4 c	·	·

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
					Barrow Dry Heath contiued						
Draba lactea	1997	·	·	·	·	181.7 a	181.6 a	·	·	·	·
	1998	164.0 ab	161.3 b	·	·	·	·	·	·	198.8 a	189.4 a
	1999	167.3 ab	171.2 a	·	·	183.0 a	185.7 a	196.3 a	194.7 a	192.5 a	192.0 a
	2000	167.2 ab	169.7 ab	·	·	185.8 a	182.0 a	196.8 a	190.3 a	201.0 a	195.0 a
Draba micropetala	1994	·	·	·	·	186.0 a	182.3 abc	·	·	198.2 a	195.4 ab
	1995	167.7 a	167.9 a	170.2 b	172.4 b	172.8 de	174.3 cde	·	·	190.4 bc	189.7 cd
	1997	166.2 a	164.9 a	167.9 b	167.7 b	176.3 bcd	174.6 cde	·	·	188.0 cd	188.0 cd
	1998	156.2 b	156.8 b	160.9 c	160.0 c	171.7 de	166.7 e	·	·	185.3 cd	185.9 cd
	1999	168.1 a	166.4 a	181.7 a	173.2 b	182.6 ab	177.4 bcd	190.9 a	190.0 a	189.1 cd	185.9 cd
	2000	163.6 a	163.7 a	171.1 b	168.9 b	175.6 bcd	173.9 de	181.6 b	179.9 b	186.0 cd	184.5 d
Luzula arctica	1994	176.3 a	175.0 a	190.2 a	187.3 a	193.6 a	189.1 ab	·	·	·	·
	1995	166.9 b	167.0 b	177.0 b	174.8 bc	183.7 bc	182.3 bc	·	·	·	·
	1996	155.3 e	155.3 e	162.7 e	164.4 de	169.7 e	171.0 de	·	·	·	·
	1997	162.6 d	163.4 cd	168.3 cde	168.4 cde	179.7 c	178.9 c	188.6 b	185.9 bc	·	·
	1998	157.4 e	156.0 e	164.0 de	164.4 de	180.2 c	177.0 cd	183.7 c	183.7 c	216.4 a	218.3 a
	1999	167.3 b	165.4 bc	173.1 bc	170.5 bcd	183.3 bc	181.6 c	193.5 a	194.0 a	198.4 b	196.6 b
	2000	166.3 b	166.4 b	172.6 bc	172.0 bc	179.8 c	177.6 cd	185.8 bc	184.2 bc	200.8 b	198.5 b
Luzula confusa	1994	178.9 a	176.7 ab	194.4 a	190.5 ab	198.9 a	196.7 ab	·	·	·	·
	1995	169.0 de	168.6 de	182.4 cd	182.1 cd	192.2 bcd	186.9 defg	·	·	·	·
	1996	158.4 g	156.7 g	170.2 gh	166.5 h	185.3 fg	176.0 h	·	·	·	·
	1997	166.0 ef	165.0 f	179.5 cde	176.8 def	189.3 cdef	185.2 fg	194.4 bc	191.9 cd	·	·
	1998	160.0 g	159.5 g	173.2 fg	171.8 fgh	183.6 g	182.4 g	191.0 cd	189.4 d	215.2 a	215.7 a
	1999	173.5 bc	171.7 cd	184.7 bc	181.9 cd	191.2 bcde	190.1 cdef	200.6 a	197.8 ab	209.3 b	207.8 b
	2000	166.7 ef	166.6 ef	176.9 def	175.3 efg	194.5 abc	186.2 efg	201.7 a	196.2 b	211.0 b	208.4 b

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
				Barrow Dry Heath contiued							
Papaver hultenii	1994	180.4 a	177.8 ab	193.6 a	180.9 bc	208.3 a	198.1 ab	212.6 a	208.8 ab	·	·
	1995	167.8 cd	167.6 cd	173.0 bcde	174.8 bcd	199.3 ab	197.1 bc	206.2 abc	204.8 bcd	·	·
	1996	159.9 efg	154.6 g	167.8 defg	161.9 g	186.6 cde	176.8 e	196.2 cde	186.4 e	·	·
	1997	164.8 de	164.4 def	171.7 cdef	171.8 cdef	196.3 bc	189.4 bcd	·	·	·	·
	1998	158.3 fg	158.7 efg	162.9 fg	164.4 efg	188.9 bcd	183.9 de	197.9 cd	194.4 de	210.2 a	210.1 a
	1999	172.6 bc	167.9 cd	181.3 b	178.3 bc	196.8 bc	191.3 bcd	202.5 bcd	199.3 bcd	·	·
	2000	168.0 cd	167.7 cd	172.4 bcde	173.0 bcde	199.3 ab	192.3 bcd	205.2 abc	201.1 bcd	211.6 a	209.6 a
Pedicularis kanei	1995	167.0 ab	166.0 abc	·	·	·	·	·	·	·	·
	1996	154.6 e	154.8 e	·	·	·	·	·	·	·	·
	1997	164.6 abcd	160.8 bcde	·	·	·	·	·	·	·	·
	1998	158.6 cde	158.4 de	·	·	·	·	·	·	·	·
	1999	170.4 a	167.2 a	·	·	·	·	·	·	·	·
	2000	166.5 ab	165.8 abcd	·	·	·	·	·	·	·	·
Poa arctica	1994	185.7 a	182.6 a	206.5 a	208.8 ab	·	·	·	·	·	·
	1995	167.6 cd	168.2 bcd	204.8 ab	201.8 ab	·	·	·	·	·	·
	1996	159.8 e	158.8 e	199.4 ab	187.4 cde	218.8 a	213.6 ab	·	·	·	·
	1997	165.2 d	165.5 cd	·	·	213.3 ab	206.0 bc	·	·	·	·
	1998	160.0 e	159.1 e	184.3 de	183.5 e	196.1 c	198.9 c	·	·	·	·
	1999	171.5 b	169.0 bc	197.4 abc	195.4 bcd	·	·	·	·	·	·
	2000	165.7 cd	165.7 cd	201.4 ab	199.4 ab	·	·	·	·	·	·
Potentilla hyparctica	1994	175.1 a	175.0 a	192.4 a	190.6 a	199.0 a	191.9 b	·	·	·	·
	1995	166.6 cd	167.0 cd	177.7 bc	175.6 cd	191.6 b	185.4 cde	·	·	·	·
	1996	153.8 ef	152.2 f	170.1 ef	167.5 fg	181.9 ef	172.0 g	·	·	·	·
	1997	164.6 d	163.7 d	175.1 cd	172.5 de	189.3 bc	180.5 ef	195.5 a	189.6 bc	·	·
	1998	156.5 e	156.0 ef	165.4 fg	163.6 g	182.0 ef	176.5 fg	193.7 ab	187.6 c	·	·
	1999	171.0 b	168.4 bc	181.4 b	178.6 bc	188.0 bcd	183.5 de	195.9 a	193.5 ab	218.2 a	215.6 a
	2000	165.0 cd	164.0 d	175.4 cd	173.8 cde	189.3 bc	183.4 de	195.2 a	189.7 bc	209.4 b	208.3 b

Table E-1. Continued.

			Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species		Year	C	W	C	W	C	W	C	W	C	W
						Barrow Dry Heath contiued						
Salix rotundifolia	Female	1994	180.4 a	175.2 b	·	·	188.0 a	183.0 b	·	·	·	·
		1995	171.1 c	170.2 cd	·	·	180.0 bc	177.0 cde	·	·	·	·
		1996	159.0 f	162.3 e	·	·	167.1 h	168.8 gh	·	·	·	·
		1997	170.0 cd	167.1 d	·	·	176.9 cde	175.9 de	187.7 b	187.3 b	190.4 c	190.2 c
		1998	160.5 ef	160.9 ef	161.6 c	161.6 c	173.7 ef	171.7 fg	·	·	186.4 d	184.6 d
		1999	175.4 b	172.8 bc	176.7 a	174.7 a	183.5 b	180.5 b	195.2 a	195.0 a	196.1 ab	196.0 ab
		2000	170.2 cd	170.4 cd	166.0 b	165.8 b	179.5 bcd	177.5 cde	190.0 b	188.7 b	198.3 a	194.0 b
	Male	1994	·	·	·	·	190.3 a	184.8 bc	195.0 a	192.0 ab	·	·
		1995	·	·	·	·	185.5 ab	180.4 cde	188.1 bc	183.2 d	·	·
		1996	·	·	·	·	166.8 h	169.9 h	170.9 e	172.2 e	·	·
		1997	169.4 b	168.2 b	·	·	179.4 def	176.9 ef	183.4 d	182.9 d	·	·
		1998	160.0 c	160.8 c	161.4 c	160.6 c	175.0 fg	171.3 gh	184.2 cd	184.1 cd	·	·
		1999	176.0 a	173.0 ab	177.4 a	173.7 a	182.6 bcd	179.0 def	192.0 ab	190.7 b	·	·
		2000	170.3 b	169.9 b	166.0 b	165.7 b	178.3 def	176.7 ef	182.6 d	181.7 d	·	·
Saxifraga foliolosa		1996	159.6 d	165.5 bcd	·	·	·	·	·	·	·	·
		1998	161.7 cd	161.8 cd	·	·	·	·	·	·	·	·
		1999	173.7 a	169.8 ab	·	·	·	·	·	·	·	·
		2000	168.6 abc	169.3 abc	·	·	·	·	·	·	·	·
Saxifraga punctata		1994	190.3 a	186.9 a	196.7 a	192.8 ab	207.4 a	202.2 ab	214.9 a	210.9 ab	·	·
		1995	172.9 bc	173.3 bc	174.9 efg	178.5 cdef	194.9 bc	193.4 cd	206.9 ab	204.9 bc	·	·
		1996	167.5 defg	165.7 efg	172.0 fg	169.9 g	184.7 ef	182.7 f	198.5 cd	195.9 d	·	·
		1997	176.4 b	169.5 cdef	183.3 cd	176.8 defg	190.0 cde	187.6 def	208.0 ab	197.6 cd	215.3 a	213.0 a
		1998	164.2 fg	163.3 g	169.9 g	168.9 g	186.3 def	183.6 ef	·	·	·	·
		1999	177.3 b	175.0 bc	185.0 bc	182.8 cde	192.4 cd	189.7 cdef	205.4 bc	203.8 bcd	204.6 b	204.8 b
		2000	170.4 cde	170.7 cde	173.1 fg	173.9 fg	196.5 bc	192.3 cd	205.6 bc	204.1 bcd	211.3 a	211.8 a

Table E-1. Continued.

Species	Year	Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
		C	W	C	W	C	W	C	W	C	W
Barrow Dry Heath contiued											
Senecio atropurpureus	1994	187.5 ab	188.6 a	192.3 a	194.8 ab	215.7 a	211.2 ab	226.7 a	223.3 ab	.	.
	1995	171.2 de	172.0 de	180.1 abc	185.7 abc	.	.	.	.	.	.
	1996	165.2 ef	167.4 def	.	.	.	.	.	.	.	.
	1997	169.9 def	171.0 def	175.7 c	181.0 abc	191.4 d	194.1 cd	222.0 abc	216.0 bc	.	.
	1998	163.6 f	166.7 def	.	.	195.4 cd	191.6 d	217.1 bc	213.8 c	.	.
	1999	180.9 bc	183.1 ab	182.7 abc	184.0 abc	209.5 ab	203.0 bc	226.9 a	226.0 a	.	.
	2000	173.1 d	173.9 cd	177.7 c	178.6 bc	217.3 a	213.9 a	230.8 a	229.3 a	.	.
Stellaria laeta	1994	179.0 a	177.8 a	205.9 a	199.8 ab	217.5 ab	211.8 bcd	222.5 ab	219.1 b	.	.
	1995	166.5 bcd	166.8 bc	194.3 bc	194.6 bc	224.1 a	216.3 abc	231.3 a	219.0 b	.	.
	1996	161.5 ef	158.8 f	189.2 cd	177.3 e	201.0 def	191.0 f	208.4 cd	205.0 d	.	.
	1997	164.7 bcde	163.4 de	188.2 cd	189.6 cd	204.9 de	201.3 def	223.0 ab	219.4 b	.	.
	1998	158.9 f	159.0 f	188.1 cd	182.4 de	197.0 ef	192.2 f	207.7 cd	208.4 cd	.	.
	1999	168.0 b	165.7 bcd	196.1 abc	190.4 bcd	201.5 def	195.7 ef	208.3 cd	206.7 cd	.	.
	2000	164.5 bcd	164.2 cde	190.3 bcd	189.9 bcd	211.6 bcd	205.4 cde	216.2 bc	214.4 bcd	.	.
Barrow Wet Meadow											
Cardamine pratensis	1995	180.0 bc	180.4 bc	204.4 bcd	199.4 cde	.	.	.	.	.	.
	1996	170.5 fg	169.9 g	.	.	.	.	.	.	.	.
	1997	176.8 cd	176.3 de	198.7 cde	197.5 cde	224.8 a	221.7 a	234.0 a	230.2 ab	.	.
	1998	176.2 de	175.7 de	195.5 de	193.3 e	218.6 ab	213.1 b	224.9 ab	222.5 c	.	.
	1999	181.4 a	180.5 ab	217.4 a	203.5 bcd	225.9 a	219.1 ab	.	.	.	.
	2000	173.8 def	173.1 efg	209.0 ab	206.4 abc	.	.	.	.	.	.
Carex aquatilis/stans	1995	180.0 bc	179.6 c	195.2 ab	199.3 a	214.2 a	212.0 a	.	.	.	.
	1996	168.7 e	167.3 e	187.5 cd	181.1 d	197.6 de	188.2 f	201.2 e	192.0 f	.	.
	1997	182.8 ab	182.0 abc	195.2 ab	192.1 bc	207.7 abc	200.8 cde	214.7 ab	207.3 cd	.	.
	1998	176.0 d	176.2 d	188.8 bc	186.8 cd	202.9 cd	194.3 ef	210.8 bc	203.0 de	.	.
	1999	182.8 a	181.9 abc	191.7 bc	191.9 bc	204.8 bcd	199.7 bcd	218.8 a	214.7 ab	.	.
	2000	176.0 d	176.3 d	195.5 ab	195.1 ab	211.2 ab	204.4 bcd	218.0 a	209.0 c	.	.

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
					Barrow Wet Meadow continued						
Cerastium beeringianum	1995	178.8 bc	179.3 bc	·	·	·	·	·	·	·	·
	1996	165.6 c	165.8 c	·	·	·	·	·	·	·	·
	1997	176.0 bc	178.0 bc	·	·	·	·	·	·	·	·
	1998	174.9 bc	173.6 bc	·	·	·	·	·	·	·	·
	1999	188.6 a	182.0 ab	·	·	·	·	·	·	·	·
	2000	175.6 bc	180.0 b	·	·	·	·	·	·	·	·
Cochlearia officinalis	1995	180.7 abc	181.1 abc	·	·	·	·	·	·	·	·
	1996	166.1 e	167.8 de	·	·	·	·	·	·	·	·
	1997	178.4 bcd	179.3 abcd	·	·	·	·	·	·	·	·
	1998	178.1 bcd	177.9 bcde	·	·	·	·	·	·	·	·
	1999	188.3 ab	191.1 a	·	·	·	·	·	·	·	·
	2000	172.6 cde	175.3 cde	·	·	·	·	·	·	·	·
Draba lactea	1995	179.4 ab	180.0 ab	185.1 ab	184.3 ab	195.5 a	193.1 ab	·	·	207.5 ab	203.0 b
	1996	163.0 d	163.2 d	169.8 e	169.4 e	181.5 cd	180.0 d	·	·	192.4 cd	188.4 d
	1997	176.5 bc	178.8 c	182.9 abc	184.9 ab	196.4 a	195.8 a	206.0 a	204.3 a	207.8 ab	205.9 ab
	1998	173.7 c	173.4 c	177.6 d	177.2 d	190.3 ab	187.5 bc	201.0 a	191.7 b	202.4 b	195.5 c
	1999	181.4 a	179.0 ab	186.6 a	184.2 ab	194.8 a	193.3 ab	203.5 a	202.8 a	211.8 a	208.0 ab
	2000	172.9 c	172.8 c	180.2 bcd	178.5 cd	194.9 a	191.3 ab	204.8 a	200.7 a	206.6 ab	202.8 b
Dupontia fisheri	1995	177.5 bc	178.0 b	200.4 abc	200.1 abc	230.0 a	227.7 a	·	·	·	·
	1996	164.3 e	164.8 e	188.4 d	187.1 d	209.4 de	205.2 e	210.3 e	208.1 e	·	·
	1997	176.3 bc	177.4 bc	204.1 a	202.1 ab	220.2 bc	215.9 cd	225.5 ab	223.7 bc	·	·
	1998	171.5 d	174.0 cd	195.1 c	197.2 bc	213.7 cd	210.4 de	220.6 c	215.7 d	·	·
	1999	180.7 a	182.3 a	202.3 ab	201.0 abc	224.0 ab	215.8 cd	228.7 a	226.6 ab	·	·
	2000	171.1 d	172.2 d	203.0 ab	202.7 ab	224.6 ab	217.1 c	225.5 ab	220.2 c	·	·

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
				Barrow Wet Meadow continued							
Eriophorum angustifolium/triste	1995	180.2 b	180.0 b	196.1 a	194.8 a	·	·	·	·	·	·
	1996	167.2 d	166.1 d	188.0 ab	181.7 b	199.4 bc	191.3 c	202.8 cd	194.6 d	·	·
	1997	180.3 b	179.7 b	196.7 a	194.2 a	206.0 ab	201.1 bc	213.7 abc	210.0 abc	·	·
	1998	175.2 c	175.4 c	191.0 ab	187.4 ab	·	·	206.0 bcd	201.4 cd	·	·
	1999	184.7 a	185.6 a	196.3 a	190.8 ab	202.7 b	198.9 bc	220.6 a	210.1 abc	231.5 a	220.1 b
	2000	174.5 c	174.3 c	191.7 ab	187.5 ab	213.4 a	202.0 b	218.8 ab	210.4 abc	230.9 a	221.1 b
Eriophorum russeolum	1995	186.6 a	185.7 a	·	·	·	·	·	·	·	·
	1996	166.2 e	163.5 e	·	·	·	·	·	·	·	·
	1997	178.2 bc	179.8 b	192.6 a	191.4 a	200.0 ab	192.7 b	204.8 ab	202.0 ab	·	·
	1998	175.0 cd	175.6 cd	·	·	·	·	·	·	·	·
	1999	183.6 a	183.6 a	199.3 a	196.4 a	196.8 ab	196.3 ab	211.6 a	207.1 ab	224.8 a	219.8 a
	2000	172.9 d	173.3 d	188.3 a	184.7 a	203.5 a	194.4 ab	209.3 ab	199.5 b	223.4 a	214.2 a
Hierochloe pauciflora	1995	·	·	201.1 a	198.2 ab	219.4 a	211.9 ab	·	·	·	·
	1996	·	·	187.7 d	181.4 e	195.1 ef	187.6 f	198.5 d	191.3 e	·	·
	1997	182.7 b	184.3 b	198.3 ab	197.3 ab	205.8 bc	202.9 cd	213.4 bc	210.6 c	·	·
	1998	180.4 bc	180.3 bc	193.5 bcd	191.1 cd	196.7 de	195.3 e	213.7 bc	215.4 abc	·	·
	1999	190.4 a	193.5 a	198.4 ab	198.3 bcd	206.1 bc	204.1 cd	222.2 a	218.4 ab	228.0 a	228.0 a
	2000	174.6 cd	174.0 d	197.1 ab	196.2 abc	209.1 bc	208.6 bc	210.1 c	209.7 c	226.5 a	226.4 a
Juncus biglumis	1995	188.3 c	187.3 c	196.6 cde	197.5 bcde	198.1 e	199.6 de	205.0 b	204.3 b	220.6 abc	214.6 c
	1996	172.3 d	171.1 d	188.0 ef	185.0 f	188.0 f	185.8 f	·	·	197.0 d	193.3 d
	1997	184.6 c	186.4 c	203.4 abcd	202.0 abcd	205.8 bcde	204.6 cde	209.7 b	207.1 b	215.6 c	215.3 c
	1998	182.1 c	182.7 c	196.2 de	203.0 abcd	202.7 de	204.3 cde	·	·	215.0 c	216.9 bc
	1999	198.0 ab	201.6 a	206.5 abc	210.2 a	208.1 bcd	215.0 ab	·	·	224.5 ab	225.0 a
	2000	187.8 c	190.2 bc	199.9 bcd	206.8 ab	212.9 abc	218.8 a	222.0 a	224.0 a	·	·

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
				Barrow Wet Meadow continued							
Luzula arctica	1995	179.0 ab	178.8 b	188.3 a	183.3 abc	193.1 a	191.3 a	199.9 abc	198.1 abcd	·	·
	1996	164.3 d	161.3 d	174.9 de	168.6 f	180.2 cd	173.7 d	186.1 fg	180.5 g	·	·
	1997	176.9 b	177.0 b	182.2 bc	182.2 bc	193.3 a	190.0 ab	202.6 a	200.6 ab	215.9 ab	215.6 abc
	1998	172.4 c	172.5 c	178.3 cde	173.7 ef	189.9 ab	184.3 bc	193.3 de	189.3 ef	205.3 cd	202.2 d
	1999	182.0 a	178.1 ab	186.7 ab	183.4 abc	192.8 a	190.1 ab	200.1 ab	195.1 bcd	221.3 a	213.2 abc
	2000	172.7 c	172.2 c	180.6 cd	181.5 bc	189.8 ab	188.6 ab	197.3 abcd	194.5 cde	207.4 bcd	206.0 bcd
Luzula confusa	1995	182.5 bc	184.0 bc	200.3 a	195.0 a	201.6 a	198.0 ab	216.4 a	211.2 a	·	·
	1996	171.7 de	166.8 e	188.8 ab	177.9 b	192.4 bc	187.2 c	197.7 b	194.4 b	·	·
	1997	183.3 bc	184.3 bc	197.3 a	193.9 a	205.1 a	200.9 ab	211.5 a	210.4 a	228.0 ab	224.0 abc
	1998	182.3 bc	180.3 bc	192.6 a	189.7 ab	200.7 ab	201.9 a	211.0 a	212.7 a	215.8 c	216.9 c
	1999	196.6 a	186.5 b	198.9 a	196.0 a	199.2 ab	201.0 a	214.0 a	212.9 a	230.2 a	229.5 a
	2000	176.6 cd	175.9 cd	191.7 a	190.2 a	204.9 a	202.7 a	211.3 a	209.8 a	221.0 abc	218.8 bc
Poa arctica	1996	·	·	·	·	·	·	·	·	·	·
	1997	180.0 b	184.7 ab	211.3 a	206.0 a	·	·	·	·	·	·
	1998	182.9 ab	178.5 b	207.6 a	201.5 a	·	·	·	·	·	·
	1999	184.0 ab	195.4 a	202.2 a	208.4 a	·	·	·	·	·	·
	2000	192.1 ab	186.7 ab	208.5 a	210.0 a	·	·	·	·	·	·
Salix rotundifolia	1995	192.3 a	187.2 ab	·	·	·	·	·	·	·	·
	1996	170.0 c	169.2 c	·	·	·	·	·	·	·	·
	1997	189.0 ab	186.8 ab	·	·	·	·	·	·	·	·
	1998	183.0 ab	183.3 ab	·	·	·	·	·	·	·	·
	2000	188.5 ab	179.8 bc	·	·	·	·	·	·	·	·
Saxifraga cernua	1995	181.9 ab	181.1 b	·	·	·	·	·	·	·	·
	1996	172.7 cd	170.6 d	202.0 ab	201.4 ab	215.7 c	214.6 c	·	·	·	·
	1998	180.5 b	177.5 bc	199.6 ab	198.6 b	217.3 bc	217.1 bc	·	·	·	·
	1999	180.1 b	186.1 a	212.9 ab	208.4 a	226.2 a	223.9 ab	·	·	·	·
	2000	176.5 bc	179.3 b	206.8 ab	206.3 ab	·	·	·	·	·	·

Table E-1. Continued.

		Leaf		Inflorescence / Bud		Flower		Withered Flower		Seed	
Species	Year	C	W	C	W	C	W	C	W	C	W
		Barrow Wet Meadow continued									
Saxifraga foliolosa	1995	178.1 bcd	178.5 bc	·	·	·	·	·	·	·	·
	1996	164.5 f	163.8 f	209.3 a	202.8 ab	215.0 ab	211.7 b	·	·	·	·
	1997	176.6 cde	178.2 bcd	205.9 ab	205.0 ab	223.3 a	214.6 ab	229.3 a	227.9 a	·	·
	1998	173.9 e	174.3 de	197.1 ab	194.1 b	217.0 ab	212.8 b	222.0 ab	217.8 b	·	·
	1999	181.1 a	180.0 ab	199.6 ab	200.7 ab	·	·	·	·	·	·
	2000	172.8 e	175.5 cde	205.0 ab	198.0 ab	·	·	·	·	·	·
Saxifraga hieracifolia	1995	177.9 ab	177.4 abc	185.7 cd	185.3 cd	205.9 ab	201.7 abc	·	·	·	·
	1996	164.1 f	162.3 f	170.8 e	168.0 e	191.5 de	185.8 e	·	·	·	·
	1997	177.1 abc	176.1 bcd	184.6 cd	184.3 cd	204.4 ab	200.8 abc	·	·	·	·
	1998	172.1 de	171.8 e	188.2 bc	189.8 abc	199.2 bcd	195.3 cd	209.5 b	209.8 b	213.2 dc	210.8 d
	1999	178.8 ab	178.4 a	195.8 ab	196.0 a	208.4 a	203.4 abc	222.0 a	217.2 ab	231.2 a	228.6 ab
	2000	171.4 e	173.6 cde	179.3 d	179.5 d	205.9 ab	203.6 ab	218.4 a	214.6 ab	222.0 abc	219.6 bcd
Saxifraga hirculus	1995	179.2 bc	180.3 bc	190.8 c	190.8 c	220.7 a	217.8 a	·	·	·	·
	1996	168.1 de	166.7 e	180.9 de	175.6 e	196.4 de	190.0 e	215.6 c	211.7 c	·	·
	1997	180.1 bc	182.3 b	188.9 cd	187.7 cd	211.6 abc	200.5 cde	226.0 a	225.0 ab	·	·
	1998	174.5 cd	175.2 bcd	197.2 abc	194.2 bc	205.5 bcd	200.0 de	217.9 bc	214.3 c	·	·
	1999	182.1 bc	192.0 a	·	·	·	·	·	·	·	·
	2000	176.3 bc	181.8 bc	205.4 a	200.8 ab	216.7 ab	211.8 abc	223.9 ab	227.0 a	·	·
Stellaria laeta	1995	178.9 bc	178.7 bc	·	·	·	·	·	·	·	·
	1996	167.9 ef	166.2 f	197.8 ab	195.6 b	212.0 c	212.2 c	·	·	·	·
	1997	176.4 cd	176.5 cd	·	·	·	·	·	·	·	·
	1998	173.5 cde	173.0 de	201.6 ab	205.4 ab	219.5 abc	215.0 bc	·	·	·	·
	1999	181.8 ab	183.4 a	210.6 a	217.4 ab	226.3 a	223.5 ab	·	·	·	·
	2000	178.3 bcd	177.7 bcd	207.0 ab	209.0 ab	·	·	·	·	·	·

Table E-2. Average growth and reproductive traits of the plant species within the four sites for each year and treatment (C - control plots, W - warmed plots). Growth measurements included the number of leaves, the length of the longest leaf, and the change in size. The change in size metric differed depending on the growth morphology of the species: it represented the number of individuals (ramets or tillers), number of branches, or diameter of rosette. Reproductive measurements included the percentage of the population flowering, the number of inflorescences within a plot, and the length of the tallest flowering stalk. Letters represent the statistical difference between the populations calculated with a Tukey's studentized range test (HSD, p-value <0.05); if two populations do not have the same letter then they are significantly different.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
						Atqasuk Dry Heath							
Carex bigelowii	1997	·	·	7.9 a	11.4 a	·	·	·	·	·	·	·	·
	1998	4.2 a	3.0 a	12.6 a	11.8 a	-1.3 bc	-1.9 c	·	·	·	·	·	·
	1999	4.0 a	3.5 a	11.5 a	12.1 a	0.0 a	-0.3 ab	·	·	·	·	·	·
	2000	3.1 a	3.5 a	11.7 a	11.9 a	0.6 a	-0.1 a	·	·	·	·	·	·
Cassiope tetragona	1996	·	·	0.5 ab	0.5 b	·	·	·	·	21.2 b	21.3 b	·	·
	1997	·	·	0.6 ab	0.6 a	·	·	·	·	18.1 b	6.4 b	·	·
	1998	·	·	0.5 ab	0.6 ab	3.3 a	4.9 a	0.19	0.13	23.2 b	10.0 b	·	·
	1999	·	·	0.6 ab	0.5 b	1.8 ab	2.8 ab	0.44	0.14	53.2 a	12.6 b	·	·
	2000	·	·	0.5 b	0.5 b	-3.6 c	-0.3 bc	·	·	15.7 b	23.8 b	·	·
Diapensia lapponica	1996	·	·	·	·	·	·	·	·	6.9 c	6.2 c	2.1 b	2.0 b
	1997	·	·	·	·	·	·	·	·	20.7 abc	9.1 c	2.7 a	2.8 a
	1998	·	·	0.8 c	0.9 c	·	·	0.80	0.48	21.3 abc	8.7 c	2.9 a	2.9 a
	1999	·	·	1.0 ab	1.1 a	3.8 a	5.7 a	0.69	0.39	26.9 ab	13.9 bc	3.0 a	3.0 a
	2000	·	·	1.0 b	1.0 ab	-5.0 b	-3.3 b	0.61	0.52	36.0 a	25.8 ab	2.9 a	3.1 a
Hierochloe alpina	1996	·	·	·	·	·	·	·	·	2.6 b	3.3 b	20.3 d	23.4 cd
	1997	·	·	10.3 b	12.3 ab	·	·	·	·	1.4 b	4.2 b	24.1 cd	26.6 bc
	1998	2.0 a	2.2 a	11.2 ab	12.8 ab	0.1 a	0.0 a	0.32	0.46	3.8 b	7.9 ab	26.5 bc	32.0 a
	1999	2.2 a	2.2 a	12.3 ab	13.5 a	-0.3 a	0.0 a	0.44	0.67	6.6 ab	11.8 a	27.2 bc	30.8 ab
	2000	2.0 a	2.0 a	9.7 b	10.6 ab	-0.3 a	-0.8 a	0.55	0.44	6.7 ab	12.1 a	23.2 cd	29.3 ab

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
						Atqasuk Dry Heath							
Ledum palustre	1996	·	·	·	·	·	·	·	·	5.3 ab	4.4 b	·	·
	1997	·	·	1.0 c	1.0 abc	·	·	·	·	6.0 ab	4.2 b	2.8 b	3.1 ab
	1998	·	·	1.0 c	1.1 ab	·	·	0.47	0.32	10.3 a	6.0 ab	·	·
	1999	·	·	1.0 abc	1.1 a	0.3 a	0.7 a	0.10	0.12	9.2 ab	6.4 ab	·	·
	2000	·	·	1.0 bc	1.1 abc	-1.2 b	-1.0 b	0.15	0.16	7.1 ab	5.8 ab	3.0 ab	3.6 a
Luzula arctica	1997	·	·	2.1 a	2.0 a	·	·	·	·	·	·	·	·
	1998	6.6 a	6.0 ab	2.4 a	2.4 a	-0.3 a	-0.1 a	0.33	0.25	2.7 a	2.6 a	13.2 a	11.5 a
	1999	5.4 abc	5.0 bcd	2.6 a	2.6 a	0.9 a	0.5 a	0.32	0.20	6.7 a	2.0 a	11.3 a	11.0 a
	2000	3.6 d	3.9 cd	2.1 a	2.3 a	-0.4 a	0.2 a	0.30	0.24	3.8 a	2.8 a	10.0 a	8.2 a
Luzula confusa	1996	·	·	·	·	·	·	·	·	4.5 a	5.6 a	16.6 abcd	14.0 d
	1997	·	·	6.1 b	7.1 ab	·	·	·	·	2.3 a	4.6 a	17.5 abc	15.8 cd
	1998	2.0 b	2.2 b	8.7 a	8.6 a	0.1 a	-0.1 a	0.28	0.24	7.7 a	7.8 a	19.4 a	19.3 ab
	1999	2.9 a	2.9 a	8.3 a	8.2 a	-0.1 a	-0.1 a	0.34	0.31	11.3 a	7.0 a	18.5 abc	16.1 bcd
	2000	2.3 b	2.3 b	7.1 ab	7.3 ab	-0.2 a	0.1 a	0.25	0.17	13.0 a	7.0 a	16.7 abcd	17.0 abcd
Polygonum bistorta	1996	·	·	·	·	·	·	·	·	1.4 a	2.7 a	8.7 ab	12.2 ab
	1997	·	·	5.3 a	5.2 a	·	·	·	·	·	·	·	·
	1998	1.4 b	1.4 b	5.9 a	6.9 a	0.0 a	0.0 a	0.19	0.17	2.1 a	3.0 a	10.3 ab	13.3 a
	1999	1.9 ab	1.7 ab	6.2 a	7.1 a	0.1 a	0.1 a	0.27	0.34	2.0 a	5.0 a	14.0 a	13.7 a
	2000	1.9 ab	2.2 a	5.0 a	5.9 a	0.0 a	0.0 a	·	·	2.3 a	3.3 a	6.1 b	9.5 ab
Trisetum spicatum	1997	·	·	13.8 a	15.6 a	·	·	·	·	·	·	·	·
	1999	2.8 a	2.9 a	15.6 a	15.7 a	·	·	·	·	·	·	·	·
	2000	2.9 a	2.8 a	12.9 a	13.5 a	·	·	·	·	·	·	·	·
Vaccinium vitis-idaea	1998	·	·	0.6 a	0.6 a	0.6 a	0.3 ab	0.19	0.00	10.2 ab	3.3 c	·	·
	1999	·	·	0.7 a	0.6 a	-0.3 abc	-0.1 abc	0.25	0.10	14.3 a	6.5 bc	·	·
	2000	·	·	0.6 a	0.6 a	-1.1 c	-0.5 bc	0.08	0.08	4.2 c	2.6 c	·	·

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
						Atqasuk Wet Meadow							
Carex aquatilis	1996	·	·	·	·	·	·	·	·	4.5 ab	5.2 a	21.7 de	24.3 bcde
	1997	·	·	18.1 d	20.5 cd	·	·	·	·	1.8 c	1.6 c	21.2 e	22.6 cde
	1998	3.0 ab	3.1 ab	22.5 abc	24.3 ab	·	·	0.14	0.11	6.3 a	3.9 abc	27.4 abc	30.2 a
	1999	3.3 a	3.1 ab	22.7 abc	24.6 a	-0.3 b	0.0 ab	0.07	0.04	2.3 bc	1.7 c	26.5 abcd	26.5 abcd
	2000	2.9 ab	2.7 b	21.2 bcd	23.4 abc	0.5 a	0.6 a	0.10	0.08	4.0 abc	4.8 ab	25.8 abcd	29.2 ab
Dupontia fisheri/psilosantha	1996	·	·	·	·	·	·	·	·	1.6 a	2.9 a	23.0 a	24.6 a
	1997	·	·	7.3 c	9.2 bc	·	·	·	·	·	·	·	·
	1998	1.7 c	1.9 bc	11.4 ab	13.5 a	-0.2 a	0.0 a	0.06	0.05	1.2 a	1.5 a	27.7 a	30.7 a
	1999	2.5 a	2.4 ab	10.5 abc	14.2 a	-0.2 a	0.0 a	0.11	0.10	1.5 a	1.9 a	26.8 a	29.3 a
	2000	2.4 ab	2.2 abc	11.1 abc	11.0 abc	0.3 a	-0.1 a	·	·	1.3 a	1.0 a	·	·
Eriophorum angustifolium	1996	·	·	·	·	·	·	·	·	2.3 a	2.2 a	15.8 bc	17.0 abc
	1997	·	·	20.9 c	21.4 bc	·	·	·	·	1.0 a	1.3 a	20.3 abc	16.2 abc
	1998	3.2 ab	3.5 a	23.7 abc	25.2 ab	0.0 a	0.0 a	0.08	0.12	2.9 a	1.6 a	20.2 abc	21.0 abc
	1999	3.4 ab	3.5 a	23.8 abc	25.8 a	0.1 a	0.0 a	0.13	0.20	3.3 a	1.9 a	16.8 abc	22.7 ab
	2000	2.8 b	3.2 ab	21.3 bc	24.1 abc	0.0 a	0.1 a	·	·	2.1 a	1.8 a	13.0 c	24.6 a
Eriophorum russeolum	1997	·	·	13.1 b	14.5 ab	·	·	·	·	·	·	·	·
	1998	1.9 ab	1.8 ab	15.1 ab	16.2 a	-0.3 c	-0.2 ab	0.12	0.09	6.8 a	8.9 a	18.2 ab	20.4 a
	1999	2.0 a	2.0 a	14.7 ab	16.2 a	-0.4 c	-0.7 c	0.03	0.07	3.3 a	5.7 a	17.9 ab	21.2 a
	2000	1.5 b	1.9 ab	12.9 b	15.9 ab	0.6 ab	1.3 a	·	·	1.5 a	8.1 a	13.5 b	21.5 a
Luzula wahlenbergii	1998	2.5 b	2.7 ab	4.7 a	5.1 a	·	·	·	·	·	·	·	·
	1999	3.5 a	3.1 ab	4.8 a	5.5 a	0.0 a	-0.2 a	·	·	·	·	·	·
	2000	3.2 ab	3.4 a	4.1 a	4.7 a	0.3 a	0.1 a	·	·	·	·	·	·
Pedicularis sudetica	1997	·	·	5.5 a	5.6 a	·	·	·	·	1.4 a	2.0 a	·	·
	1998	·	·	6.9 a	7.1 a	·	·	·	·	1.4 a	3.4 a	·	·
	1999	3.5 a	3.6 a	6.1 a	7.5 a	·	·	·	·	1.5 a	2.6 a	·	·
	2000	2.6 a	2.9 a	5.2 a	7.3 a	·	·	·	·	1.6 a	4.3 a	·	·

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
						Atqasuk Wet Meadow continued							
Polygonum viviparum	1998	·	·	6.9 a	5.0 a	·	·	·	·	·	·	·	·
	1999	2.0 a	2.2 a	5.6 a	4.1 a	·	·	·	·	2.5 a	1.3 a	·	·
	2000	1.9 a	1.8 a	3.8 a	4.9 a	·	·	·	·	2.9 a	2.0 a	·	·
						Barrow Dry Heath							
Arctagrostis latifolia	1996	·	·	11.3 ab	11.5 ab	·	·	·	·	·	·	12.9 d	14.6 cd
	1997	·	·	7.5 d	9.7 bcd	·	·	0.07	0.18	2.7 a	7.5 a	10.3 d	21.3 abc
	1998	2.3 b	3.3 a	11.6 ab	12.4 ab	-0.2 a	-0.1 a	0.20	0.29	5.2 a	4.8 a	16.6 cd	24.5 ab
	1999	2.8 ab	2.8 ab	8.4 cd	10.1 abcd	-1.4 a	0.1 a	·	·	8.8 a	7.8 a	20.4 bc	27.4 a
	2000	2.6 b	2.5 b	10.7 abc	12.7 a	-0.5 a	-0.3 a	·	·	3.1 a	5.2 a	14.8 cd	20.4 bc
Cassiope tetragona	1994	·	·	·	·	·	·	0.96	1.00	·	·	·	·
	1995	·	·	0.5 c	0.5 bc	·	·	0.21	0.92	·	·	·	·
	1996	·	·	0.5 bc	0.5 bc	·	·	0.00	0.21	3.7 d	76.6 cd	·	·
	1997	·	·	0.7 a	0.6 b	·	·	0.44	0.83	150.9 bc	298.4 a	·	·
	1998	·	·	·	·	0.6 a	-0.9 ab	0.38	0.77	86.6 cd	217.0 ab	·	·
	1999	·	·	0.5 c	0.5 c	-0.7 ab	-0.2 a	·	·	196.0 ab	215.1 ab	1.7 b	2.3 a
	2000	·	·	0.3 d	0.3 d	-2.6 b	-2.4 b	0.21	0.42	89.8 cd	199.0 ab	1.3 c	1.9 b
Draba lactea	1997	·	·	0.8 ab	0.7 ab	·	·	·	·	4.5 a	3.3 a	3.4 ab	3.4 ab
	1999	·	·	0.6 b	0.6 b	-0.6 a	-0.8 a	·	·	6.0 a	3.0 a	5.5 a	4.5 ab
	2000	·	·	1.0 a	0.8 ab	-1.8 a	-0.1 a	0.91	0.67	3.8 a	5.9 a	3.1 b	3.9 ab
Draba micropetala	1997	·	·	0.7 a	0.8 a	·	·	0.85	0.85	8.0 a	6.3 a	3.2 c	5.3 abc
	1998	·	·	·	·	0.4 a	0.7 a	0.79	0.85	·	·	5.1 bc	5.1 bc
	1999	·	·	0.8 a	0.8 a	-0.6 a	0.6 a	0.45	0.63	6.6 a	8.4 a	5.0 bc	7.5 a
	2000	·	·	0.9 a	0.9 a	-1.3 a	-1.5 a	0.60	0.52	3.3 a	5.3 a	4.1 bc	6.2 ab

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Dry Heath continued													
Luzula arctica	1995	·	·	·	·	·	·	·	·	·	·	7.0 bc	9.7 ab
	1996	·	·	·	·	·	·	·	·	·	·	10.0 ab	8.4 abc
	1997	·	·	2.1 c	2.2 bc	·	·	0.72	0.51	5.3 a	6.3 a	6.2 c	9.8 ab
	1998	·	·	3.1 a	3.0 ab	-0.9 cd	-0.3 bc	0.51	0.49	3.4 a	3.2 a	7.1 bc	9.2 abc
	1999	3.7 a	4.5 a	2.8 abc	3.0 a	1.9 a	0.7 ab	0.51	0.42	5.9 a	6.6 a	9.6 ab	11.4 a
	2000	4.5 a	4.7 a	3.1 a	3.2 a	-1.6 d	-0.6 cd	0.60	0.56	6.2 a	8.3 a	5.8 c	9.7 ab
Luzula confusa	1994	·	·	·	·	·	·	·	·	·	·	7.7 e	11.3 bcd
	1995	·	·	·	·	·	·	·	·	·	·	8.1 e	11.9 bc
	1996	·	·	6.9 ab	7.4 a	·	·	·	·	·	·	10.1 cde	11.1 cde
	1997	·	·	4.5 c	5.5 bc	·	·	0.39	0.38	4.9 a	6.1 a	8.3 de	11.9 bc
	1998	3.4 ab	3.7 a	5.8 bc	7.4 a	-0.3 ab	-0.5 ab	0.43	0.36	9.1 a	6.6 a	11.7 bc	14.4 ab
	1999	2.3 c	2.5 bc	5.7 bc	6.6 ab	0.1 a	0.4 a	0.32	0.24	10.4 a	6.2 a	12.2 abc	15.2 a
	2000	3.4 ab	4.0 a	6.3 ab	7.4 a	-0.9 b	-1.0 b	0.28	0.31	6.8 a	6.3 a	10.4 cde	12.9 abc
Papaver hultenii	1995	·	·	·	·	·	·	·	·	·	·	10.9 c	17.0 abc
	1996	·	·	·	·	·	·	·	·	·	·	11.1 c	15.7 abc
	1997	·	·	·	·	·	·	0.68	0.92	1.6 b	2.3 b	10.8 c	16.1 abc
	1998	·	·	·	·	-1.0 a	-0.6 a	0.72	0.89	·	·	14.8 abc	19.9 ab
	1999	·	·	·	·	0.5 a	0.7 a	0.32	0.59	4.9 ab	8.1 ab	15.0 abc	21.8 a
	2000	·	·	·	·	0.4 a	-0.7 a	0.74	0.78	5.8 ab	10.3 a	12.2 bc	19.7 ab
Poa arctica	1996	·	·	·	·	·	·	·	·	·	·	14.5 bc	15.7 abc
	1997	·	·	3.8 c	4.3 abc	·	·	0.07	0.04	3.3 a	3.9 a	10.0 d	13.6 bcd
	1998	2.1 b	2.9 a	4.1 abc	4.9 a	0.1 ab	-0.3 ab	0.10	0.24	3.2 a	4.9 a	14.0 bcd	17.4 ab
	1999	1.9 b	2.1 b	3.9 bc	4.9 a	-0.2 ab	0.3 a	·	·	8.7 a	8.0 a	16.8 ab	19.3 a
	2000	2.0 b	2.2 b	4.1 abc	4.8 ab	-0.7 b	-0.6 ab	·	·	5.0 a	6.3 a	12.0 cd	14.7 bc

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Dry Heath continued													
Potentilla hyparctica	1994	·	·	·	·	·	·	·	·	·	·	8.5 cde	10.8 bcd
	1995	·	·	·	·	·	·	·	·	·	·	5.9 e	10.2 bcd
	1996	·	·	·	·	·	·	·	·	·	·	8.3 de	12.9 ab
	1997	·	·	·	·	·	·	0.86	0.93	6.7 a	5.7 a	6.6 e	10.4 bcd
	1998	·	·	·	·	-2.5 d	-1.6 cd	0.69	0.91	8.2 a	8.1 a	8.2 de	11.5 bc
	1999	·	·	·	·	1.9 a	1.7 a	0.76	0.77	21.1 a	19.6 a	8.5 cde	14.6 a
	2000	·	·	·	·	-0.3 b	-0.6 bc	0.78	0.86	22.5 a	20.1 a	6.0 e	10.1 bcd
Salix rotundifolia female	1994	·	·	0.8 de	1.0 abc	·	·	1.00	1.00	·	·	·	·
	1995	·	·	0.9 cde	1.0 abc	·	·	0.79	0.75	·	·	·	·
	1996	·	·	0.9 bcd	0.9 bcd	·	·	0.96	0.96	·	·	·	·
	1997	·	·	0.7 e	0.8 de	·	·	0.99	0.90	73.8 bc	65.0 c	1.6 b	1.8 b
	1998	·	·	·	·	·	·	0.92	0.93	105.0 abc	144.5 a	·	·
	1999	·	·	1.0 abc	1.1 a	·	·	0.82	0.71	78.8 bc	51.1 c	2.1 a	2.2 a
	2000	·	·	0.9 bcd	1.1 ab	·	·	0.85	0.81	132.3 ab	81.9 abc	0.9 c	1.2 c
male	1994	·	·	0.7 c	0.9 bc	·	·	0.92	0.92	·	·	·	·
	1995	·	·	0.8 bc	0.9 bc	·	·	0.83	0.71	·	·	·	·
	1996	·	·	·	·	·	·	0.71	0.79	·	·	·	·
	1997	·	·	0.7 c	0.9 bc	·	·	0.97	0.92	60.6 a	43.2 a	1.7 a	1.8 a
	1998	·	·	·	·	·	·	0.88	0.90	78.7 a	86.4 a	·	·
	1999	·	·	0.9 ab	1.1 a	·	·	0.73	0.69	50.4 a	54.8 a	1.5 a	1.8 a
	2000	·	·	1.0 ab	1.1 a	·	·	0.82	0.72	90.6 a	70.2 a	·	·
Saxifraga foliolosa	1997	·	·	1.0 abc	1.2 ab	·	·	·	·	2.8 a	1.5 a	6.5 a	7.8 a
	1998	5.0 ab	8.3 a	1.0 abc	1.0 abc	·	·	·	·	·	·	8.8 a	9.5 a
	1999	4.5 b	4.9 b	0.7 bc	0.6 c	-0.1 a	0.0 a	0.29	0.46	2.1 a	1.3 a	9.6 a	11.6 a
	2000	6.9 ab	6.5 ab	1.3 a	1.2 ab	0.1 a	0.4 a	·	·	·	·	·	·

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Dry Heath continued													
Saxifraga punctata	1994	·	·	·	·	·	·	·	·	·	·	5.7 g	12.3 bc
	1995	·	·	·	·	·	·	·	·	·	·	8.3 defg	12.2 bc
	1996	·	·	·	·	·	·	·	·	·	·	9.1 cdef	12.0 bcd
	1997	3.4 a	3.6 a	1.5 d	1.7 cd	·	·	0.51	0.66	4.1 a	4.4 a	7.7 efg	12.5 bc
	1998	3.9 a	3.6 a	1.7 cd	2.0 bc	0.7 a	0.8 a	0.46	0.48	·	·	10.0 bcde	16.6 a
	1999	3.0 a	3.1 a	3.0 a	3.2 a	0.2 a	0.7 a	0.49	0.44	7.3 a	5.4 a	11.8 bcd	13.7 ab
	2000	3.6 a	3.7 a	2.0 bc	2.3 b	-0.6 a	-1.0 a	0.54	0.57	7.3 a	6.1 a	6.6 fg	11.0 bcde
Senecio atropurpureus	1997	4.5 a	3.6 ab	1.4 a	1.3 a	·	·	0.61	0.44	3.7 a	2.8 a	6.9 a	8.1 a
	1998	·	·	1.3 a	1.3 a	1.3 a	0.9 a	0.12	0.15	7.3 a	2.0 a	·	·
	1999	2.4 bc	2.1 c	1.6 a	1.6 a	-0.5 ab	0.6 ab	0.32	0.20	4.1 a	3.4 a	8.7 a	9.0 a
	2000	2.4 bc	3.2 bc	1.2 a	1.3 a	-2.4 b	-1.2 ab	0.07	0.18	2.6 a	3.6 a	7.0 a	8.4 a
Stellaria laeta	1997	·	·	·	·	·	·	0.22	0.34	9.7 c	17.8 bc	·	·
	1998	·	·	·	·	0.0 a	-1.4 ab	0.32	0.44	16.9 bc	38.5 ab	·	·
	1999	·	·	0.7 ab	0.6 b	-4.1 ab	-4.3 b	0.21	0.24	15.9 bc	41.1 a	·	·
	2000	·	·	0.7 ab	0.7 a	-1.6 ab	-1.1 ab	0.06	0.22	12.0 c	24.7 abc	·	·
Barrow Wet Meadow													
Cardamine pratensis	1995	·	·	3.2 d	3.3 cd	·	·	·	·	1.5 b	1.6 ab	3.6 c	6.3 bc
	1996	·	·	3.8 bcd	4.3 abc	·	·	·	·	·	·	·	·
	1997	·	·	3.8 bcd	4.3 abc	·	·	0.09	0.21	2.2 ab	3.2 ab	8.6 b	12.3 a
	1998	·	·	4.4 ab	5.0 a	·	·	0.11	0.21	1.8 ab	3.8 a	7.7 b	14.7 a
	1999	·	·	3.2 d	3.8 bcd	·	·	0.06	0.14	1.8 ab	3.1 ab	8.8 b	13.6 a
	2000	·	·	·	·	·	·	·	·	1.1 b	1.4 b	·	·

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Wet Meadow continued													
Carex aquatilis/stans	1995	·	·	·	·	·	·	0.10	0.13	4.6 d	5.1 cd	8.6 e	11.3 de
	1996	·	·	11.1 e	12.3 de	0.0 ab	-0.8 bc	0.18	0.26	5.3 cd	7.4 bcd	12.7 cd	16.5 bc
	1997	·	·	10.9 e	12.2 de	-0.5 bc	-1.0 bc	0.31	0.40	16.5 a	18.8 a	13.9 cd	18.9 ab
	1998	·	·	15.8 b	18.2 a	2.4 a	1.3 ab	0.15	0.19	4.8 d	5.8 cd	16.5 bc	21.7 a
	1999	·	·	11.4 e	14.0 bcd	-3.1 c	-0.4 bc	0.32	0.18	13.6 ab	12.8 abc	15.5 bc	22.5 a
	2000	·	·	12.8 cde	14.7 bc	2.5 a	2.6 a	0.18	0.16	7.0 bcd	8.4 bcd	14.7 cd	19.0 ab
Cerastium beeringianum	1998	·	·	·	·	-1.7 a	-2.9 a	·	·	·	·	·	·
	1999	·	·	·	·	-2.9 a	-2.0 a	·	·	·	·	·	·
	2000	·	·	·	·	-0.3 a	-0.4 a	·	·	·	·	·	·
Cochlearia officinalis	1996	·	·	·	·	0.7 a	0.3 a	·	·	·	·	·	·
	1997	·	·	·	·	0.3 a	-0.3 a	·	·	·	·	·	·
	1998	·	·	·	·	0.7 a	0.4 a	·	·	·	·	·	·
	1999	·	·	·	·	-1.1 a	-0.8 a	·	·	·	·	·	·
	2000	·	·	·	·	1.0 a	1.0 a	·	·	·	·	·	·
Draba lactea	1995	·	·	1.1 a	1.0 a	·	·	0.87	0.84	·	·	4.3 d	4.8 cd
	1996	·	·	1.0 a	1.0 a	·	·	0.80	0.85	·	·	4.8 cd	6.3 abcd
	1997	·	·	1.0 a	1.0 a	·	·	0.87	0.80	9.1 a	10.9 a	5.6 bcd	6.7 abc
	1998	·	·	1.1 a	0.9 a	-0.2 a	0.6 a	0.63	0.52	·	·	6.7 abc	8.5 a
	1999	·	·	1.0 a	1.1 a	-1.1 a	-2.2 a	0.47	0.56	10.2 a	7.5 a	5.4 bcd	8.4 a
	2000	·	·	1.1 a	1.1 a	-1.9 a	0.5 a	0.46	0.44	9.3 a	8.2 a	5.3 bcd	7.1 ab
Dupontia fisheri	1995	·	·	9.0 cd	9.2 cd	·	·	0.07	0.14	6.1 b	8.4 ab	11.5 g	16.1 f
	1996	·	·	8.8 cd	8.9 cd	·	·	0.11	0.11	14.5 ab	11.3 ab	16.2 ef	19.7 bcd
	1997	·	·	8.2 d	8.9 cd	·	·	0.15	0.14	18.9 a	10.3 ab	17.9 cdef	19.1 bcde
	1998	·	·	13.3 a	14.8 a	-0.1 a	-0.1 a	0.12	0.05	17.4 a	8.1 ab	21.1 bc	25.2 a
	1999	·	·	10.3 bc	11.1 b	-0.6 a	0.2 a	0.01	0.03	10.3 ab	9.7 ab	17.8 def	21.7 b
	2000	·	·	9.7 bcd	10.4 bc	0.0 a	-0.1 a	0.03	0.01	15.4 ab	8.2 ab	17.7 def	19.4 bcde

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Wet Meadow continued													
Eriophorum angustifolium/triste	1995	·	·	9.6 c	9.9 bc	·	·	·	·	·	·	7.0 c	7.4 c
	1996	·	·	8.9 c	9.3 c	·	·	0.24	0.31	·	·	7.1 c	9.1 bc
	1997	·	·	8.6 c	9.4 c	·	·	0.01	0.11	2.3 a	4.2 a	8.4 bc	11.2 bc
	1998	·	·	12.2 ab	13.3 a	-0.1 ab	0.0 ab	0.03	0.09	2.3 a	3.7 a	·	·
	1999	·	·	12.1 ab	13.0 a	-0.2 ab	-0.5 b	0.06	0.04	9.8 a	12.3 a	12.4 ab	16.5 a
	2000	·	·	8.9 c	9.4 c	0.0 ab	0.1 a	0.10	0.10	31.5 a	37.4 a	12.4 ab	16.6 a
Eriophorum russeolum	1995	·	·	·	·	·	·	·	·	·	·	4.8 c	5.7 bc
	1997	·	·	6.1 d	6.8 cd	·	·	0.03	0.08	4.0 a	9.9 a	6.8 bc	9.8 abc
	1998	·	·	9.8 ab	11.2 a	0.0 a	-0.1 a	·	·	2.5 a	7.0 a	·	·
	1999	·	·	8.2 bc	9.6 ab	-0.3 a	-0.1 a	0.03	0.07	3.6 a	18.8 a	11.6 ab	13.3 a
	2000	·	·	8.1 bc	8.7 bc	0.4 a	0.0 a	0.03	0.07	8.0 a	20.1 a	9.8 abc	13.0 a
Hierochloe pauciflora	1995	·	·	·	·	·	·	0.42	0.37	·	·	8.8 d	10.4 cd
	1996	·	·	·	·	·	·	0.96	0.88	7.9 ab	25.8 ab	11.0 cd	13.9 abc
	1997	·	·	3.2 c	4.0 c	·	·	0.58	0.62	39.7 a	33.1 ab	12.8 abc	12.6 abcd
	1998	·	·	6.9 a	7.9 a	·	·	0.10	0.04	9.3 ab	4.4 b	15.9 a	12.1 abcd
	1999	·	·	4.3 bc	5.4 b	·	·	0.16	0.24	24.5 ab	14.9 ab	13.5 abc	15.1 ab
	2000	·	·	4.1 bc	4.1 c	·	·	0.10	0.11	12.9 ab	6.2 b	11.8 bcd	13.1 abc
Juncus biglumis	1995	·	·	·	·	·	·	0.91	0.68	·	·	8.4 d	9.4 bcd
	1996	·	·	·	·	·	·	0.65	0.58	·	·	10.5 abcd	12.4 ab
	1997	·	·	4.6 ab	5.1 ab	·	·	0.76	0.68	11.4 a	7.2 a	8.9 cd	10.2 bcd
	1998	·	·	5.8 ab	6.5 ab	-1.6 ab	-1.1 ab	0.39	0.44	·	·	11.8 abc	13.3 a
	1999	·	·	3.8 b	4.0 ab	-1.2 ab	-2.9 b	0.26	0.16	5.6 a	3.1 a	8.2 d	9.3 cd
	2000	·	·	5.8 ab	6.2 a	0.3 ab	1.1 a	0.33	0.21	4.4 a	4.1 a	10.1 bcd	10.3 bcd

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Wet Meadow continued													
Luzula arctica	1995	·	·	2.1 c	2.5 bc	·	·	0.52	0.46	·	·	6.1 b	9.6 ab
	1996	·	·	2.4 bc	2.8 bc	·	·	0.46	0.75	·	·	8.3 ab	12.3 a
	1997	·	·	2.2 c	2.2 c	·	·	0.60	0.66	4.3 a	5.0 a	9.3 ab	11.3 ab
	1998	·	·	2.8 bc	3.3 ab	-1.6 a	-2.8 a	0.38	0.36	4.4 a	4.2 a	11.7 a	12.3 a
	1999	·	·	·	·	0.0 a	0.7 a	0.30	0.59	4.4 a	4.1 a	7.7 ab	9.8 ab
	2000	·	·	3.4 ab	4.1 a	-0.4 a	-1.6 a	0.40	0.38	3.9 a	3.6 a	8.6 ab	10.5 ab
Luzula confusa	1995	·	·	·	·	·	·	0.88	0.65	·	·	8.1 d	12.4 abc
	1996	·	·	7.0 ab	6.3 b	·	·	0.68	0.60	·	·	10.1 bcd	13.7 ab
	1997	·	·	6.5 ab	6.3 b	·	·	0.60	0.76	5.6 a	4.7 a	12.9 abc	14.7 a
	1998	·	·	9.4 a	9.0 ab	-0.2 ab	-1.0 b	0.29	0.36	3.5 a	3.6 a	12.9 abc	15.1 a
	1999	·	·	·	·	0.3 ab	1.4 a	0.32	0.43	3.0 a	4.0 a	9.8 cd	12.1 abc
	2000	·	·	6.9 ab	7.4 ab	-0.6 b	-0.8 b	0.47	0.44	3.2 a	4.7 a	10.5 bcd	12.7 abc
Poa arctica	1996	·	·	·	·	·	·	·	·	·	·	12.0 cd	17.5 abc
	1997	·	·	4.0 a	5.0 a	·	·	·	·	6.1 a	9.6 a	13.0 cd	17.2 abc
	1998	·	·	6.2 a	7.1 a	·	·	·	·	5.2 a	4.8 a	13.9 bcd	19.5 ab
	1999	·	·	4.4 a	5.8 a	·	·	·	·	11.8 a	7.3 a	13.6 cd	22.0 a
	2000	·	·	6.0 a	5.8 a	·	·	·	·	8.5 a	3.8 a	9.7 d	13.6 cd
Salix rotundifolia	1997	·	·	0.9 a	0.9 a	·	·	·	·	·	·	·	·
	1998	·	·	0.9 a	1.2 a	·	·	·	·	·	·	·	·
	1999	·	·	0.9 a	0.9 a	·	·	·	·	·	·	·	·
	2000	·	·	0.6 a	0.8 a	·	·	·	·	·	·	·	·
Saxifraga cernua	1995	·	·	0.8 bcd	0.8 abcd	·	·	·	·	4.2 bc	2.0 c	6.6 d	9.3 bcd
	1996	·	·	0.9 abc	1.0 a	·	·	0.04	0.08	6.1 abc	4.8 bc	8.7 bcd	11.3 b
	1997	·	·	0.7 bcd	0.9 abc	·	·	·	·	11.0 ab	12.2 a	9.8 bc	14.4 a
	1998	·	·	·	·	·	·	0.03	0.04	7.1 abc	6.7 abc	9.5 bcd	11.1 b
	1999	·	·	0.9 ab	0.8 bcd	0.0 a	-0.1 a	0.02	0.03	8.8 abc	9.3 ab	7.6 cd	10.3 bc
	2000	·	·	0.7 cd	0.6 d	0.0 a	0.0 a	·	·	8.7 abc	6.7 abc	·	·

Table E-2. Continued.

		Growth						Reproductive Effort					
		Leaf				Change in Size		Percentage Flowering		Inflorescence			
		No.		Length (cm)						No./Plot		Length (cm)	
Species	Year	C	W	C	W	C	W	C	W	C	W	C	W
Barrow Wet Meadow continued													
Saxifraga foliolosa	1995	·	·	1.6 a	1.5 a	·	·	·	·	·	·	6.4 e	8.8 cde
	1996	·	·	1.4 ab	1.5 a	·	·	0.03	0.06	7.1 a	6.8 a	9.7 cd	11.8 abc
	1997	·	·	1.3 ab	1.3 ab	·	·	0.07	0.14	8.4 a	8.7 a	10.2 bcd	13.3 ab
	1998	5.8 a	5.8 a	1.0 b	1.3 ab	-0.6 a	0.1 a	0.03	0.11	4.9 a	5.9 a	9.2 cde	14.2 a
	1999	·	·	1.3 ab	1.5 a	-0.1 a	-0.9 a	·	·	5.3 a	7.6 a	9.9 cd	13.2 ab
	2000	7.4 a	6.6 a	1.4 ab	1.3 ab	-0.4 a	-0.5 a	·	·	3.8 a	3.4 a	8.5 de	8.8 cde
Saxifraga hieracifolia	1995	·	·	4.9 b	4.7 b	·	·	0.76	0.83	·	·	9.8 c	14.3 bc
	1996	·	·	5.3 ab	5.4 ab	·	·	0.77	0.68	·	·	17.2 ab	18.2 ab
	1997	4.3 a	4.5 a	4.9 b	5.2 ab	·	·	0.70	0.76	3.2 a	3.4 a	18.5 ab	21.7 a
	1998	5.4 a	5.1 a	5.9 ab	6.6 a	0.1 a	-2.6 a	0.74	0.83	3.9 a	4.5 a	17.1 ab	21.5 a
	1999	5.2 a	5.1 a	5.4 ab	5.2 ab	-3.1 a	-0.7 a	0.31	0.43	2.9 a	2.7 a	16.4 ab	16.5 ab
	2000	5.7 a	5.2 a	5.3 ab	5.6 ab	0.3 a	-1.2 a	0.59	0.59	2.3 a	2.4 a	13.8 bc	18.4 ab
Saxifraga hirculus	1995	·	·	·	·	·	·	0.91	0.73	11.7 a	18.2 a	7.6 e	8.8 cde
	1996	·	·	·	·	·	·	0.72	0.80	42.4 a	30.0 a	9.3 bcde	11.5 bcd
	1997	·	·	·	·	·	·	0.76	0.81	70.6 a	87.7 a	8.3 de	10.4 bcde
	1998	·	·	·	·	·	·	0.63	0.69	47.8 a	30.3 a	11.6 bcd	15.4 a
	1999	·	·	1.2 a	1.3 a	·	·	·	·	57.0 a	57.6 a	9.7 bcde	12.3 ab
	2000	·	·	1.5 a	1.3 a	·	·	0.32	0.47	50.1 a	35.0 a	10.0 bcde	11.9 bc
Stellaria laeta	1996	·	·	·	·	·	·	0.00	0.17	4.6 a	8.3 a	·	·
	1997	·	·	·	·	·	·	·	·	1.4 a	3.3 a	·	·
	1998	·	·	·	·	-3.0 ab	-4.4 b	0.03	0.00	5.0 a	4.6 a	·	·
	1999	·	·	·	·	-1.7 ab	-0.8 a	0.02	0.02	3.6 a	4.3 a	·	·
	2000	·	·	·	·	-0.5 a	-0.5 a	·	·	1.4 a	3.0 a	·	·

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