Effects of long-term experimental warming on three High Arctic plant communities.

by

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Abstract

Arctic regions are experiencing faster rates of atmospheric warming than any other biome. Increasing temperatures will affect the biomass, phenology, and composition of Arctic vegetation, which in turn will alter ecosystem functions such as greenhouse gas flux and nutrient cycling. These functional changes are likely to affect feedbacks to terrestrial and atmospheric systems. Responses are expected to occur at a range of scales and are likely to show close coupling to environmental conditions. In this thesis I compare ecosystem response in three plant communities after 18 years of experimental warming on Ellesmere Island, Canada. Warming response was measured at peak season in a dry, mesic and wet community. Biomass, height, and composition were measured using a point-intercept method and CO₂ flux was measured using an infrared gas analyzer and a custom made chamber. Environmental and NDVI data were collected from all three communities as well as being sampled across the entire lowland to map environmental heterogeneity and identify predictors of NDVI. All three plant communities showed structural responses to warming. Total above-ground biomass and height did not show significant changes but growth form composition shifted in all cases. Increases were observed for graminoids and forbs at the dry site; graminoids, deciduous shrubs and bryophytes at the mesic site; and deciduous shrubs and bryophytes at the wet site. Lichen abundance decreased at all sites. CO₂ flux responses were largely explained by compositional changes. All sites were CO₂ sinks at peak season and the dry and wet sites became stronger sinks as a result of warming. Landscape scale mapping successfully displayed the variation in environmental variables and NDVI across the landscape. Soil moisture was identified as an important determinant of
NDVI signal and NDVI showed potential as a predictor of CO$_2$ flux. These results support the prediction that climate change response will be ecosystem specific. While some general trends existed across multiple communities, each community had a unique response to warming. Large scale climate change predictions will have to account for such variability.
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Glossary

ANOVA Analysis of Variance, a set of statistical techniques to identify sources of variability between groups.

DOY Day of Year.

GEP Gross Ecosystem Photosynthesis, CO₂ taken into the ecosystem by photosynthesis.

GIS Geographical Information System, computer software for dealing with geographically referenced data.

GWR Geographically Weighted Regression, a localized regression technique.

LAI Leaf Area Index, ratio of total upper leaf surface to area of land on which vegetation grows.

NDVI Normalized Difference Vegetation Index, a spectral technique for analyzing the structural properties of vegetation.

NEE Net Ecosystem Exchange, the net difference between CO₂ influx through photosynthesis and CO₂ efflux through autotrophic and heterotrophic respiration.

NMDS Non-metric Multidimensional Scaling, a non-parametric ordination technique.

NPP Net Primary Production, the net difference between primary production and
autotrophic respiration in an individual plant.

**OLS** Ordinary Least Squares, a regression technique using the least squares method.

**OTC** Open-top Chamber, ITEX method for warming experiments.

**PAR** Photosynthetically Active Radiation, the amount of solar radiation available for photosynthesis.

**PERMANOVA** Permutational Multivariate Analysis of Variance, an extension of ANOVA used to identify differences in community composition.

**RE** Ecosystem Respiration, CO₂ released from the ecosystem by respiration.

**RMSE** Root Mean Squared Error, indicates how closely an interpolated model matches the measured data points.

**TLH** Total Live Hits, total number of live vegetation hits detected in the ITEX point frame method.
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Chapter 1

Introduction

1.1 Overview

Climate change is affecting ecosystems around the globe at a range of scales. The Arctic is an area of particular interest and concern given its current and projected rates of warming. As the Arctic warms, ecosystem structures and functions are expected to change. Such changes include shifts in species distribution, changes in community composition, phenological changes, and changes in vegetation productivity. Responses are likely to vary between plant communities, and between species within those communities. Many Arctic ecosystems show a high degree of heterogeneity in both environmental conditions and in plant community types. If community type is tightly linked to environmental conditions, a relatively small area could show high variation in climate change response. Understanding vegetation heterogeneity and ecosystem response not only informs us about ecological processes, but also improves our ability to predict change and take relevant action. Ecological changes in Arctic ecosystems have impacts for floral and faunal biodiversity, biogeochemical cycling and both local and global changes in atmospheric conditions.

In this thesis I investigate the warming responses of three Arctic plant communi-
ties along a natural soil moisture gradient. I also investigate vegetation and environmental heterogeneity at the landscape scale. Chapter 1 reviews the relevant literature and outlines the objectives for the study. Chapter 2 investigates the response of above-ground vegetation structure to warming. Chapter 3 looks at the CO\(_2\) flux response in each ecosystem. Chapter 4 outlines a landscape scale study to map environmental variables and plant productivity. Chapter 5 summarizes the findings and draws conclusions.

### 1.2 The Arctic environment

The Arctic tundra biome is the circumpolar region north of the Taiga, it is characterized by low temperatures, long cold winters and short cool summers. The tundra is made up of glacial areas (29%), lakes (1%), un-vegetated barren regions (15%), and vegetated areas of graminoid tundra, shrub tundra and sedge wetlands (55%; Walker et al. 2005). The southern boundary of the Arctic is alternately defined as the boreal forest timberline, the 10°C July isotherm, the summer mean position of the Arctic front, or the Arctic circle (66°33’N) (Pagnan, 2000).

Arctic regions are experiencing environmental change due to shifts in climatic conditions. Marine, terrestrial and atmospheric studies show that the Arctic has experienced significant warming in the past 30 years (Serreze et al., 2000). Future climate predictions are difficult due to the complex coupling between atmospheric and terrestrial processes (Hinzman et al., 2005). General Circulation Models (GCM) predict that warming will be amplified in polar regions due to a number of factors collectively referred to as polar amplification. Arctic temperatures are predicted to increase 1.5 - 2 times faster than the global average (Kaplan and New, 2006). Reductions in sea ice, glacial extent, and terrestrial snow and ice could be rapid as warming is amplified by decreasing albedo (Lindsay and Zhang, 2005; Serreze et al., 2007, 2000). Higher temperatures in Arctic ecosystems are expected to increase winter precipitation (Kattsov and Walsh, 2000), soil moisture content, soil temperature, active layer depth, nutrient availability, and growing season length (Serreze et al., 2000). Changes in moisture regimes could be dramatic as patterns in the permafrost boundary shift at both local and regional scales (Callaghan and
Some studies have already reported changes in precipitation, soil moisture and growing season length (Kattsov and Walsh, 2000; Myneni et al., 1997; Nicholls et al., 1996), however these changes are uncertain and are likely to vary in magnitude and direction between different Arctic ecosystems (Callaghan and Jonasson, 1995).

### 1.3 Arctic plants

Biodiversity in the Arctic is low. Just 900 (0.4%) of the world’s vascular plant species are found in this region (Billings, 1997; Bliss, 1979; Polumun, 1951). Vegetation is made up of dwarf shrubs, grasses, sedges, mosses and lichens. Plant species tend to be long-lived, slow-growing, polycarpic perennials (Molau, 1993). Reproductive traits vary widely among Arctic plants but tend to correlate with flowering phenology and therefore snow cover (Molau, 1993). Early flowering plants tend to adopt dioecious outbreeding strategies whereas later flowering species are restricted to apomixis and vivipary (Molau, 1993).

The general pattern of decreasing floristic richness and ecosystem productivity towards higher latitudes can be explained by environmental conditions and the evolutionary responses to these conditions by plants (Billings, 1987; Bliss, 1971). When averaged over a year, incident solar radiation and therefore temperature, decrease from the equator to the poles. Precipitation is highly variable across the Arctic, but when constrained to the Canadian Arctic Archipelago, trends show dramatic decreases in precipitation from south to north (Serrezee and Hurst, 2000).

Tundra plants need to tolerate extremely low temperatures through the winter and maximize growth and reproduction during the cool summer growing season. Vascular plants cope with extreme winter temperatures by producing a large proportion of their biomass below ground (Dennis and Johnson, 1970). Small size allows some Arctic plants to maintain a boundary layer 3 - 8°C warmer than the surrounding air temperature (Molgaard, 1982). Small size also maximizes insulation from snow cover during the winter (Sturm et al., 2005), and minimizes damage and desiccation from wind exposure (Oberbauer and Dawson, 1992; Sonesson and
Plants adapted to Arctic conditions can have a lower optimum temperature for shoot growth (Kummerow et al., 1980), and overwintering species are cold hardened to temperatures as low as -60°C (Billings and Mooney, 1968).

Soil moisture in the High Arctic is generally low due to decreasing precipitation at higher latitudes (Bovis and Barry, 1974). Species adapted to dry Arctic conditions are able to maintain higher concentrations of carbohydrates and have lower transpiration rates than those of wetter environments. They are also able to lower water potentials to resist drought (Billings and Mooney, 1968). Soil moisture can however show high variability due to the effects of snow melt and permafrost on water regimes. This variability influences the spatial extent and productivity of plant communities found in Arctic ecosystems (Oberbauer and Dawson, 1992).

The amount of solar radiation available for Arctic plants during the growing season varies with the frequency of cloud cover. Arctic plants manage photosynthesis in a similar way to shade-adapted plants of temperate regions: by maintaining photosynthesis at low light levels, and by achieving photosynthetic saturation at low light intensities (Chapin and Shaver, 1985).

Growing seasons are short at high latitudes due to snow cover. Plants cannot take advantage of incoming sunlight until temperatures exceed freezing and the winter snow cover has melted; they therefore have much less time for growth and reproduction than plants inhabiting temperate regions. The production of roots and photosynthetic tissue must be rapid to repay the carbon and nutrient costs of synthesis and provide a net benefit to the plant (Chapin, 1987). Plant growth and flowering occur rapidly when spring temperatures increase and snow cover melts (Bliss, 1971). The perennial nature of most Arctic plants allow carbohydrates stored in roots and rhizomes to be immediately released to developing shoots at the onset of growth (Mooney and Billings, 1960). Pre-formed shoots and flower buds can overwinter and therefore emerge early in the growing season to maximize growth and reproduction.

Organic matter build up is common in Arctic ecosystems due to low decomposition rates, this is despite low levels of input. Elements such as nitrogen and phosphorus are therefore key limitations to increases in carbon fixation and biomass accumu-
lation (Callaghan et al., 2004a). Temperature and moisture have strong influences on the availability of soil nutrients. Arctic soils gain a large proportion of their nutrients from nitrogen fixation and the nutrient content of rain water. Both these inputs are reduced by low temperatures making internal nutrient recycling an important process in Arctic soils (Chapin et al., 1980a). Arctic plants compensate for low nutrient availability by maintaining a high capacity for nutrient uptake by roots (Chapin, 1974).

1.4 Arctic plant communities

Arctic vegetation shows strong heterogeneity at a range of scales, from the physiological properties of individual species to the biome scale patterns in vegetation type (Muc et al., 1989; Walker et al., 2005). Broad transitions in Arctic ecosystem types are primarily due to changes in climate, soil parent material, permafrost, and hydrology (Epstein et al., 2004; Walker et al., 2005). Dominant growth forms in Arctic ecosystems could be vascular or non-vascular, deciduous or evergreen, woody or herbaceous (Bliss, 1981; Shaver and Chapin, 1991). It is therefore unique in that it cannot be described by a single dominant vegetation type, as is the case in many other biomes (Shaver and Chapin, 1991).

Species level differences in physiological properties can cause different growth form groups to show different patterns of internal element cycling, tissue turn-over rates and growth (Chapin et al., 1996, 1980b; Shaver and Chapin, 1980). Similar physiological variation is seen at the level of whole Arctic vegetation types (Dowd- ing et al., 1981; Henry et al., 1986; Jonasson, 1983; Shaver and Chapin, 1991). These variations translate to differences in ecosystem properties such as CO$_2$ flux (Oberbauer et al., 2007; Welker et al., 2004), normalized difference vegetation index (NDVI; Boelman et al., 2005; Walker et al., 2003, 2005), leaf area index (LAI; Van Wijk et al., 2004; Walker et al., 2003) and total plant biomass (Shaver et al., 1996).

At the landscape scale, environmental gradients can be steep. Small changes in topography can be associated with large changes in microclimate and plant stress
Topographic variation in the Arctic has been correlated with changes in air temperature, wind, soil moisture, and snow cover (Billings, 1973). More recent studies have also highlighted the availability of soil nutrients as an important variable which is influenced by topography (Giblin et al., 1991; Shaver et al., 1991; Walker and Everett, 1991). Studies along toposequences in the Arctic have shown significant variation in plant community type, nutrient pool sizes, distribution and cycling rates (Giblin et al., 1991), and in the amounts of total plant biomass, vascular plant biomass, and above ground plant production (Shaver et al., 1996).

### 1.5 Arctic plants and climate change

Changes in climate affect the phenology, productivity, spatial extent, and species composition of Arctic vegetation. A number of climate induced range shifts have already been documented around the globe (Walther et al., 2002) and observations indicate that some Arctic ecosystems are greening due to increased temperatures. Jia et al. (2003) show a 16.9% increase in peak vegetation greenness in the Alaskan Arctic which corresponds to increases in temperature over a 21 year period. Other studies in Arctic Alaska have found similar increases in shrub abundance (Sturm et al., 2001b; Verbyla, 2008). Myneni et al. (1997) show an increase in photosynthetic activity at high latitudes between 1981 and 1991 with the largest increase between 45 - 70°N, correlating with springtime warming. Experimental warming and nutrient addition treatments predict changes in phenology and increases in shrub abundance, gross ecosystem photosynthesis (GEP) and above ground biomass (Henry et al., 1986; Marchand et al., 2004; Walker et al., 2006; Welker et al. 2004 1997). These changes are not consistent throughout all communities and some communities show reverse trends (Oberbauer et al., 2007).

The individualistic nature of Arctic plant species means long term responses cannot easily be generalized and predictions must consider the indirect effect of climate change on resource supply (Chapin et al., 1995). The different growth forms and evolutionary histories of Arctic plants mean many species have unique factors limiting growth and dispersal (Chapin et al., 1996). While short term changes may be
observed within plant communities, community composition itself is expected to change in the long term due to species specific responses to climate change.

Vegetation changes are likely to act as a feedback mechanism to climate change as shrub abundance has a major influence on regional energy and CO$_2$ fluctuations (McFadden et al., 1998). Two important mechanisms contributing to climate change feedbacks on the Arctic and global climate systems are albedo (ratio of incoming radiation reflected by surface), and the biological emissions and uptake of greenhouse gases (Callaghan et al., 2004b). Terrestrial Arctic regions experience extreme seasonal changes in energy exchange. In late winter, snow reflects large amounts of incoming radiation (albedo about 0.7) whereas in summer, ecosystems absorb large amounts of radiation (albedo about 0.15; Callaghan et al. 2004b). Approximately 90% of the energy absorbed in summer is transferred to the atmosphere, the rest is transferred to the soil and released to the atmosphere during winter (Eugster et al., 2000). Changes in ecosystem type and the accompanying change in albedo can have dramatic impacts on climate-forcing. Chapin et al. (2000b) for example found that the difference in net climate-forcing between shrub tundra and forest tundra as a result of albedo change, is roughly equivalent to a doubling of global atmospheric CO$_2$ concentrations. The strong summer warming effect of tundra ecosystems on regional atmosphere can create a positive feedback, whereby an increased snow-free period, an increasing cover of shrubs, or a northerly migration of the tree line would act to decrease albedo and lead to further regional warming (Callaghan et al., 2004b; Sturm et al., 2001a,b).

Similar feedbacks are possible with greenhouse gas flux, however the direction of this feedback depends on whether an ecosystem has a net influx or efflux of gas. The main greenhouse gases in Arctic ecosystems are CO$_2$ and CH$_4$. Methane is a stronger greenhouse gas but it is far less abundant and climate models do not deal with methane flux as well as they do with CO$_2$. Models to predict future CO$_2$ flux are uncertain, but a number of models conclude that the Arctic will continue to be a net sink of CO$_2$ in the coming century (Grant et al., 2011; McGuire et al., 2000; Qian et al., 2010; Sitch et al. 2007, 2003; White et al., 2000). These models have high levels of uncertainty due to the complex response mechanisms of ecosystem photosynthesis and respiration to climate drivers. Callaghan et al.
summarize model predictions as follows. In polar desert areas, increases in growing season temperatures and CO\textsubscript{2} will lead to increased vegetation growth and northward migration. This will increase carbon storage through increases in net primary production (NPP). This is offset by the heterotrophic respiration of soil microorganisms which is also expected to increase with warming. Areas currently containing large stocks of soil carbon are therefore expected to release more CO\textsubscript{2} as decomposition increases. The net flux in the active layers of Arctic ecosystems is therefore a balance between the increased productivity associated with longer growing seasons, higher temperatures and increased CO\textsubscript{2}; and temperature enhanced respiration.

The current and future cycling of carbon through Arctic ecosystems varies by plant growth form and therefore plant community (Dorrepaal, 2007; Shaver and Chapin, 1991). Large scale changes in community composition could have consequences for carbon flux dynamics and climate change feedbacks. Vegetation change can occur as a direct effect of climatic change (e.g. Hudson and Henry, 2009; Sturm et al., 2001b) or through indirect disturbances such as permafrost degradation and changes in hydrological regimes (Barrett et al., 2008; Beilman, 2001; Lantz et al., 2009). Accurate predictions for Arctic ecosystems therefore rely on an understanding of community specific responses to expected climatic change.

1.6 ITEX

The International Tundra Experiment (ITEX) is a network of over 20 Arctic and alpine sites established in 1990 to investigate the response of tundra ecosystems to high-latitude warming. The primary objective of ITEX is to monitor changes in growth, phenology, and reproduction in circumpolar vascular plant species in response to environmental manipulations and climatic variation (Henry and Molau, 1997). Passive warming of tundra ecosystems is achieved using open-top chambers (OTCs, Marion et al., 1997), growing season length is altered using snow manipulations, and soil nutrient content is altered through nutrient addition. OTCs have been shown to simulate predicted climatic change by warming near-surface air temperatures by 1 - 3\textdegree C (Henry and Molau, 1997). Standard protocols for experimental
design, measurements, and statistical analysis allow data from multiple ITEX sites to be combined in large scale analyses. This approach has been used to predict ecosystem responses in growth, phenology and reproduction (Arft et al., 1999); carbon flux (Oberbauer et al., 2007); and composition and biodiversity (Walker et al., 2006).

1.7 Alexandra Fiord

All research for this study was conducted within the Alexandra Fiord lowland on Ellesmere Island, Nunavut (78°53'N, 75°55'W; Figure 1.1). This High Arctic site is part of the ITEX network. The lowland is an 8 km² periglacial outwash plain bordered to the south by the Prince of Wales ice cap, and to the north by the waters of Alexandra Fiord. The topography rises gently from north to south and the site is enclosed by bare upland areas to the east and west. The site includes two rivers, a number of streams and creeks, granite outcrops, frost boils, sorted polygons, and a number of glacial erratics of varying size.

Alexandra Fiord is a polar oasis with a warmer climate, greater primary productivity, higher species diversity, and greater plant cover than the surrounding area (Freedman et al., 1994). It receives between 10 - 20 cm of precipitation annually and approximately 1 - 5 cm during the growing season. Growing season average temperatures are between 5 - 8°C (G. Henry, unpublished data). The site is rich in plant, animal and insect life. A total of 96 species of vascular plant have been recorded (Ball and Hill, 1994), common species include Salix arctica, Cassiope tetragona, Dryas integrifolia, and Luzula arctica.

The lowland is covered by closed, or semi-closed vegetation across 90% of its area (Muc et al., 1989). Plant community composition varies considerably across the lowland and is largely influenced by moisture regimes (Muc et al., 1989). Drainage of spring melt water is limited horizontally by the gentle slopes of the lowland (1-3%) and vertically by permafrost and a frozen active layer at snowmelt (Freedman et al., 1994). Soil moisture is greatest at snowmelt and is thereafter influenced by localized drainage properties, topography and vegetation. Soils are young and
Figure 1.1: Overview of Alexandra Fiord showing site locations, plot locations within each site, growth form breakdowns for control plots at each site, and dominant species.
poorly developed but have relatively large amounts of organic matter compared to
surrounding areas (Muc et al., 1994).

This study was conducted in three distinct plant communities. A sedge meadow
site had a 10 - 25 cm organic layer over sand-gravel substrate. Soils were water
saturated throughout the growing season, had a hummocky topography, and a max-
imum active layer of 80 cm (Henry et al., 1986). This community was dominated
by the hydrophilic sedges *Eriophorum angustifolium triste, Carex membranacea,*
and *Carex aquatilis stans.* A combination of relatively high NPP, low decompo-
sition, and the absence of large herbivores at the site has allowed thick layers of
litter and organic matter to accumulate (Henry, 1998; Hill and Henry, 2011). This
community covers approximately 28% of the lowland (Muc et al., 1989).

A dry site was characterized by low snow deposition, early snow melt, deep early
season active layer depth, and sandy soils. This ecosystem covers approximately
4% of the lowland and is dominated by *Salix arctica, Dryas integrifolia, Saxifraga
oppositifolia,* and a few graminoid and forb species (Muc et al., 1989). This ecosys-
tem type is found throughout the lowland on river banks and raised slopes.

The mesic site for this study is found on flood plains and seepage slopes with
less moisture than the sedge meadow sites. Communities are dominated by *Dryas
integrifolia, Cassiope tetragona, Salix arctica* and graminoid species such as *Arc-
togrostis latifolia.* This site was affected by a flood event in the summer of 2000.
Prior to this event, the site was dominated by *Dryas integrifolia* but now *Cassiope
tetragona* and graminoid species such as *Eriophorum angustifolium triste, Arc-
togrostis latifolia,* and *Carex* species are more abundant. This community covers
approximately 19% of the lowland (Muc et al., 1989).

1.8 Objectives

Many Arctic ecosystems exist in landscapes with highly heterogeneous environ-
mental conditions which contribute to spatial heterogeneity in vegetation com-
position and productivity. Future changes in Arctic conditions could be dramatic and
shifts in community composition may be expected. The direction and magnitude of
climate change response is likely to be species specific; responses are not therefore expected to be consistent across ecosystems. To investigate how the structure and functions of Arctic ecosystems may respond to future changes I asked the following questions:

1. How does above-ground vegetation structure differ between tundra communities and how will warming change this vegetation structure? (Chapter 2)

2. How does CO$_2$ flux differ between tundra ecosystems and how will this change in response to warming? (Chapter 3)

3. How do environmental variables and vegetation productivity vary throughout this landscape and what environmental factors contribute to changes in vegetation productivity? (Chapter 4)

For questions 1 and 2, passive warming was achieved using open top chambers (1992-2010). Plant communities were described by abundance and composition. CO$_2$ flux was described by net ecosystem exchange (NEE), gross ecosystem photosynthesis (GEP), and ecosystem respiration ($R_E$). To address question 3, a systematic sampling grid was used to collect data estimating vegetation abundance. Environmental data were also collected to estimate near-surface air temperature and soil moisture.
Chapter 2

Vegetation structure

2.1 Introduction

The Arctic has warmed 1.6°C in the past 40 years and is expected to increase further in the coming century (Kattsov et al., 2005; McBean et al., 2005). Species specific responses to warming will cause changes to both the structure and function of ecosystems (Callaghan et al., 2004a). Ecosystem structure can be thought of as the physical components of the vegetation whereas ecosystem functions are the processes within, and interactions between these components. The link between structural components and ecosystem function will be discussed in Chapter 3.

A common prediction is that Arctic warming will increase vegetation biomass as plants grow larger and spread to previously bare ground. This has been shown at the plot scale for some ecosystems under both warmed (Arft et al., 1999) and ambient (Hill and Henry, 2011; Hudson and Henry, 2009) conditions. Biomass response is variable however, and results differ with latitude (Arft et al., 1999), and even by community type within a study site (Hollister and Flaherty, 2010; Hudson and Henry, 2009, 2010). Findings at the plot level can be linked to broader scale analyses using remote sensing techniques (Laidler et al., 2008). Results from Alaska using photographic techniques and satellite data indicate broad scale in-
creases in shrub abundance (Jia et al., 2003; Sturm et al., 2001b), however these results are also likely to be region and ecosystem specific.

Changes in community composition are expected as environmental conditions change and species ranges shift. Compositional changes could occur due to direct changes in temperature (Brooker and van der Wal, 2003), temperature induced changes in environmental regimes (e.g. hydrological cycles; Grime, 2001), or due to temperature induced disturbance (Beilman, 2001). Circumpolar warming experiments have shown increases in the cover and heights of graminoids and shrubs, and decreases in lichen and bryophyte cover (Walker et al., 2006). Responses in the Low Arctic are stronger than those in the High Arctic, but not all sites show the same patterns of response (Walker et al., 2006). Changes in community composition will affect net primary production (NPP), nutrient cycling, and species interactions (Eviner and Chapin, 2003).

The normalized difference vegetation index (NDVI) allows long term monitoring of vegetation structure at a range of scales. It was developed by Rouse et al. (1974) and has been used at a global scale to detect and quantify plant and ecosystem processes (Myneni et al., 2001, 1997). NDVI applies a numerical indicator to a remotely sensed image which is related to the fraction of absorbed photosynthetically active radiation (fAPAR; Sellers, 1987). NDVI has been widely applied in the Arctic to monitor ecosystem structure through community categorization (e.g. Walker et al., 2002) and vegetation abundance (e.g. Jia et al., 2003; Verbyla, 2008). It is usually calculated from satellite data to monitor broad scale patterns and climate change response (Walker et al., 2005), but can also be applied at fine scales to monitor individual plots of land (e.g. Boelman et al., 2003).

The relationships between NDVI and ecological variables are likely to be community specific (Hope et al., 1993). A plot-based NDVI approach not only allows comparison of NDVI between plant communities, but also allows investigation into the relationship between NDVI and other measures of biomass and CO₂ flux within plant communities. Some plot level studies have linked NDVI not only to structural measures like biomass (Hope et al., 1993; Walker et al., 2003) and cover (Laidler et al., 2008), but also to functions such as photosynthesis (Whiting et al., 1992),
respiration (McMichael et al., 1999), and phenology (Marchand et al., 2004). More plot level research is needed to compare responses between different plant communities and link findings at different scales. Analyzing NDVI and other measures of ecosystem structure along environmental gradients could reveal important relationships determining variations in plant community properties.

The amount and composition of above-ground vegetation in an ecosystem has a strong effect on ecosystem function and is tightly coupled with regional and global atmospheric conditions (Bonan et al., 1995, 1992). A number of potential positive and negative land-atmosphere feedbacks exist in the Arctic (Lashof et al., 1997). Callaghan et al. (2004c) identify four of the most important feedbacks as albedo changes, biological greenhouse gas fluxes, greenhouse gas emissions from melting permafrost, and fluxes in freshwater systems. Of these feedbacks, albedo change is most directly linked to vegetation structure. Albedo is a measure of the reflectivity of a surface; snow and ice for example reflect more solar radiation than vegetation. Vegetation albedo is determined by vegetation density, LAI, canopy height, and canopy spectral properties (Lashof et al., 1997). A positive feedback exists whereby increased vegetation cover decreases albedo and leads to increases in local warming as more heat is retained in the ecosystem. A number of studies have found changes in atmospheric warming due to albedo changes from transitions in vegetation zones (Beringer et al., 2005; Chapin et al., 2000b, 2005). Vegetation changes have reportedly increased sensible heat flux and atmospheric heating (Beringer et al., 2005; Chapin et al., 2000b), and are predicted to further increase atmospheric heating in the future (Chapin et al., 2005).

The aim of this chapter is to compare the warming response of three Arctic plant communities in terms of ecosystem structure. Structure is described using biomass estimation, growth form composition and vegetation height. These components are compared between communities under both ambient and experimentally warmed conditions. Temperature and soil moisture are also recorded to quantify the environmental differences between sites.
2.2 Methods

2.2.1 Study site

Field work was conducted at the Alexandra Fiord lowland on Ellesmere Island, Nunavut (78°53'N, 75°55'W). This site is an 8 km² polar oasis and therefore has warmer temperatures and more diverse vegetation than the surrounding areas. The site is bounded by glaciers, steep ridges and coastal ice and water. Vegetation covers 90\% of the lowland; community distributions are heterogeneous and largely determined by soil moisture status (Muc et al., 1989). Vegetation is composed of small shrubs, graminoids, forbs, lichen and bryophytes.

2.2.2 Experimental design

Ecosystem structure was surveyed in three plant communities: a wet site, mesic site and dry site. The wet site was a sedge-meadow community where soils were water saturated throughout the growing season. Vegetation at the sedge meadow was dominated by the hydrophilic sedges. Common species included Eriophorum angustifolium triste, Carex membranacea, and Carex aquatilis stans. The mesic site was located on a flood plain and had the most variable soil moisture content. Vegetation here was dominated by Dryas integrifolia, Cassiope tetragona, Salix arctica and graminoid species such as Arctagrostis latifolia. The dry site was on a raised river bank and had the lowest levels of soil moisture. Its vegetation was dominated by the deciduous shrub Salix arctica, and smaller numbers of evergreen shrubs, forbs and graminoids.

Each site consisted of ten warmed and ten control plots. Warming was achieved using the ITEX open-top chamber (OTC) method (Marion et al., 1997). These six sided chambers are made of 1 mm thick fibreglass sheets. This material has low solar transmittance in the infrared wavelengths (<5\%) and high transmittance in the visible wavelengths (>85\%). They are constructed into inclined hexagonal cones standing 0.5 m tall with a diameter of 1.5 m. This structure allows transmittance of
solar energy, trapping of convective heat, and a reduction in wind speed (Marion et al., 1997). The open-top design allows ‘near-normal’ levels of precipitation and gas exchange and raises average surface air temperatures by 1-3°C during the growing season (Henry and Molau, 1997). OTCs were installed at these sites in 1992. The ITEX OTC approach is the preferred method for Arctic and alpine warming experiments, a review of this method and some of limitations are summarized by Wookey (2008). Control plots were sections of tundra with no chambers installed. Control and warmed plots were randomly assigned within each site at the start of the experiment. Each plot contained a permanent 1m² section which is used for long term monitoring of vegetation structure.

2.2.3 Data collection

Environmental data

Surface air temperature was collected in a sub-sample of plots at each site. HOBO air temperature sensors (Onset, Bourne, MA, USA) recorded temperature every two minutes for the entire growing season (day of year, DOY 174 - 228). Sensors were elevated 10 cm from the soil surface and were shaded to avoid direct sunlight. Temperature data were collected from two OTC and two control plots at the dry site, two OTC and three control plots at the mesic site, and two OTC and one control plot at the wet site.

The date of snowmelt was recorded at each plot as the date that 90% of the plot was free of snow cover. Soil moisture was recorded using a portable soil moisture sensor (CS620 HydroSense unit, Campbell Scientific, Edmonton, AB, Canada). This system combines a handheld display with a 12 cm water sensing probe. Measurements are averaged along the length of the probe and are reported as the percentage of volumetric water content in the soil. Measurements are accurate to 3% and have a resolution of 0.25%. Soil moisture measurements were recorded in all plots on three days during the peak growing season (DOY 210/211, 218, 230). Plot values were averaged from three individual measurements taken in each plot.
Point-framing

All structural data were collected between DOY 204 and 209 at the peak of the growing season. Structural data were collected at each plot using the ITEX point-intercept technique (Molau and Molgaard, 1996). This technique uses a 1m$^2$ frame containing a grid of points 10 cm apart. At each point, the vegetation type is recorded for all layers of the canopy. Almost all vegetation was recorded to the species level. Exceptions were the bryophytes and lichens. Vegetation height was also measured at each point. Above-ground vegetation biomass was estimated using the total number of live vegetation hits recorded in each plot. There is a strong correlation between the point intercept method and measures of biomass from harvests (Jonasson, 1988; Shaver et al., 2001). Both of these methods have shown the same results in biomass analyses (Pedersen and Post, 2008). Plant species were grouped into 6 common growth form groups for analysis: deciduous shrubs, evergreen shrubs, graminoids, forbs, bryophytes and lichen.

NDVI

NDVI is calculated from reflectance data and represents the abundance of photosynthetically active vegetation (Rouse et al., 1974). The formula for NDVI uses the difference between reflectance in the red region of the spectrum (620 nm - 700 nm) and reflectance in the near infra-red region (NIR, 700 nm - 1000 nm). Healthy green vegetation has low reflectance in the red region because red light is being absorbed. It has high reflectance in the NIR due to the structural properties of the spongy mesophyll layer. In unhealthy vegetation the converse is true, reflectance in the red region increases and in the NIR decreases. The relationship between these two spectral regions is represented by the NDVI formula as follows:

$$\text{NDVI} = (NIR - red)/(NIR + red)$$

(2.1)

NDVI values range from -1 to 1 with values below zero corresponding to water or dark surfaces lacking vegetation. Sparsely vegetated areas can have values as low as 0.05 while well vegetated areas can range from 0.4 to 0.7 (Boelman et al., 2005).
The actual NDVI value recorded is influenced by the instrument used, the wavelengths chosen for the formula, sun angle, background reflectance and canopy structure (Boelman et al., 2003).

Canopy reflectance properties were measured using a field portable spectrometer (Tetracam ADC, Chatsworth, CA, USA). This spectrometer has a $46^\circ \times 35^\circ$ field of view (FOV) that detects wavelengths between 520 nm and 920 nm. These wavelengths are split into three spectral bands (520-600nm; 630-690nm; 790-920nm). Camera calibration uses an image of a standard white surface to normalize for changes in light conditions. The spectrometer was used to collect images of the $1m^2$ plots within one day of point frame sampling. NDVI data were collected around midday on DOY 204 from the exact same plots that were point framed. Images were processed using Tetracam’s PixelWrench 2.0 software. Non-vegetated areas such as bare ground, rocks and standing water were masked out of each image before NDVI was calculated. Only the vegetation within each $1m^2$ plot was used in the calculation. Four images had to be removed from analysis. There are therefore only eight control plot images and nine warmed plot images from the wet site, and nine warmed plot images from the dry site.

### 2.2.4 Statistical analysis

**Environmental**

Environmental variables were collected to quantify the differences in snowmelt, soil moisture and temperature between each site. Snowmelt and soil moisture averages were calculated for each site and for each treatment at each site. Mean daily temperatures were calculated for each treatment at each site to show temperature change through the growing season. The average difference in surface air temperature between control and warmed treatments was also calculated for the entire growing season.
Biomass

Fixed effects 2-way Analysis of Variance (ANOVA) was used to test for differences and interactions across all sites and treatments for Total Live Hits (TLH), NDVI and height variables. A type three sum of squares procedure was used due to the unbalanced design. Any significant interactions would suggest that communities were responding to warming in different ways. Any significant variables identified with the 2-way ANOVA were tested with one-way ANOVA and Tukey tests to investigate differences. T-tests were used to test for differences between control and warmed plots within each site for each of the three biomass variables. Any datasets that did not meet the statistical assumptions were log or square root transformed. In some cases the non-parametric Wilcoxon test was used in place of a t-test if assumptions could not be met. P-values were interpreted at the 95% confidence level ($\alpha = 0.05$).

Simple linear regression was used to investigate the relationship between NDVI and TLH. Regressions were produced using all data combined and data grouped by site. Multiple regression was used to identify the vegetation growth forms that were driving changes in NDVI. This was done for all sites combined and for sites individually. If two variables showed high levels of correlation, one of them was removed from the model to avoid multicollinearity.

Composition

TLH data grouped by growth form were used to analyze community composition using ordinations and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). PERMANOVA was done using the ‘adonis’ procedure in the vegan package (1.17-7; Oksanen 2011) and the Bray-Curtis method for dissimilarities. Ordinations were plotted with nonmetric multidimensional scaling (NMDS; Kruskal 1964) using the ‘metaMDS’ procedure in vegan 1.17-7. The Bray-Curtis method was used to calculate dissimilarities and a 95% confidence interval ellipse was drawn around the centroid of each ordination class. If the ellipses do not overlap the communities are likely to be different at $\alpha = 0.05$. All data analysis and
graphing was done using R version 2.12.2.

2.3 Results

2.3.1 Environmental

Warming advanced the growing season at the dry site by an average 2 days (Control = 164.7 ± 0.9, Warmed = 162.7 ± 0.4; mean ± 1 standard error) and at the mesic site by an average 1.4 days (Control = 168.4 ± 0.3, Warmed = 167.0 ± 0.5). Snowmelt was not significantly different at the wet site (Control = 163.0 ± 0.0, Warmed = 163.2 ± 0.5). There were no significant differences between the soil moisture content of the control and warmed plots at any site (Figure 2.1). The average growing season volumetric water content, for all treatments, at the dry site was 15.95 ± 0.65%, at the mesic site was 21.57 ± 1.00%, and at the wet site was 80.02 ± 2.20%.

All sites showed similar surface air temperature trends with the highest temperatures occurring earlier in the season and the lower temperatures later (Figure 2.2). The highest temperatures occurred between DOY 180 and 187 at all sites. The warming treatment appeared to have a greater effect at higher temperatures, especially at the mesic and wet sites. The average temperature difference between control and warmed plots was 0.99 ± 0.06°C at the dry site, 1.54 ± 0.15°C at the mesic site, and 1.73 ± 0.16°C at the wet site. OTC warming in 2010 was therefore consistent with previous years at this site (1-3°C; Henry and Molau 1997).

2.3.2 Biomass

Results from the 2-way ANOVA model showed significant differences between sites (2-way ANOVA, Site $F_{54,2} = 6.77$, $p = 0.002$) but not treatments (2-way ANOVA, Treatment $F_{54,1} = 3.61$, $p = 0.063$). No interactions were found. The biggest within site treatment difference was at the dry site (t-test, $t_{18} = 3.43$, $p = 0.08$) which showed a 17.8% difference between the control (108.7 ± 6.9) and
Figure 2.1: Average soil moisture content for the 2010 growing season from three sites with two treatments. Each bar is averaged from ten plots and three sample days (210/11, 218, 230). Error bars represent one standard error.

warmed (130.8 ± 12.7) plots (Figure 2.3). When investigated with one-way ANOVA, the control plots at the wet site had significantly more live hits than the dry and mesic sites (ANOVA, $F_{2,7} = 7.49, p = 0.003$) but there were no differences in the warmed plots and no differences between the dry and mesic sites for either treatment.

Control and warmed plots within each site showed similar NDVI values and no warming response was detected (Figure 2.4). NDVI averages differed by site but did not show the same trends as the TLH data. When treatments were grouped the mesic site showed significantly lower NDVI values than the dry and wet sites.
Figure 2.2: Mean daily temperature in control and warmed plots throughout the growing season. Dry site control n=2, warmed n=2; Mesic site control n=3, warmed n=2; Wet site control n=1, warmed n=2.
Figure 2.3: Peak season live hit averages across three sites and two treatments. Total live hits recorded using the ITEX point intercept method. Each bar is the average of ten plots. Error bars represent one standard error.

(2-way ANOVA, Site $F_{50.2} = 5.98$, $p = 0.005$).

Heights were greatest at the wet site for both treatments (ANOVA, $F_{27.2}$, $p<0.001$ for both treatments) with no difference between the dry and mesic sites (Figure 2.5). Plants in warmed plots were slightly taller at the dry (Control, 5.16 ± 1.01 cm; Warmed, 6.65 ± 0.66 cm) and mesic (Control, 4.08 ± 0.45 cm; Warmed, 4.63 ± 0.46 cm) sites but shorter at the wet site (Control, 14.79 ± 0.78 cm; Warmed, 11.34 ± 1.76 cm). None of these differences were significant but an interaction existed whereby an increase in soil moisture led to a decrease in height response to warming. This interaction was due to the negative response at the wet site and
Figure 2.4: Peak season average NDVI from three sites and two treatments. Dry site control n=10, warmed n=9; Mesic site control n=10, warmed n=10; Wet site control n=8, warmed n=9. Error bars represent one standard error.

shows that warming response is not consistent across all plant communities (2-way ANOVA, Site:Treatment $F_{33,2} = 3.65$, $p = 0.03$).

TLH and NDVI showed a significant relationship when sites were grouped together (Figure 2.6; Regression, $R^2 = 0.36$, $F_{34} = 30.83$, $p<0.001$). The relationship was such that an increase in NDVI of 0.05 signified a TLH increase of 22.3 (Regression equation, TLH = -151.7 + 445.44 × NDVI). This relationship was weak due to error around the regression line, part of this error can be explained by site differences. The dry and wet sites had different regression slopes and the mesic site showed little evidence of a relationship (Figure 2.7). The dry site showed a sig-
Figure 2.5: Peak season average canopy height from three sites and two treatments. Each bar shows the average of ten plots. Error bars represent one standard error.

A significant relationship ($R^2 = 0.26$, $F_{17} = 6.13$, $p = 0.02$) and a slope of 394.1. The wet site showed a significant relationship ($R^2 = 0.52$, $F_{15} = 16.50$, $p = 0.001$) and a slope of 566.4. The mesic site did not show a significant relationship ($R^2 = 0.12$, $F_{18} = 2.55$, $p = 0.13$) and had a slope of 365.5. Regression for the mesic site was weakened by the small range of NDVI at this site.

Multiple regression analyses identified graminoids and deciduous shrubs as important drivers of NDVI (Table 2.1). These variables were both significant in the combined model (All sites all treatments multiple regression, $R^2 = 0.54$, $F_{49} = 9.50$, $p < 0.001$). Deciduous shrubs were the only significant variable at the dry site (Dry site all treatments, $R^2 = 0.63$, $F_{12} = 3.35$, $p = 0.04$). Graminoids were the only
Figure 2.6: Regression relationship between TLH and NDVI. Includes plots from all sites and treatments. Each point represents a single plot. $R^2 = 0.36$, $F_{54} = 30.83$, $p<0.001$. 
Figure 2.7: Regression relationship between TLH and NDVI at each site. Each graph includes plots from both treatments. A = Dry site ($R^2 = 0.26$, $F_{17} = 6.13$, $p = 0.02$); B = Mesic site, ($R^2 = 0.12$, $F_{18} = 2.55$, $p = 0.13$); C = Wet site, ($R^2 = 0.52$, $F_{15} = 16.50$, $p = 0.001$).
significant variable at the wet site (Wet site all treatments, $R^2 = 0.53$, $F_{12} = 3.41$, $p = 0.04$). The mesic site did not produce a significant model.

Table 2.1: Multiple regression results identifying growth forms that drive NDVI increase. Explanatory variables are the number of hits for each growth form at peak season in each plot. df = degrees of freedom.

<table>
<thead>
<tr>
<th>Site</th>
<th>$R^2$ full model</th>
<th>$F_{df}$</th>
<th>p-value</th>
<th>Significant variables</th>
<th>Slope</th>
<th>$R^2$ variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>0.54</td>
<td>9.5</td>
<td>9.49</td>
<td>&lt;0.001</td>
<td>Graminoids 0.0011</td>
<td>0.39</td>
</tr>
<tr>
<td>Dry</td>
<td>0.63</td>
<td>3.35</td>
<td>12</td>
<td>0.04</td>
<td>Deciduous shrubs 0.0013</td>
<td>0.12</td>
</tr>
<tr>
<td>Mesic</td>
<td>0.35</td>
<td>1.15</td>
<td>13</td>
<td>0.39</td>
<td>Deciduous shrubs 0.0022</td>
<td>0.62</td>
</tr>
<tr>
<td>Wet</td>
<td>0.53</td>
<td>3.41</td>
<td>12</td>
<td>0.04</td>
<td>Graminoids 0.0011</td>
<td>0.32</td>
</tr>
</tbody>
</table>

2.3.3 Composition

Growth form abundances differed by site (Figure 2.8) and the three sites contained three distinct plant communities (PERMANOVA, $F_{57,2} = 40.13$, $R^2 = 0.58$, $p<0.001$). Communities were dominated by deciduous shrubs at the dry site, evergreen shrubs at the mesic site, and graminoids at the wet site (Figure 2.9, NMDS, stress = 0.16, $k = 2$, nonmetric $R^2 = 0.98$, linear $R^2 = 0.87$). The dry site ordination showed a decrease in lichen and evergreen shrubs, and an increase in graminoids and forbs in the warmed plots (Figure 2.10, NMDS, stress = 0.11, $k = 2$, nonmetric $R^2 = 0.99$, linear $R^2 = 0.93$). Despite these differences community composition in the warmed plots was not significantly different to that of the controls (PERMANOVA, $F_{18,1} = 1.77$, $R^2 = 0.09$, $p = 0.14$). The mesic site did show significant shifts in composition (PERMANOVA, $F_{18,1} = 3.44$, $R^2 = 0.16$, $p = 0.01$) with the warmed plots having less lichen, and more bryophytes and deciduous shrubs than the control plots (Figure 2.11, NMDS, stress = 0.13, $k = 2$, nonmetric $R^2 = 0.98$, linear $R^2 = 0.91$). The warmed plots at the wet site also showed compositional differences (PERMANOVA, $F_{18,1} = 3.29$, $R^2 = 0.15$, $p = 0.02$) with more bryophytes and deciduous shrubs, and fewer graminoids than the controls (Figure 2.12, NMDS, stress = 0.09, $k = 2$, nonmetric $R^2 = 0.99$, linear $R^2 = 0.97$).
Figure 2.8: Total live hits divided between growth forms for three sites and two treatments. C = control plots, W = warmed plots. Each bar segment represents the average number of hits for a given growth form. Each segment is the average of ten plots.
Figure 2.9: NMDS of 60 plots showing three distinct plant communities at the three different sites (stress = 0.16, $k = 2$, nonmetric $R^2 = 0.98$, linear $R^2 = 0.87$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
Figure 2.10: NMDS of ten control and ten warmed plots at the dry site (stress = 0.11, $k = 2$, nonmetric $R^2 = 0.99$, linear $R^2 = 0.93$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
Figure 2.11: NMDS of ten control and ten warmed plots at the mesic site (stress = 0.13, $k = 2$, nonmetric $R^2 = 0.98$, linear $R^2 = 0.91$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
Figure 2.12: NMDS of ten control and ten warmed plots at the wet site (stress = 0.09, $k = 2$, nonmetric $R^2 = 0.99$, linear $R^2 = 0.97$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
2.4 Discussion

The major warming response at this site was a change in growth form composition, and not an increase in above-ground biomass or height. These results suggest that all three of the communities displayed a unique structural response to experimental warming. Only one of the communities studied offers evidence for total biomass change, whereas all three communities show both increases and decreases in the abundance of specific growth form groups.

The dry site showed the biggest increase in total above-ground biomass under warming, followed by a small increase at the mesic site and a small decrease at the wet site. The increases seen at the dry and mesic site were due to increased abundance of graminoids and forbs; and graminoids, bryophytes and deciduous shrubs respectively. While both of these sites showed decreases in lichen and evergreen shrubs, these decreases were small and outweighed by those growth forms that increased. It is likely that the open vegetation at these sites allowed growth forms to increase without compensatory decreases in other groups. This does not appear to be the case at the wet site where the large decrease in graminoids and small decrease in evergreen shrubs outweigh the increases in bryophytes and deciduous shrubs. One possible explanation for this is that the increases in deciduous shrubs and bryophytes are causing compensatory decreases in the sedge species. The deciduous shrubs - and to a lesser extent the bryophytes - found in the warmed plots tend to grow on raised hummocks or on beds of accumulated litter which are raised above the water level. An increase in these raised areas could be facilitating a decrease in the hydrophilic sedges, either through changes in abiotic conditions or through competition. This could also explain the decrease in average height in the warmed plots if, on the highest points within a plot, the tall graminoids are being replaced by smaller shrubs and bryophytes.

The graminoid and forb increase observed at the dry site is consistent with the meta-analysis by Arft et al. (1999) who found positive herbaceous responses in all four years of study. The later meta-analysis by Walker et al. (2006) also found graminoid increases at High Arctic sites. Both these papers were based on short term warming experiments (<7 years) and while other authors have found differ-
ences between short and long term responses (Chapin et al., 1995; Hollister et al., 2005), the graminoids here appear to have shown a consistently positive response to warming at dry and mesic sites.

One consistent change across all groups was a decrease in lichen cover. Lichen decline is a widespread observation in Arctic warming studies (Elmendorf et al., 2012a,b; Walker et al., 2006) and is likely due to increased shading by vascular plants (Cornelissen et al., 2001), or increased competition from bryophytes (Hudson and Henry, 2010). Lichen declines could be important as they have been shown to influence soil temperature, nitrogen fixation, moisture regimes and biogeochemical cycling (Longton, 1997). They also provide winter forage for Arctic herbivores.

Bryophytes showed a warming response at both the mesic and wet sites. This is inconsistent with many other reports which find bryophytes decrease under warming (Hollister et al., 2005; Walker et al., 2006). Hollister et al. (2005) state that an increase in graminoids was responsible for their observed decrease in bryophytes. In this study, both graminoids and bryophytes increased at the mesic site, likely due to the open nature of the vegetation. Bryophyte species tend to grow in warm and wet environments (Potter et al., 1995) so the increases observed here are likely due to OTCs increasing temperatures but not decreasing soil moisture.

Overall the evergreen shrubs showed small decreases and the deciduous shrubs small increases in OTC plots. The total abundance of shrubs at each site was approximately the same in control and warmed plots. Arft et al. (1999) found decreases in woody shrubs after four years of warming and suggested that the flexible morphology and greater storage reserves in herbaceous plants allowed them to respond to short-term warming. At this site it appears the herbaceous response has been sustained, and any negative short-term response of woody shrubs has not been maintained. A replacement of evergreen with deciduous shrubs could be due to an increase in nutrient levels under warming which would favour deciduous shrub growth (Chapin et al., 1996).

The use of NDVI showed mixed results at this site. It was not able to distinguish the small changes in TLH between control and warmed plots, however across all sites it
did show a positive relationship with TLH. This relationship had moderate residual error caused by the individual signatures of each plant community which suggests that caution should be used when applying NDVI at the landscape level. The plots and communities with greater abundances of deciduous shrubs and graminoids had the highest NDVI values and community specific signals are likely driven by these groups at this site. Arctic studies using NDVI to estimate biomass should consider the effect of different communities on the NDVI signal.

This chapter has shown that three plant communities along a soil moisture gradient are all responding to experimental warming, but not in the same ways. This has implications for future predictions in Arctic ecosystems because it shows that long-term responses will be community specific. Community specific responses to climate change will have important consequences for ecosystem functions such as albedo and CO$_2$ flux, as well as for habitat availability for large herbivores and birds.
Chapter 3

Net Ecosystem Exchange

3.1 Introduction

Carbon dioxide is an important contributor to radiative forcing (Forster et al., 2007) which is causing widespread environmental change (Walther et al., 2002), especially at high-latitudes (Post et al., 2009b; Serreze et al., 2000). The carbon cycle includes the fluxes of carbon between the atmosphere, the ocean, fossil carbon and the terrestrial biosphere (Schimel, 1995). Estimates of land-atmosphere fluxes suggest a net uptake of 0.2 PgC yr$^{-1}$ in the 1980s (with ocean-atmosphere uptake of 1.9 PgC yr$^{-1}$ and emissions of 5.4 PgC yr$^{-1}$) and 1.4 PgC yr$^{-1}$ in the 1990s (with ocean-atmosphere uptake of 1.7 PgC yr$^{-1}$ and emissions of 6.3 PgC yr$^{-1}$; Prentice et al., 2001). Most models predict the continuation of this terrestrial sink (Grant et al., 2011; McGuire et al., 2000; Qian et al., 2010; Sitch et al., 2007, 2003; White et al., 2000), except under the most extreme climate forcing scenarios where this sink becomes a net source in the 21st century (Scholze et al., 2006; Sitch et al., 2008). These models carry large uncertainties due to the biological complexities associated with terrestrial carbon flux and climate change response (Schimel, 1995; Sitch et al., 2008).

Arctic ecosystems have a strong role in the global climate system (Chapin et al.,
Four potential climate change feedbacks between the Arctic system and the global climate system are albedo, greenhouse gas fluxes in ecosystems, methane release from melting permafrost, and the effect of freshwater fluxes on thermohaline circulation (Callaghan et al., 2004c). All of these interactions are influenced in part by changes in ecosystem characteristics, especially large scale shifts in vegetation zones (Callaghan et al., 2004c). Most relevant for this chapter are the changes in greenhouse gas fluxes within ecosystems, specifically CO$_2$ flux.

Net ecosystem exchange (NEE) represents the balance between the respiratory losses of CO$_2$ from plants and soils (ecosystem respiration, $R_E$) and gross ecosystem photosynthesis (GEP, also known as gross ecosystem production):

$$NEE = GEP - R_E$$  \hspace{1cm} (3.1)

$$R_E = R_a + R_h$$  \hspace{1cm} (3.2)

where $R_a$ is autotrophic respiration from plants and $R_h$ is heterotrophic respiration from the soil. Increases in GEP can result from both increases in leaf area and increases in photosynthetic capacity. $R_E$ and GEP may be affected differently by warming and NEE is expected to be influenced by species composition as well as environmental conditions (Oberbauer et al., 2007).

Warming of the tundra biome is predicted to increase the rates of plant primary production and microbial respiration in soils. The balance of these two processes will affect feedbacks to atmospheric concentrations of CO$_2$ and methane (Shaver et al., 1992). If the increase in primary production is greater than that of respiration, CO$_2$ will be removed from the atmosphere and stored as terrestrial biomass. If the opposite occurs, CO$_2$ will be lost to the atmosphere. The future net carbon exchange will depend on the relative responses of photosynthesis and respiration to climate change. These responses are likely to be community specific due to differences in resource allocation (Chapin et al., 1995; Shaver et al., 1991), photosynthetic and respiration rates (Oberbauer et al., 2007) and environmental differences (Callaghan et al., 2004c). Soil moisture status is especially important in determining CO$_2$ flux status (Huemmrich et al., 2010). Some wet sites for example have lower respiration
levels due to soil anoxia (Oberbauer et al., 2007).

Long term studies in Alaska have shown ecosystems shifting from sinks to sources of CO$_2$ (Oechel et al., 1993), however these ecosystems also appear to have acclimatized to warming by reducing their net efflux of CO$_2$ (Oechel et al., 2000). Oberbauer et al. (2007) investigated CO$_2$ flux at different latitudes. They did not find any strong latitudinal trends, but did find that dry sites generally had stronger respiration responses than wet sites. All sites showed warming responses in respiration and photosynthesis but the direction and magnitude were ecosystem dependent. Data from Alexandra Fiord for example showed the dry and wet sites to be net sinks of CO$_2$ during the growing season, whereas the mesic site was a net source (Welker et al., 2004).

Terrestrial and climate change research in the Arctic require an improved understanding of how land-atmosphere interactions, and vegetation dynamics in general, vary across geographical space (Post et al., 2009b). This chapter will focus on the warming response of CO$_2$ flux in three Arctic plant communities along a soil moisture gradient. These functional results will be linked to the structural properties of each ecosystem in terms of vegetation abundance and growth form composition.

### 3.2 Methods

#### 3.2.1 Study site

The data were collected at an 8 km$^2$ lowland in Alexandra Fiord on Ellesmere Island (78°53′N, 75°55′W). Alexandra Fiord is a polar oasis with more developed vegetation than the surrounding polar desert. Vegetation extent at this site is limited by glaciers, upland plateaus, coastal water and glacial rivers. Soil moisture status is influenced by topography and fed by runoff from snow and ice melt.
3.2.2 Experimental design

Data were collected from three sites, each located in a different plant community along a soil moisture gradient. A dry site was located on a raised river bank and received the least runoff throughout the growing season due to low snow deposition and early snow melt. This community had a deep active layer, sandy soils, and was dominated by *Salix arctica*, *Dryas integrifolia* and *Saxifraga oppositifolia*. It was found throughout the lowland on river banks and raised slopes and represented approximately 4% of the land cover (Muc et al., 1989).

A mesic site was located on a flood plain and received variable levels of runoff. The vegetation at this site was in a transitional stage due to flood water damage in 2000. Previously the site was dominated by *Dryas integrifolia*, however flooding caused *Cassiope tetragona* and graminoids such as *Arctagrostis latifolia* to become more common. This community covered approximately 19% of the lowland (Muc et al., 1989).

A wet site was located on a seepage slope and was waterlogged throughout the growing season. Sandy substrate was found below a thick layer of litter and organic matter and vegetation was dominated by the sedge species *Eriophorum angustifolium triste*, *Carex membranacea* and *Carex aquatilis stans*. This community represented approximately 28% of the lowland plant cover (Muc et al., 1989).

The dry and mesic sites had four warmed and four control plots. The wet site had three warmed and three control plots. Warming was achieved passively using hexagonal open-top chambers (OTCs). These chambers were 1.5 m in diameter and simulated predicted climate warming by increasing surface air temperatures by 1 - 3°C during the growing season (Henry and Molau, 1997). These plots were installed in 1992 and treatments were randomly assigned within each site.
3.2.3 Data collection

CO₂ flux

Ecosystem-level CO₂ flux was measured using a portable photosynthesis system (Li 840, LiCor, Lincoln, Neb., USA) attached to a custom made transparent chamber (75 x 75 x 30 cm) as described by Welker et al. (2004). Each CO₂ plot contains a permanent metal collar (75 x 75 cm) installed in the ground to a depth of 15 cm creating a closed system when the chamber is attached. The LiCor instrument measures CO₂ parts per million (ppm) within the chamber. Data were recorded after letting the LiCor stabilize for a few seconds, then measurements were made for 2 minutes per plot to calculate the average rate of CO₂ change within the chamber. Linear regression was used to calculate the rate of NEE and \( R_E \) at each plot. The initial measurement represents NEE because the transparent chamber allows both photosynthetic and respiration processes to continue as normal. The chamber was removed, allowed to stabilize to atmospheric conditions, then \( R_E \) measurements were made with a black cover installed over the chamber to prevent photosynthesis. GEP was calculated as the difference between NEE and \( R_E \). Results are expressed from the ecosystem perspective (as per Boelman et al. 2005, 2003; Oberbauer et al. 2007; Shaver et al. 1998) in \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) of CO₂. Fluxes into the atmosphere are treated as negative and fluxes into the ecosystem as positive. For analysis purposes, \( R_E \) is given a positive sign in linear regression analyses.

Measurements were made on warm sunny days between 10:00 and 17:00, twice during the peak growing season (DOY 189 and 205). Incoming solar radiation never fell below 0.27 kWm² during these measuring periods. 0.27 kWm² is roughly equivalent to a photosynthetically active radiation (PAR) measurement of 1285 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) (these units are not directly comparable but can be roughly approximated). Other studies have found photosynthesis in Arctic vegetation to become light saturated at 600-800 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) (Alaska, Johnson et al. 2000) and 200-400 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) (Svalbard, Muraoka et al. 2002), it is therefore very likely that photosynthesis was light saturated for the measurements at this site.
Some field data were lost due to an electrical fault which prevented correct transfer of data between the LiCor and the storage module. Some plots were therefore missing data for NEE, $R_E$, or both. Data from DOY 189 and 205 were pooled to create peak season average NEE and $R_E$ values for each plot. This is justified as flux values were similar between these two sample periods. GEP values were calculated by subtracting the $R_E$ average from the NEE average for each plot. Some plots lost data at both peak season sample periods so sample size was reduced for some sites as shown in Table 3.1.

**Table 3.1: Sample sizes for CO$_2$ flux data after data loss.**

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>$n_{\text{netexchange}}$</th>
<th>$n_{\text{respiration}}$</th>
<th>$n_{\text{photosynthesis}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>Control</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Mesic</td>
<td>Control</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Wet</td>
<td>Control</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

**Point framing**

Data detailing vegetation structure was collected twice (between DOY 191-193 and between DOY 203-207) in the exact same plots where CO$_2$ flux was measured. Point-framing data were collected using 5625 cm$^2$ sampling grids with points 7.5 cm apart. Vegetation was surveyed within the metal collars used for the CO$_2$ measurements. Vegetation type was recorded to the species level (except for bryophytes and lichen) for all layers of the canopy. Above-ground vegetation biomass was estimated for each plot using the total number of live hits. Composition was analyzed in each plot by grouping species into 6 common growth form classes: deciduous shrubs, evergreen shrubs, graminoids, forbs, bryophytes and lichen.
3.2.4 Statistical analysis

CO₂ Flux

Fixed effects 2-way ANOVA was used to test for interactions and differences in CO₂ components (NEE, ER, GEP) between different sites and treatments. Significant 2-way ANOVAs were further investigated using one-way ANOVAs and Tukey tests. One-way ANOVAs were also used to test for site differences for each treatment individually however low sample size limited the power of this analysis. Transformations were used when ANOVA assumptions were not met. Differences between GEP and ER were tested with t-tests at each site to investigate the significance of carbon storage. Treatments were combined to increase power and transformations or non-parametric tests were used when assumptions were violated. Simple linear regression was used to analyze the relationship between GEP and ER across all sites and treatments.

Relationship to structure

Average TLH were calculated for each site and treatment, and TLH were divided between six growth form groups for visual analysis. Community composition was analyzed using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) and nonmetric multidimensional scaling (NMDS; Kruskal 1964). The Bray-Curtis method was used to calculate dissimilarities and a 95% confidence interval was drawn around the centroid of each ordination class.

Linear regression was used to look for relationships between flux components and vegetation structure. Regressions were done between flux components and TLH to see if there was a direct relationship between CO₂ flux and above-ground biomass. Regressions were then used to look for specific growth form categories that could be influencing flux values. This was done using the live hits of each vascular plant growth form in each plot. Live hit averages were calculated using the same peak season averaging method as the corresponding CO₂ flux data. Finally, peak season NDVI was regressed against flux components to see if NDVI could be used as a
predictor of CO$_2$ flux. All data analysis and graphing was done using R version 2.12.2.

3.3 Results

3.3.1 CO$_2$ flux

There were site specific differences in all components of CO$_2$ flux (Figure 3.1). The mesic site had significantly lower values than the dry or wet sites for NEE (2-way ANOVA, Site $F_{13,2} = 6.86, p = 0.009$) and GEP (2-way ANOVA, Site $F_{10,2} = 8.60, p = 0.007$). When GEP was analyzed by treatment the dry site had significantly greater values in the control plots than either the mesic or wet sites (ANOVA, $F_{6,2} = 9.79, p = 0.01$). In the warmed plots all sites had significantly different GEP with the dry site having the highest values and the mesic site the lowest (ANOVA, $F_{4,2} = 11.19, p = 0.02$). R$_E$ was greater at the dry site than at the mesic or wet sites, this result was close to significance (2-way ANOVA, Site $F_{13,2} = 3.39, p = 0.065$). Flux values and standard errors can be viewed in numerical form in Appendix A.1.

When testing for treatment effects across all sites, the warmed and control plot values were significantly different for GEP (2-way ANOVA, Treatment $F_{10,1} = 17.82, p = 0.002$), and close to significance for R$_E$ (2-way ANOVA, Treatment $F_{13,1} = 4.01, p = 0.066$). NEE did not show a significant warming response across sites due to low sample size and the lack of response at the mesic site. However when the dry and wet sites were combined, the difference between control and warmed values approached significance (Wilcoxon, $p = 0.07$). A significant interaction term for the GEP model (2-way ANOVA, Site: Treatment $F_{10,2} = 4.66, p = 0.04$) indicated that sites were not all responding to warming in the same way. The mesic site showed no change in GEP as a result of warming whereas the dry and wet sites both showed GEP increases.

Site GEP was significantly greater than R$_E$ in all cases (Dry site t-test, $t_{11} = 6.92, p<0.001$; Mesic site t-test, $t_{10} = 5.61, p<0.001$; Wet site Wilcoxon, $p = 0.008$) showing that all sites were significant sinks for CO$_2$ at peak season. GEP and R$_E$
showed strong correlation ($R^2 = 0.72$) and GEP values were at least double $R_E$ in most plots (Figure 3.2).

### 3.3.2 Relationship to structure

Structural data trends were consistent across the first and second sample periods so only structural data from the second sample period is being reported. Sample sizes are low for these analyses which limits power in significance tests.

Biomass estimates were similar between sites and the only site showing a warming response was the wet site (Figure 3.3). Control plots at the wet site had an average TLH count of 110.0 ± 1 and warmed plots an average of 148.7 ± 9.6 (mean ± one standard error). Growth form composition shifted in the dry and wet sites, but not at the mesic site (Figure 3.4). The dry site showed significant community shifts (PERMANOVA, $F_{6,1} = 5.30$, $R^2 = 0.47$, $p = 0.047$) with increased numbers of graminoids, deciduous shrubs and bryophytes, and decreases in lichens and evergreen shrubs (Figure 3.5, NMDS, stress = 0.024, $k = 2$, nonmetric $R^2 = 1.00$, linear $R^2 = 0.99$). NMDS at the mesic site showed no shift in composition under warming (Figure 3.6, NMDS, stress = 0.010, $k = 2$, nonmetric $R^2 = 1.00$, linear $R^2 = 1.00$) and no significant changes in PERMANOVA analysis (PERMANOVA, $F_{6,1} = 0.24$, $R^2 = 0.04$, $p = 0.892$). The community at the wet site shifted towards deciduous shrubs and bryophytes (Figure 3.7, NMDS, stress = 0.004, $k = 2$, nonmetric $R^2 = 1.00$, linear $R^2 = 1.00$). PERMANOVA analysis at the wet site did not show a significant difference ($F_{4,1} = 4.80$, $R^2 = 0.55$, $p = 0.086$) between treatments due to low sample size, but the NMDS results were supported by the raw data which showed increases in the counts of deciduous shrubs and bryophytes under warmed conditions (Figure 3.4). Graminoids also increased from 90.0 ± 4.2 in control plots to 121.3 ± 9.0 in warmed plots and it was still graminoids which dominated this site under warmed conditions. NMDS did not identify composition as shifting towards graminoids due the the high numbers of this group across all plots.

No direct relationship existed between TLH and components of CO$_2$ flux. When
Figure 3.1: Peak season CO$_2$ flux values averaged by site and treatment. Error bars represent one standard error. NEE = net ecosystem exchange; GEP = gross ecosystem photosynthesis; ER = ecosystem respiration. C = control; W = warmed. Table 3.1 shows the sample size for each site and treatment.
Figure 3.2: Relationship between $R_E$ and GEP across all sites and treatments. Each point represents a single plot at the peak of the growing season. $R^2 = 0.72$. Regression equation: $\text{GEP} = 0.44 + 2.5 \times R_E$
analyzed at the growth form level however, some patterns emerged. The abundance of deciduous shrubs was correlated with all three components of CO$_2$ flux. When analyzed across all sites the abundance of deciduous shrubs showed significant positive relationships with NEE (Regression, $R^2 = 0.29$, coefficient = 0.03, $F_{1,7} = 7.00$, $p = 0.02$), GEP ($R^2 = 0.47$, coefficient = 0.05, $F_{1,4} = 12.55$, $p = 0.003$), and $R_E$ ($R^2 = 0.49$, coefficient = 0.02, $F_{1,7} = 16.53$, $p<0.001$). These relationships were noisy due to residual error caused by plots that had few or no deciduous shrubs but high flux values (Figure 3.8). When analyzed at the dry site alone, where all plots had some deciduous shrubs, the relationship was stronger (Regression NEE,
Figure 3.4: Total live hits divided between growth forms for three sites and two treatments in the CO₂ plots. C = control plots, W = warmed plots. Each bar segment represents the average number of hits for a given growth form. Segments at the dry and mesic sites are averages of four plots, segments at the wet site are averages of 3 plots.
Figure 3.5: NMDS of four control and four warmed plots at the dry site (stress = 0.024, k = 2, nonmetric $R^2 = 1.00$, linear $R^2 = 0.99$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
Figure 3.6: NMDS of four control and four warmed plots at the mesic site (stress = 0.01, $k = 2$, nonmetric $R^2 = 1.00$, linear $R^2 = 1.00$). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
Figure 3.7: NMDS of three control and three warmed plots at the wet site (stress = 0.004, \(k = 2\), nonmetric \(R^2 = 1.00\), linear \(R^2 = 1.00\)). Each point is an individual plot. Ordination used TLH data grouped by growth form and the Bray-Curtis dissimilarity procedure. Ellipses represent 95% confidence intervals around the centroid of each ordination class.
$R^2 = 0.65$, coefficient = 0.05, $F_5 = 9.20$, $p = 0.03$; GEP, $R^2 = 0.86$, coefficient = 0.07, $F_4 = 25.06$, $p = 0.007$; $R_E$, $R^2 = 0.38$, coefficient = 0.01, $F_3 = 3.01$, $p = 0.14$), although p-values were higher due to low sample sizes. Other significant, but weak relationships across all sites were a negative relationship between graminoids and $R_E$ (Regression, $R^2 = 0.25$, coefficient = -0.01, $F_{17} = 5.66$, $p = 0.03$), and a positive relationship between forbs and NEE (Regression, $R^2 = 0.27$, coefficient = 0.14, $F_{17} = 6.19$, $p = 0.02$). Bryophytes showed a negative relationship with NEE ($R^2 = 0.54$, coefficient = -0.6, $F_{17} = 19.99$, $p < 0.001$), GEP ($R^2 = 0.53$, coefficient = -0.10, $F_{14} = 15.93$, $p = 0.001$), and $R_E$ ($R^2 = 0.28$, coefficient = -0.02, $F_{17} = 6.53$, $p = 0.02$); and across all sites bryophytes showed negative correlation with deciduous shrubs ($R^2 = 0.17$, coefficient = -0.50, $F_{58} = 11.99$, $p = 0.001$). It could be that bryophytes were less abundant in the plots that had high flux values because they were replaced in these plots by deciduous shrubs which contributed more to CO$_2$ flux.

NDVI had a significant relationship with all flux components across all sites (Figure 3.9). This relationship was largely explained by the fact that NDVI and CO$_2$ were both influenced by deciduous shrub abundance. For NEE the relationship had a slope of 49.04 (Regression, $R^2 = 0.41$, $F_{15} = 10.53$, $p = 0.005$), for GEP a slope of 78.90 (Regression, $R^2 = 0.51$, $F_{13} = 13.65$, $p = 0.003$), and for $R_E$ a slope of 23.45 (Regression, $R^2 = 0.44$, $F_{16} = 12.69$, $p = 0.003$). Slopes were steep due to the narrow range of NDVI values at this study site (0.60 - 0.67).

### 3.4 Discussion

Each site had a unique set of flux values and warming response was community specific. All three sites acted as CO$_2$ sinks at the peak of the growing season. NEE in the OTC plots was an average 29% higher than controls at the dry site and 46% higher at the wet site. The mesic site was an average 27% lower in warmed plots than controls. Warmed plots had higher GEP and $R_E$ at the dry and wet sites but GEP showed a stronger response in both cases. The mesic site showed minimal warming response with no change in $R_E$ and a slightly lower GEP under warmed conditions. Alaskan studies have reported limited $R_E$ response at wet sites due to soil anoxia (Oberbauer et al., 2007), this does not appear to be the case here as the
Figure 3.8: Relationship between components of CO₂ flux and the abundance of deciduous shrubs. Plotted for all sites combined and for the dry site individually. Each point represents the peak season average of a single plot. R²: A = 0.29, B = 0.65, C = 0.47, D = 0.86, E = 0.49, F = 0.38.
Figure 3.9: Relationship between components of CO$_2$ flux and NDVI across all sites. Each point represents the peak season averages of a single plot. $R^2$: A = 0.41 , B = 0.51 , C = 0.44.
wet and dry sites showed similar R\textsubscript{E} responses at peak season.

These findings partly agree with previous measurements from this site which found the dry site to be the largest sink at peak season (Oberbauer et al., 2007; Welker et al., 2004). The wet site however shows different results; in the previous study OTCs decreased NEE because respiration responded to warming and GEP did not. In this study the wet site NEE increased due to a strong GEP response.

The observed CO\textsubscript{2} fluxes are largely explained by the point frame data. Rather than being influenced by the total amount of above-ground vegetation, CO\textsubscript{2} flux was dependant on the relative abundances of certain growth form groups at each site. The lack of response at the mesic site was due to minimal changes in community composition. CO\textsubscript{2} flux response at the dry and wet sites appear to be linked to the abundance of deciduous shrubs and to a lesser extent graminoids. The higher rates of GEP in OTCs at the dry site is likely due to the warmed plots having 64\% more deciduous shrubs than the controls. Likewise, the GEP increase at the wet site corresponds to the appearance of deciduous shrubs at this site as well as a additional 35\% of graminoids in the warmed plots. The wet site was the only site to show a large increase in total biomass but this increase was almost entirely due to graminoid and deciduous shrub increase. The only deciduous shrub recorded throughout these sites was \textit{Salix arctica}. This woody, prostrate species has relatively large green leaves and forms mats approximately 10 cm tall. It has been shown to influence NEE in other areas by increasing LAI and GEP (Steltzer et al., 2008). Although bryophytes increased in all plots under warmed conditions, they were more abundant in the plots with lower flux activity. The negative relationship with deciduous shrubs suggests that bryophytes are being reduced in areas where shrubs are increasing. Although bryophytes may be contributing to CO\textsubscript{2} flux, they are not an important driver at this site.

If the CO\textsubscript{2} sinks observed at peak season are maintained throughout the growing season (as suggested by Welker et al., 2004 for the dry and wet ecosystems), and if the warmed plots are consistently stronger sinks than the controls, we may expect to see greater biomass accumulation in plots experiencing warming. Warmed plots at the wet site do have higher levels of above-ground vegetation but the dry and
mesic sites show little change. It is not possible to track the fate of CO$_2$ influx with a single year of data but it is possible to compare control and warmed plots. At the dry site for example, both treatments have similar amounts of above-ground biomass but the warmed plots have much higher CO$_2$ influx suggesting a higher photosynthetic capacity per unit biomass. The higher proportion of *Salix arctica* in the warmed plots and the apparently higher photosynthetic capacity of this species increases the amount of CO$_2$ absorbed which increases NEE. Different species and growth forms have different photosynthetic capacities and will allocate resources differently so the amount of CO$_2$ influx and the relationship between influx and new biomass will not be consistent across ecosystems (Maessen et al., 1983). The allocation of resources to different phenological stages and to vegetative tissue versus reproduction may also differ between species (Suzuki and Kudo, 2005). Additionally, growth may be limited by nutrient availability which could constrain climate change response (Callaghan et al., 2004a).

Not all accumulated biomass is detectable using the point-intercept technique. The woody biomass stored in shrubs for example can only be accurately estimated by harvesting which is not possible in long-term study plots. The point-intercept method tends to underestimate woody biomass because the woody sections of shrubs such as *Salix arctica* have high biomass content but low proportional cover relative to leaves. It is likely that woody biomass is higher in the plots with high shrub abundance. This, along with differences in below ground biomass accumulation, could partly account for insignificant biomass differences between warmed and control plots at the dry site. It is also important to note that these results are exclusive to the peak of the growing season and the seasonal CO$_2$ budget at each site could be a better indicator of above-ground biomass accumulation. Flux rates (especially GEP) differ throughout the season (Welker et al., 2004) so the sites studied here may not be such strong sinks for the entire growing season.

There was evidence to suggest significant relationships between NDVI and all components of CO$_2$ flux when data were pooled across sites and treatments. This was expected for GEP given that GEP is the rate of photosynthetic activity and NDVI is a proxy for LAI and therefore photosynthetic potential (Gitelson and Merzylak, 1996). The correlation with NEE was also reasonable given that GEP values are
higher than $R_E$ at this site, and show a stronger warming response. The only surprising result was the correlation between NDVI and $R_E$. This relationship has also been observed in Alaska by Boelman et al. (2003) who suggest it could be due to: 1) a fixed amount of all photosynthates per day going towards growth respiration (Waring et al., 1998); 2) total plant biomass accounting for the majority of $R_E$ at peak season (Johnson et al., 2000); or 3) increased biomass producing more litter and potentially more labile carbon substrates for soil microbes, leading to higher microbial respiration. The present results do not allow investigation into these or other hypotheses as autotrophic and heterotrophic respiration cannot be differentiated. Nevertheless there is evidence to suggest that NDVI could be a useful predictor for CO$_2$ flux at this site. In order to integrate this relationship into larger scale predictions, NDVI-flux relationships would be needed from each major plant community at the site. This is not possible with the current data as sample sizes are not large enough to establish a reliable relationship.

This chapter has shown that peak season CO$_2$ flux and warming response at this site is community specific. Warming increased NEE in two of the communities, if this increase applies to similar communities across the High Arctic there could be implications for the regional carbon budget and for feedbacks to local and regional changes in climate. The changes observed at this site can be explained in part by changes in the abundances of specific growth forms. The deciduous shrub Salix arctica appears to be an important determinant of CO$_2$ flux. Extrapolation of the community specific results seen here would allow broader scale patterns to be investigated, this would first require an accurate relationship to be established between NDVI and CO$_2$ flux at each site.
Chapter 4

Landscape

4.1 Introduction

Climate change response shows high levels of heterogeneity across the Arctic (Elmendorf et al., 2012a,b; Post et al., 2009b; Walker et al., 2006). Some regions have shown dramatic changes whereas others have remained the same. This can partly be attributed to variation in climatic conditions, but variation in climate change response can also be expected within climatically homogenous areas (Post et al., 2009a). Ecosystem structure and function can vary within a region due to abiotic factors such as topography (Shaver et al., 1996) and soil moisture (Muc et al., 1989). We can expect climate change response to vary across the landscape because different ecosystems will respond in different ways to abiotic change. An increase in soil moisture across an area for example, could cause a large change to dry ecosystems but a minimal change in wetter ones.

The results of ecological studies depend on the temporal and spatial scales being used (Ludwig et al., 2000). The distribution and abundance of species for example can show different patterns when analyzed at different scales (Wiens et al., 1985). Understanding how patterns differ with scale has implications if data are to be extrapolated through time or space, or used to make predictions and influ-
ence management. The ability to map environmental variables allows small scale findings to be linked to the wider landscape. This can reveal patterns of structure and function which may not have been apparent at finer scales. Models using NDVI have been created with varying success. Some studies have found NDVI alone to be insufficient to estimate CO$_2$ flux response to climate change (La Puma et al., 2007). Other simple models incorporating temperature and photon flux density have found NDVI to be a good predictor of CO$_2$ flux, even in the absence of community specific NDVI signatures (Shaver et al., 2007). Studies combining fine and coarse scale data offer the potential to develop upscaling techniques so that ecosystem processes measured in the field can be transferred onto readily available satellite data (Williams et al., 2008).

Site specific studies such as the ITEX approach provide a detailed understanding of how specific species and communities will respond to climate change, and broad scale mapping projects such as the circumpolar vegetation map (Walker et al., 2005) offer the potential for biome-wide inventories. An important step to link these two approaches lies at the landscape scale where site specific results are up-scaled to the smallest resolvable scale in regional models or global observation systems (Williams et al., 2008). This provides a detailed account of ecosystem properties across the landscape which is especially important in the Arctic given the high levels of heterogeneity in plant communities, ecosystem functions and climate change response. A single, global model is insufficient to make large scale predictions in the Arctic and community and landscape scale information is crucial if models are to be accurate.

Three tools useful for the spatial analysis of environmental and ecological data are geographic information systems (GIS), spatial interpolation, and local regression techniques. GIS is a software tool which allows the management, display and analysis of spatial data. It is used across many geographic disciplines and is becoming increasingly powerful and popular in ecology and biogeography. Interpolation is a method that is used in conjunction with GIS to create continuous maps from a series of points. This reduces the amount of data that need to be collected, provided data quality and quantity is high enough to create accurate interpolation surfaces. These spatial tools are particularly useful for visualizing environmental and biotic
variables which are known to have high variability through space. Analysis of these variables using traditional statistical techniques would apply global models across the entire spatial extent of data. Local regression techniques such as geographically weighted regression (GWR) allow relationships and trends to be investigated within the spatial extent of data, so that local relationships can vary throughout the dataset. This is useful in Arctic ecosystems where variables of interest can have steep gradients, and processes and interactions may show significant change throughout a region of study.

At Alexandra Fiord a large amount of data have been gathered in individual communities, but less work has been done across the entire lowland. Landscape maps of the peak season growing conditions at this site could be an important first step towards extrapolating site level findings to the wider area, especially given that plant processes in the High Arctic are largely controlled by environmental conditions (Chapin, 1987). Muc et al. (1989) produced a community map of the lowland and suggested that plant community type is largely determined by soil moisture status. Mapping the variation in soil moisture could therefore be an important step toward understanding plant processes across the lowland.

This chapter reports results of an environmental mapping technique using field sampling and spatial interpolation. Maps are produced for a small number of easily monitored variables during the peak of the growing season. Maps are then used to investigate variable distribution and quantify heterogeneity. The raw sample data are also used to identify correlations between variables and to see if simple environmental data can be used to predict NDVI values across the lowland. This allows identification of environmental factors that influence NDVI and therefore ecosystem structure and function.
4.2 Methods

4.2.1 Study site

The Alexandra Fiord lowland is a polar oasis on the east coast of Ellesmere Island in Nunavut, Canada (78°53’N, 75°55’W). The site is an 8 km² periglacial outwash plain with a gentle upward slope from north to south. The north of the site is bordered by the waters of Alexandra Fiord. To the east and west are steep cliffs rising to upland plateaus. At the south of the lowland are glacial tongues from the Prince of Wales ice cap. Vegetation covers 90% of the lowland (Muc et al., 1989) and has greater continuity in the north of the site. Vegetation is sparse in the southern, moraine covered areas closer to the glacier. Annual precipitation is low and water regimes are primarily driven by melting snow and ice. Two rivers and a number of creeks and streams run from the glaciers and feed into the fiord. Soil moisture varies spatially due to topography, the drainage properties of the soil, and vegetation cover. Soils are immature and poorly developed but have relatively thick organic layers in comparison to surrounding areas (Muc et al., 1994).

4.2.2 Sample design

A systematic sampling method was used to collect data across the entire lowland. Weaknesses of this method are that patches smaller than the sampling distance can be underrepresented, and points are often said to be non-independent which can limit the use of inferential statistics. Systematic sampling has been shown to be the most effective method at this site (Bean, 2002) and is logistically the most appropriate method in this case. Two sampling grids were used for data collection, one for temperature sensor locations and one for the collection of other environmental variables. The distance between sampling grid points was determined by the time available to collect the data and the logistics of installing and collecting data from temperature sensors. Temperature sensors were installed at 27 locations using an evenly spaced grid with approximately 530 m between points (Figure 4.1). If a point fell in a river or could not be installed it was moved to the nearest appropriate
location. A second grid was laid over the temperature grid for the collection of elevation, soil moisture and NDVI data. This grid contained 180 points approximately 180 m apart. Some NDVI data were not suitable for analysis so only 171 points had NDVI information. These 171 points were used to create the NDVI map and to carry out the regression analysis (Figure 4.1). Maps for other environmental variables were created using the original 180 points. Sampling grids were made using global positioning system (GPS) software (MobileMapper Office, Magellan, Santa Clara, CA, USA). Sampling locations were identified in the field to the nearest metre using a handheld GPS (Magellan, Santa Clara, CA, USA) and marked with a 1m² quadrat. Each point was then accurately recorded using a differential global positioning system (DGPS; ProMark 3, Magellan, Santa Clara, CA, USA). Data were later entered into ARCGIS v.10 for analysis.
4.2.3 Data collection

Temperature

Air temperature was measured every 5 minutes for most of the snow-free growing season (DOY 179 to 226) using HOBO pendant temperature sensors (Onset, Bourne, MA, USA). Sensors were mounted 10 cm above the ground and shaded from direct sunlight.

Elevation

Elevation was recorded using a DGPS unit (ProMark 3, Magellan, Santa Clara, CA, USA). The DGPS combined a fixed beacon with a portable receiver to calculate location and elevation. An error calculated from the fixed unit is used in post-processing to correct the data collected by the roaming unit. This system can produce elevation measurements accurate to less than 10 cm.

Soil moisture

Soil moisture was recorded at each point using a portable soil moisture probe (CS620 HydroSense unit, Campbell Scientific, Edmonton, AB, Canada). This system records the percentage of volumetric water content in the soil and is accurate to 3%. At each sample point 5 moisture readings were recorded, one in each corner of the quadrat and one in the centre. The average of these was used as the soil moisture value for that point. Soil moisture was recorded between days 211 - 214. No precipitation fell during data collection. Weather for the preceding week was bright with scattered clouds and no precipitation. The majority of the study site had been snow free for at least 40 days before data were collected.
NDVI

NDVI data were collected at the peak of the growing season between days 211-214 using a field portable spectrometer (Tetracam ADC, Chatsworth, CA, USA). The camera was calibrated using a standard white surface to normalize for changes in light conditions. Images were collected from each point using a 1x1 m quadrat. Images were processed using Tetracam’s PixelWrench 2.0 software and the vegetation within each quadrat was used to calculate NDVI values. Non-vegetated areas were masked out of each image before NDVI was calculated. Nine NDVI images were not suitable for analysis and discarded, leaving 171 sample points with NDVI data.

4.2.4 Statistical analysis

Exploratory data analysis

Prior to interpolation or spatial analysis, an exploratory analysis of each variable was conducted. Histograms were used to display skewness and kurtosis (the normal distribution has a skewness value of zero and kurtosis of three). Normality was checked using QQ-plots. Trend analysis and Voronoi maps were used to highlight any potential patterns or trends in the data.

Variance

Spatial analysis requires characterization of variance across the region of study. This allows any spatial autocorrelation to be identified. Spatial autocorrelation exists if points closer in geographic space have more similar values than points farther apart. Strong spatial autocorrelation suggests that similar values are clustered, whereas negative autocorrelation suggests that neighbouring values have greater dissimilarity than would be expected by chance. Three functions were used to display spatial autocorrelation: the semivariogram, covariance, and the correlogram. These functions calculate a measure of similarity for two points and plot it against
the distance between them. Semivariograms use the squared difference between two points, and covariance multiplies the differences between each point’s value and the mean. Rossi et al. (1992) suggest that variograms are sensitive to outliers and recommend using them alongside correlograms such as Moran’s I. Moran’s I is a statistical test used to determine the degree of clustering in a dataset with values close to +1 being clustered, values around zero being random, and values close to -1 being dispersed.

**Interpolation**

Interpolation techniques allow the construction of a continuous surface of data points from a sample of measured data. The interpolation technique used depends on the characteristics of the data and the time available for analysis. Techniques considered here were inverse distance weighting, second order polynomials, and ordinary kriging. A range of ordinary kriging models were tested using different parameters for the semivariogram model type, the search radius shape, and the size of the search radius. For each variable a series of models were created and tested against each other. Models were tested by removing a point (observed) and predicting the value at this location using the remaining points (predicted). The model selected was the one with the smallest error between predicted and observed points. All the selected models used ordinary kriging. All models had standardized prediction errors close to zero indicating unbiased data.

Kriging is an interpolation technique that uses a semivariogram to characterize the datasets variance and assign weights to interpolated points. Semivariograms are defined by lag number and lag size. Lags create bins for averaging semivariance values and thus influence the shape of the semivariogram. Semivariograms for the temperature data had 5 lags of 526 metres, and for the remaining variables had 11 lags of 171 metres. Interpolation parameters for each variable are shown in table 4.1. Since temperature data had fewer sample points that the other variables, temperature was resampled after interpolation so that data were available at the same survey points as the other variables. This was necessary for regression analysis. The temperature sample size of 27 makes semivariogram analysis weak and there-
fore limits the power of interpolation. Most authors suggest 30 as the minimum sample size to create a meaningful variogram (Rossi et al., 1992).

Table 4.1: Interpolation parameters for each variables final interpolation model. T=temperature.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Semivariogram model</th>
<th>Search radius (m)</th>
<th>Number of points</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean T</td>
<td>Spherical</td>
<td>1250</td>
<td>27</td>
</tr>
<tr>
<td>Max T</td>
<td>Stable</td>
<td>1250</td>
<td>27</td>
</tr>
<tr>
<td>Min T</td>
<td>Spherical</td>
<td>1250</td>
<td>27</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>Gaussian</td>
<td>500</td>
<td>180</td>
</tr>
<tr>
<td>Elevation</td>
<td>Gaussian</td>
<td>500</td>
<td>180</td>
</tr>
<tr>
<td>NDVI</td>
<td>Gaussian</td>
<td>360</td>
<td>171</td>
</tr>
</tbody>
</table>

Regression

Two regression techniques were used to test if the environmental variables measured could be used to predict NDVI. Data were used from the 171 sample points with NDVI data. Regressions used values from the original survey points and the resampled temperature data. First, ordinary least squares (OLS) regression was used to create a global model. This model used NDVI as the response variable and maximum temperature, mean temperature, minimum temperature, soil moisture and elevation as explanatory variables. We would expect variables to show some degree of spatial autocorrelation, in which case the assumption of independence required for OLS would be violated and the global model would fail to identify local variation in model parameters. A second, localized regression method was used which deals with autocorrelation and allows the regression parameters to vary through space. This method is called geographically weighted regression (GWR). It uses a search radius to create a range of localized regressions which can be visualized using GIS.

GWR does not perform well if variables are locally or globally correlated, or if a variable has clusters of similar values. For these reasons elevation and maximum temperature were removed from the model as they both correlated with mean
temperature. Mean temperature and minimum temperature values were squared to minimize clustering of similar values. OLS was repeated using the same variables as the GWR model to allow model comparison. Moran’s I analysis was done on the residuals of each model. If residuals are clustered, it is likely that important variables are missing from the model.

All variables were also regressed against NDVI individually using both OLS and GWR. This allowed identification of any variable whose relationship with NDVI could be improved using local regression methods. Finally, environmental variables were regressed against each other using both OLS and GWR to identify any environmental relationships.

4.3 Results

4.3.1 Elevation

Elevation data did not follow a normal distribution due to a skewed platykurtic histogram (Skewness=0.40, Kurtosis=2.14). Platykurtic distributions have shallow tails and more values around the mean. Ordinary kriging does not require data to be normally distributed. Trend analysis and Veronoi diagrams showed that elevation increased from north to south and elevation was most variable on the east and west edges of the lowland where slopes were steep. Moran’s I test showed that the data were clustered and therefore spatially autocorrelated (Moran’s index=0.80, p<0.001). For most datasets showing spatial autocorrelation we would expect the semivariogram model to level off after a certain distance. The point where the model levels off indicates the distance above which autocorrelation is no longer present. The biggest differences in this dataset were between the most northern and most southern areas of the site, which explains why the semivariogram showed a continuous increase (Figure 4.2), and the covariance a continuous decrease with increasing distance between points.

The interpolated map showed that elevation increased gradually from sea-level in the north to over 100 m at the glacier in the south (Figure 4.3). The map also
detailed an upland area in the west of the site. This feature is a raised, vegetated plateau separated from the true lowland by rocky outcrops. The cliffs marking the edge of the lowland rise immediately upward from the western most edge of this plateau. The cliffs marking the eastern edge of the site are un-vegetated and scree covered; they were not captured by this elevation model. The root mean squared error (RMSE) for this interpolation was 2.97 m showing that the model did a relatively good job of predicting the measured points.

### 4.3.2 Temperature

Mean, maximum and minimum temperatures showed similar patterns throughout the growing season when averaged across the entire lowland (Figure 4.4). Temperatures were higher at the start of the growing season and decreased through the month of July. The difference between maximum and minimum temperature
Figure 4.3: Interpolated map of elevation. Created using 180 data points and Ordinary Kriging.
was greatest on the warmest days. The highest daily average air temperature was 18.2°C on DOY 187 and the lowest was 3.6°C on DOY 218.

**Mean temperature**

The histogram for mean temperature was skewed towards higher values (Skewness=-0.47, Kurtosis=2.81) but showed an approximately normal distribution. Trend analysis showed an increase in temperature from north to south. Covariance decreased with increasing distance between points and Moran’s I showed significant autocorrelation indicating that the data were clustered (Moran’s index=0.46, $p<0.001$). The semivariogram (Figure 4.5) showed increasing differences with distance. The two areas farthest apart, the north-west and south-east of the site, showed the largest differences in temperature which explain why the semivari-
The interpolated map (Figure 4.6) showed that average temperatures increased from the north-west corner of the lowland to the south-east. The highest temperatures were found towards the glacier at the south of the site. There were also pockets of higher temperatures in the central and western sections of the site. Temperatures were lowest in the northwest of the site along the coastline. Temperatures were not only higher, but were also more variable in the southern half of the site (Figure 4.7). The RMSE of 0.49°C suggests that the model was successful in predicting the measured points.

**Minimum temperature**

The histogram for minimum temperature was slightly platykurtic but showed minimal skew (Skewness=0.11, Kurtosis=2.75). The data followed a normal distribu-
Figure 4.6: Interpolated map of mean July temperature. Created using 27 data points and Ordinary Kriging.
Figure 4.7: Boxplots showing variation in July temperature at 27 locations ordered by mean temperature. Boxplots show median, 1st and 3rd quartiles, potential outliers (open circles) and means (red circle). Temperature sensor codes correspond to locations shown in Figure 4.1 larger numbers are farther south.
Figure 4.8: Semivariogram for minimum temperature. X = distance, Y = difference; red dots = differences binned by distance and direction, blue crosses = differences averaged in five lags, line = fitted spherical model.

 Moran’s I analysis showed a random distribution of values and no spatial autocorrelation (Moran’s index=0.04, $p = 0.4$). This was likely due to the small amount of variation across the study region. The biggest differences were found between the east and west side of the site. The north and south ends showed small differences which explain why the raw data in the semivariogram decreased at the greatest distances (Figure 4.8).

The interpolated map showed that minimum temperatures were highest in the west, and lowest in the east (Figure 4.9), however the range in minimum temperatures calculated from the raw sensor data was only 1.5°C. The RMSE was 0.40°C so the model predicted the measured points well, but not as well as the mean model given the range of data values.
Figure 4.9: Interpolated map of minimum July temperature. Created using 27 data points and Ordinary Kriging.
Maximum temperature

Maximum temperature data showed a slightly platykurtic histogram but little skew (Skewness=-0.14, Kurtosis=2.8). The data were approximately normal and maximum temperatures increased from north to south, and from east to west in the central region of the lowland. The semivariogram and covariance showed similar trends to the mean temperature data (Figure 4.10). The biggest difference was between the areas farthest apart (north-west and south). This explains why the semivariogram did not level off as would be expected for autocorrelated data. Moran’s I showed significant autocorrelation (Moran’s index=0.39, \( p < 0.001 \)). The interpolated map showed that maximum temperature was lowest along the coastal areas in the north of the site, and greatest on the raised plateau in the west and in the southern area close to the glacier (Figure 4.11). This model had the highest RMSE of the three temperature maps (1.41°C) but still did a good job of predicting the measured points. Maximum temperature appeared to influence the mean to a greater extent than the minimum temperature. Maximum and mean temperature had similar distributions (Figures 4.6 and 4.11) and boxplots for all sensors were weighted towards lower temperatures suggesting that a relatively low number of high temperature events were increasing the mean (means were greater than medians in all cases; Figure 4.7).

4.3.3 Soil moisture

The distribution of soil moisture data was slightly leptokurtic (more extreme values) and skewed to the left (Skewness=0.90, Kurtosis=3.30). There was a general trend of increasing moisture from west to east and data did not closely follow the normal distribution. There were three patches with high soil moisture, one in the north-west, one in the north-east, and one in the central section to the east of the large river. Voronoi diagrams showed that the highest variation in soil moisture was around these three patches due to the rapid transitions from wetter to drier soil. These patches can be seen in the interpolated map (Figure 4.12) and were likely caused by a combination of local and surrounding topography, permafrost regimes and patterns of runoff. The patch in the north-west for example was in a relatively
flat area which is surrounded by steep slopes and receives large amounts of snow runoff. The data were spatially autocorrelated (Moran’s index=0.22, \( p < 0.001 \)) and the semivariogram model showed an initial increase in difference which leveled off at greater distances (Figure 4.13). The soil moisture interpolation had one of the highest error values (RMSE=18.52%), likely due to the high variability in values which make interpolation of unknown points difficult.

4.3.4 NDVI

This dataset was skewed to the right and was leptokurtic due to a high number of larger NDVI values (Skewness=-1.19, Kurtosis=6.41). The distribution was normal and there were no clear trends or patterns in the raw data. The semivariogram increased and levelled off at a distance of 500 m (Figure 4.14), autocorrelation was significant (Moran’s index=0.12, \( p = 0.004 \)). The interpolated map showed that
Figure 4.11: Interpolated map of maximum July temperature. Created using 27 data points and Ordinary Kriging.
Figure 4.12: Interpolated map of soil moisture. Created using 180 data points and Ordinary Kriging.
NDVI was highly heterogeneous with multiple small areas of high and low NDVI values (Figure 4.15). These small areas were caused by individual values with large deviations from the mean. This was more apparent in the east-central and southern sections of the site where NDVI was highly variable. The western and northern areas had larger patches which indicate a number of neighbouring points with similar values. The RMSE for this variable was quite high (0.06 NDVI units) given the data range of approximately 0.4. Again, this was likely due to the high variability in the measured points for this variable.

4.3.5 Regression

When regressed against NDVI individually, each variable’s relationship was improved by the use of GWR over OLS. The only variable showing a significant relationship was soil moisture which went from an $R^2$ of 0.046 in OLS to an $R^2$ of 82

Figure 4.13: Semivariogram for soil moisture. X = distance, Y = difference; red dots = differences binned by distance and direction, blue crosses = differences averaged in eleven lags, line = fitted gaussian model.
When explanatory variables were regressed against each other, elevation showed strong positive relationships with mean and maximum temperature, and a weak negative relationship with soil moisture. As expected from the interpolation results, mean and maximum temperature also showed a strong correlation with each other (Table 4.2).

Table 4.2: Explanatory variables regressed against each other. Only significant results shown \((p<0.05)\). T = temperature.

<table>
<thead>
<tr>
<th>Variables</th>
<th>OLS Coefficient</th>
<th>OLS Standard Error</th>
<th>OLS (R^2)</th>
<th>GWR (R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean T x Elevation</td>
<td>0.02</td>
<td>0.0009</td>
<td>0.78</td>
<td>0.89</td>
</tr>
<tr>
<td>Max T x Elevation</td>
<td>0.06</td>
<td>0.001</td>
<td>0.85</td>
<td>0.95</td>
</tr>
<tr>
<td>Soil moisture x Elevation</td>
<td>-0.18</td>
<td>0.06</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>Mean T x Max T</td>
<td>0.43</td>
<td>0.01</td>
<td>0.89</td>
<td>0.89</td>
</tr>
</tbody>
</table>

Figure 4.14: Semivariogram for NDVI. X = distance, Y = difference; red dots = differences binned by distance and direction, blue crosses = differences averaged in eleven lags, line = fitted gaussian model.
Figure 4.15: Interpolated map of NDVI. Created using 180 data points and Ordinary Kriging.
The full OLS model was significant \((p = 0.01)\) but had very low \(R^2 (0.05)\). Maximum temperature was removed from this model due to redundancy. The only variable in this model that showed significance was soil moisture (Coefficient=0.0008, standard error= 0.014, \(p = 0.002\)). The full GWR model only contained three variables (mean temperature, minimum temperature, soil moisture). This model had an \(R^2\) of 0.11. An OLS regression using the same three variables was performed to compare regression methods. Soil moisture was the only significant variable in this model (Coefficient=0.0007, standard error= 0.002, \(p = 0.002\)). The GWR was the better model as it had a higher \(R^2\) (OLS \(R^2=0.04\), GWR \(R^2=0.11\)) and a lower AIC (Akaike’s information criterion; OLS AIC=-476.6 , GWR AIC=-483.3). Residuals were clustered in both the OLS (Moran’s index=0.18, \(p = 0.002\)) and GWR (Moran’s index=0.17, \(p = 0.003\)) models which suggests that the models were misspecified and need additional variables to accurately predict NDVI.

4.4 Discussion

The mapping of environmental variables was successful and the sampling and interpolation methods used gave an accurate description of heterogeneity across the study site. As expected, soil moisture and NDVI showed high levels of heterogeneity and mean temperature showed significant variation across the study site. Mapping of soil moisture and NDVI could be improved by increasing the sampling density since these variables showed rapid change over small areas. Temperature maps could also be improved with more sample locations, especially given that semivariogram analysis usually requires at least 30 sample points (Rossi et al., 1992).

The weak, negative relationship between elevation and soil moisture is due to broad topographical patterns. Areas with lower elevation tend to have higher soil moisture due to snow and ice runoff. The GWR results for this relationship would likely be improved if the maps were detailed enough to capture micro-topography and runoff channels. The correlations between elevation and temperature are less clear but are likely a function of distance from the coast and site microclimate rather than elevation itself. Mean temperature appears to be influenced by maxi-
mum, more than minimum values. Minimum temperatures are relatively consistent throughout the site, whereas maximum values show greater variation and a higher number of unique, high temperature events. Mean and maximum temperature also show similar patterns when mapped across the lowland.

Overall model performance was poor for both OLS and GWR techniques. This is likely due to a combination of two factors. Firstly, the explanatory variables were not sufficient to explain the observed variation in NDVI. Biomass in Arctic ecosystems is determined by a combination of multiple factors which differ between species (Chapin, 1987). The simple model created here was not sufficient to capture this. The clustering of model residuals suggests that the models were mis-represented and important variables were missing. Other studies have found soil acidity (Walker et al., 2003), nutrient content (Boelman et al., 2003) and season length (La Puma et al., 2007) to influence NDVI results. Incorporating these variables into the model may improve performance. A second problem could be the response variable. NDVI may not be an accurate estimator of above-ground biomass in this case. The relationship between NDVI signal and above-ground biomass is not consistent across all plant communities (see Chapter 2) and it may be necessary to develop community specific relationships between spectral properties and physical attributes such as above-ground biomass or LAI. Ideally, structural data would be collected at each sample point using the ITEX point intercept method, and community scale relationships would be developed between NDVI and LAI. This would provide detailed information on community structure and above-ground biomass across the entire lowland which could be linked to NDVI response and used to predict CO$_2$ flux. These data would be costly to collect given the time constraints of sampling across such a large area.

Temperature has been shown to influence NDVI across wider areas (Hope et al., 2005; Raynolds et al., 2008), but did not appear to be an important variable at this site. It could be that the range of temperatures found at this site were not great enough to have a significant influence on NDVI response. The only variable that showed significance at this site was soil moisture. The positive relationship between soil moisture and NDVI is somewhat surprising given that at the community scale, no linear relationship appeared to exist (see Chapter 2). Some relationships
at this site therefore appear to differ with scale. The explanation for this relationship probably lies in vegetation density. If wet areas have consistently high vegetation cover, and dry areas show a mix of high and low density, we would expect a consistently higher NDVI response in the wet areas. In the community studies (Chapter 2), the dry plots had a consistently high cover of deciduous shrubs and graminoids which translated to high NDVI values. Not all dry areas across the lowland had such dense cover of shrubs and graminoids, and the proportion of each quadrat made up of bare ground was higher in most dry areas than in the community analysis. This was especially relevant in the south of the site where soils were less developed and vegetation tended to be confined to the wetter areas. A higher proportion of bare ground and a thinner canopy reduced the NDVI response in dry areas and contributed to the positive relationship with soil moisture.

The maps created here show a snapshot of soil moisture and NDVI at the peak of the growing season. The peak season model was not especially successful in this case - a temporal model that tracked environmental variables and NDVI through an entire growing season may reveal more patterns and relationships that were not captured by the peak season data. Temporal data would require continuous sampling through the season which was not logistically possible in this study.

This chapter has shown that detailed maps of environmental variables can be produced using field based sampling techniques and spatial interpolation. The maps created here did a good job of displaying environmental heterogeneity but were not able to produce a successful model to predict NDVI. Local regression models would be improved by including more variables and collecting more detailed vegetation data at sampling locations. Landscape scale monitoring throughout the growing season may reveal relationships that were not apparent with a single sampling period. Although a full model could not be produced with the available data, soil moisture was identified as an important variable for predicting vegetation biomass at this site.
Chapter 5

Conclusions

5.1 Introduction

The aim of this project was to investigate climate change response in terms of ecosystem structure and function in the Canadian High Arctic. Climate change was simulated using passive, experimental warming for 18 years. The direction and magnitude of warming response varies by species and is not expected to be consistent across all Arctic ecosystems. Environmental conditions are important in determining plant community composition so three ecosystems along a soil moisture gradient were used to ask the following questions:

1. How does the structure of above-ground vegetation differ between tundra ecosystems and how will this structure be changed by experimental warming?

2. How do patterns of CO$_2$ flux differ between tundra ecosystems and how will warming affect this ecosystem function?

3. How do the patterns of environmental variables and vegetation productivity vary across this landscape and what environmental factors are important in determining the abundance of above-ground vegetation?
5.2 Summary of results

All three of the sites studied showed a unique response to long-term experimental warming, although some trends were consistent across multiple sites. Structural responses were characterized by changes in growth form composition. Some changes in total above-ground biomass and canopy height were recorded but average responses were minimal and the changes were largely explained by the shifts in growth form abundance.

Warmed plots at the dry site had more vegetation than control plots due to increases in graminoids and forbs. At the mesic site an increase in graminoids, bryophytes and deciduous shrubs caused a small increase in total vegetation. The results from these two sites agree with previous studies (Arft et al., 1999; Elmendorf et al., 2012a;b; Walker et al., 2006). The wet site showed decreases in graminoids and evergreen shrubs in the warmed plots, these groups were partly replaced by deciduous shrubs and bryophytes. All three sites showed decreases in lichen abundance, a result that has been widely reported in Arctic ecosystems (Cornelissen et al., 2001; Elmendorf et al., 2012a;b; Walker et al., 2006). Other studies have also recorded decreases in bryophytes with increasing temperatures (Elmendorf et al., 2012a; Lang et al., 2011; Walker et al., 2006). In this study bryophytes increased in the two wettest sites, likely due to temperature increases without decreases in soil moisture (Hudson and Henry, 2010). Total shrub abundance was approximately the same between warmed and control plots at all sites, however deciduous shrubs showed small increases at the expense of evergreen shrubs in all cases.

All three ecosystems were sinks of CO$_2$ at the peak of the growing season. Warming at the dry and wet sites caused greater increases in GEP than R$_E$, resulting in a strengthening of the CO$_2$ sink at peak season. The dry site result agrees with a previous study by Welker et al. (2004) but the wet site has shown a shift from a negative to a positive peak season NEE response. Some Low Arctic studies have found R$_E$ response to be limited in wet ecosystems (Oberbauer et al., 2007) but this does not appear to be the case at this site. The mesic site showed no significant response in CO$_2$ flux as a result of warming. The changes in CO$_2$ flux were mostly explained by changes in community composition. Total above-ground biomass increased at
the wet site due to graminoid and deciduous shrub increases which increased both GEP and \( R_E \). At the dry site, the increase in GEP was due to an increase in deciduous shrubs and not an increase in total above-ground biomass. The mesic site did not show any compositional or biomass response which explains why \( CO_2 \) flux did not change at this site. Deciduous shrubs are the most important driver of \( CO_2 \) flux at this site and are correlated with GEP, NEE and \( R_E \).

The mapping technique used to display environmental patterns was successful in revealing landscape scale trends in temperature, soil moisture, elevation and NDVI. Mean temperature increased from north to south and was driven by changes in maximum temperature. Minimum temperatures showed little variation across the study site. Soil moisture patterns were influenced by topography and all environmental relationships were improved by using local rather than global regression techniques. A full model to explain NDVI patterns could not be produced using the simple combination of environmental variables. Adding more variables such as season length or soil characteristics may improve model performance. The model could also be improved by incorporating more detailed vegetation data such as point-frame data or LAI, and by incorporating community specific biomass-NDVI relationships. Despite poor model performance, soil moisture was identified as being an important variable which influenced NDVI values. Wetter areas in this case tended to have higher NDVI values. This reinforces the statement made by Muc et al. (1989) that soil moisture is an important factor influencing vegetation at this site.

The use of NDVI had mixed results at this site. NDVI was not able to detect the small differences observed in above-ground biomass at each community and NDVI signatures were community specific. Despite this, when communities were grouped together, NDVI showed a significant positive relationship with the ITEX live hit (TLH) method, albeit with large residual errors. Across all three sites, NDVI also showed significant relationships with all three components of \( CO_2 \) flux, especially photosynthesis. NDVI is actually a better predictor of \( CO_2 \) flux across all sites than it is TLH. This is likely because the same growth form groups are driving both NDVI and GEP. NDVI has shown strong links to \( CO_2 \) flux in community specific plot level studies in the Low Arctic (Boelman et al., 2003; McMichael).
et al., 1999). The High Arctic results presented here reveal a general relationship which would be improved by investigating the relationship in all communities individually and incorporating LAI as a link between spectral properties and ecosystem functions. This would require more flux data to be recorded in each community.

The results from the mesic site showed consistent anomalies compared to the dry and wet sites. The relationship between NDVI and biomass showed similar trends between the dry and wet site but were markedly different at the mesic site. NDVI at the mesic site was less than at the dry site, despite the two communities having similar TLH values. Similarly, the mesic site was the only site not to show a CO₂ flux response after 18 years of warming. Other studies have succeeded in applying NDVI across ecosystems to predict CO₂ flux for example (Shaver et al., 2007). The results from this study offer support for this approach across the dry and wet ecosystems, but the anomalies at the mesic site would require community specific relationships in order to allow accurate extrapolation using NDVI.

5.3 Limitations

I have identified three limitations, which if solved would expand the scope and power of the analysis.

1. Biomass estimations

The biomass estimations here are limited to above ground vegetation. Destructive sampling is not possible in long term plots so the mass of below ground vegetation cannot be measured. Measuring both above and below-ground biomass would allow comparisons between warmed and control plots and between different community types. This is important since root:shoot ratios vary with vegetation type (Mokany et al., 2006), and climate change will likely effect the abundance (Van Wijk et al., 2003) and allocation (Canadell et al., 1996) of carbon, and the distribution patterns of below ground vegetation (Mack et al., 2004). More detailed biomass information may also help explain the observed CO₂ flux patterns and link plant growth to carbon intake at the ecosystem level. Measuring LAI in each plot
would improve the ability of NDVI to predict both biomass and CO$_2$ flux.

2. Temporal data collection

Structural and functional data collection was limited here to the peak of the growing season. While this is useful for investigating ecosystem processes at peak photosynthesis, structural and functional properties vary throughout the growing season (Welker et al., 2004) and analysis could be expanded by collecting data for the entire growing season. This would allow relationships between CO$_2$ flux, composition, and biomass to be investigated in greater detail.

3. CO$_2$ flux sample size

The amount of CO$_2$ flux data available was limited by the number of collars installed at each site (and by the loss of data from some plots). Data were adequate to show site differences between communities and warming response, but the power of analyses could be increased with higher sample sizes. This is especially relevant for the NDVI-CO$_2$ flux relationships which show potential but would benefit from site specific regression analysis.

5.4 Future research

There are two extensions to this work which would expand on the findings here and improve the understanding of ecosystem dynamics at this study site.

1. One possible area for expansion is to develop the relationship between community structure and CO$_2$ flux. The regressions between NDVI and CO$_2$ flux suggest the potential for extrapolation using NDVI as a predictor of CO$_2$ flux. If reliable relationships could be determined for the three communities used in this study, NDVI could potentially be used to model CO$_2$ flux across 51% of the lowland (according to the community map by Muc et al. 1989), using either NDVI directly or a combination of NDVI and simple environmental variables as has been done at other Arctic locations (e.g. Shaver et al. 2007). This would likely require an increase in the number of CO$_2$ collars to increase sample size. It may also require NDVI-LAI relationships to be
developed for each community which would allow CO$_2$ flux to be directly predicted from LAI across multiple ecosystems. A greater percentage of the lowland could be modelled if more community types were sampled for structure and CO$_2$ flux. Developing community specific relationships would also allow direct comparisons to similar ecosystems at lower latitudes (e.g. Boelman et al. 2003).

2. Another extension would be to sample vegetation structure and CO$_2$ flux throughout the growing season. Since NEE varies throughout the growing season, continuous measurements of GEP and $R_E$ would allow a growing season carbon budget to be estimated for each community. This would allow direct comparison to Welker et al. (2004) which would identify any differences between mid- and long-term warming responses. CO$_2$ flux could also be linked to phenology by sampling for structure along with CO$_2$. This would allow changes in the relative abundance of specific growth forms to be tracked along with changes in CO$_2$ flux.

5.5 Conclusion

This study provides insight into the long term (18 years) consequences of warming in three High Arctic ecosystems. The study found that warming altered the growth form composition of ecosystems, which in turn affected the rates of photosynthesis and respiration. Responses were ecosystem specific in terms of both direction and magnitude. It also provided evidence for a potential role of remote sensing in predicting ecosystem function across the wider landscape. This study, along with others in the Arctic, shows that even relatively unproductive ecosystems will respond to atmospheric warming, but responses will not be consistent across all plant communities.
References


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Appendix A

Table A.1: Peak season CO$_2$ flux values averaged by site and treatment. NEE = net ecosystem exchange; GEP = gross ecosystem photosynthesis; R$_E$ = ecosystem respiration; n = sample size. Values are means ± one standard error. Values are reported in CO$_2$ µmol m$^{-2}$ s$^{-1}$.

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>NEE(n)</th>
<th>R$_E$(n)</th>
<th>GEP(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>Control</td>
<td>3.98±0.40(4)</td>
<td>-2.28±0.23(4)</td>
<td>6.26±0.55(4)</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>5.15±1.01(3)</td>
<td>-3.05±0.38(3)</td>
<td>9.58±0.01(2)</td>
</tr>
<tr>
<td>Mesic</td>
<td>Control</td>
<td>2.04±0.17(4)</td>
<td>-1.60±0.18(3)</td>
<td>3.47±0.11(3)</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>1.49±0.47(2)</td>
<td>-1.52±0.27(4)</td>
<td>3.34±0.92(2)</td>
</tr>
<tr>
<td>Wet</td>
<td>Control</td>
<td>3.07±0.31(3)</td>
<td>-1.21±0.04(2)</td>
<td>4.27±0.57(2)</td>
</tr>
<tr>
<td></td>
<td>Warmed</td>
<td>4.46±0.45(3)</td>
<td>-1.96±0.36(3)</td>
<td>6.42±0.61(3)</td>
</tr>
</tbody>
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