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Nutrient cycling in Alaskan tundra in response to experimental manipulation of growing season length and soil temperature : a climate change scenario

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

NUTRIENT CYCLING IN ALASKAN TUNDRA IN RESPONSE TO
EXPERIMENTAL MANIPULATION OF GROWING SEASON LENGTH AND
SOIL TEMPERATURE: A CLIMATE CHANGE SCENARIO

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

by

Lorraine E. Ahlquist

2003

To: Dean R. Bruce Dunlap
College of Arts and Sciences

This thesis, written by Lorraine E. Ahlquist, and entitled Nutrient Cycling in Alaskan Tundra in Response to Experimental Manipulation of Growing Season Length and Soil Temperature: A Climate Change Scenario, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

Krish Jayachadran

David W. Lee

Steven F. Oberbauer, Major Professor

Date of Defense: 27 October 2003

The thesis of Lorraine E. Ahlquist is approved.

Dean R. Bruce Dunlap
College of Arts and Sciences

Dean Douglas Wartzok
University Graduate School

Florida International University, 2003

DEDICATION

This thesis would be incomplete without a mention of the support given to me by my cherished parents, Earle and Betty, to whom this thesis is dedicated. They have provided me with support emotionally and financially throughout this long journey called my academic career.

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A journey is easier when you travel together. Interdependence is certainly more valuable than independence. This thesis is the result of six years of work whereby I have been accompanied and supported by many people. It is with great pleasure that I now have the opportunity to express my gratitude to all of them.

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ABSTRACT OF THE THESIS

NUTRIENT CYCLING IN ALASKAN TUNDRA IN RESPONSE TO
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by

Lorraine E. Ahlquist

Florida International University, 2003

Miami, Florida

Professor Steven F. Oberbauer, Major Professor

Climate change in the Arctic is predicted to increase plant productivity through decomposition-related enhanced nutrient availability. However, the extent of the increase will depend on whether the increased nutrient availability can be sustained. To address this uncertainty, I assessed the response of plant tissue nutrients, litter decomposition rates, and soil nutrient availability to experimental climate warming manipulations, extended growing season and soil warming, over a 7 year period. Overall, the most consistent effect was the year-to-year variability in measured parameters, probably a result of large differences in weather and time of snowmelt. The results of this study emphasize that although plants of arctic environments are specifically adapted to low nutrient availability, they also possess a suite of traits that help to reduce nutrient losses such as slow growth, low tissue concentrations, and low tissue turnover that result in subtle responses to environmental changes.

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Chapter 1.

Study description and justification

Overview

Plant-soil interactions in the nutrient-limited arctic region are important because they will form the basis for our understanding of the carbon (C) exchange between the ecosystems and the atmosphere under predicted future climatic changes. The carbon balance of the Arctic depends on the equilibrium between the CO₂ uptake by primary producers and the subsequent release of CO₂ through autotrophic and heterotrophic respiration (Chapin *et al.* 2000). This balance may change in the future in response to changes in soil-moisture conditions or temperature resulting from increases in atmospheric greenhouse gases (Flanagan and Veum 1974; Heal and French 1974; Billings *et al.* 1982; Billings *et al.* 1983; Chapin *et al.* 2000).

The general tendency in many arctic nutrient cycling experiments has been to experimentally manipulate the system and address questions about plant nutrient acquisition or decomposition and mineralization processes, while few studies have integrated the processes in both the soil and plant compartments (Rastetter *et al.* 1996). This study was an attempt to determine seasonal nutrient cycling patterns of arctic plants under conditions of simulated climate change. The results of this study will help in evaluating which species are likely to persist under the predicted rapid climate changes in the Arctic (Maxwell 1992, 1996). To

address the uncertainty of plant and soil response to climate change, I assessed the response of plant tissue nutrients, litter decomposition rates, and soil nutrient availability to experimental climate warming manipulations, extended growing season and soil warming, over a 7 year period in arctic Alaska. The data from this project will be valuable in computer modeling of ecosystem carbon budgets of the Arctic in response to climate warming (Sitch *et al.* 2003). These models will help assess the future contributions of tundra ecosystems to the global carbon budget. This thesis consists of three chapters: 1) an introduction to the role of nutrient cycling in the Arctic, 2) a journal article presenting my research, and 3) a general conclusion.

Background

Climate Change in the Arctic

On a global scale, atmospheric concentrations of CO₂ have been rising since the onset of the industrial revolution (Bawa and Markham 1995; Keeling *et al.* 1995; Cubasch 2001). This increase has been primarily attributed to fossil fuel consumption and the destruction of tropical forests (Brown 1993; Bawa and Markham 1995). Atmospheric concentrations of CO₂ are predicted to double in the next three decades as a result of these anthropogenic contributions (Kerr 1988; Maxwell 1992, Keeling *et al.* 1995; Maxwell 1996). The increases in CO₂ will significantly affect the composition of the world's terrestrial ecosystems and global carbon budget (Schimel *et al.* 1994). There is increasing evidence to support the idea that terrestrial systems play a major role in global primary

productivity and, consequently, feedbacks to the global carbon cycle (Tans *et al.* 1990; Williams and Rastetter 1999).

GCMs predict that doubling of atmospheric CO₂ will result in an average annual global warming of 1.9 to 5.2 °C. This warming will be greater towards the poles. For the Arctic, the GCMs predict a winter warming at the surface 2 to 2.4 times greater than the average warming for the globe. These increases may have far reaching effects on other components of the arctic climate, such as evaporation, cloudiness, rain and snowfall. The effects of these changes on arctic plants will result in a cascade of effects through arctic ecosystems. To predict the changes to community structure and ecosystem function at these northern latitudes, we must understand the responses of tundra plants to global warming. The complexity and uncertainty associated with these predictions, including the relationships between climate elements and ecosystem components, are not well understood (Cohen 1990).

Climate changes in the Arctic may result in important changes in the snow-free season (Maxwell 1992, 1996). GCMs provide three scenarios for the effects of global warming on the arctic growing season: 1) A shortened growing season, associated with increased likelihood that snow cover will persist longer in the spring than at present, because of increased snowfall and cloud cover; 2) An extended growing season, in which the snow-free season is likely to extend further into autumn, and snow melt will occur earlier in the season; and 3) A

growing season unchanged from the current growing season because of a combination of increased snowfall counteracted by increased snow melt. The most likely scenario is an extended season with higher temperatures, increased decomposition rates, deeper active layer, and lower water tables. Greater decomposition and unfrozen soil volume will increase nutrient availability resulting in as much as twice the present net primary production (Oechel and Billings 1992). Whether such an increase can be sustained over the long term depends on the capacity of the system to maintain elevated levels of nutrients in response to warming (Jefferies *et al.* 1992).

Nutrient Pools in Arctic Ecosystems

Most arctic ecosystems have high nutrient fractions in belowground biomass compared to low pools in aboveground plant biomass. Nutrients in the soil are mostly immobilized into organic pools. In ecosystems with high accumulations of soil organic matter, such as dwarf shrub tundra, the percentage of nitrogen in the soil plus litter is between 90 to 95% (Jonasson 1982; Jonasson 1983; Jonasson and Michaelson 1996). Nutrients within the mostly slow-growing plants are held in tissues with slow turnover (Jonasson 1983; Shaver *et al.* 1996). Net nutrient mineralization is low and the residence time of nutrients in the soil is long. Low soil temperatures, high soil moisture, and the low quality of the organic matter strongly limit decomposition rates and nutrient mineralization in the Arctic (Flanagan and Veum 1974). Released nutrients are quickly immobilized in soil microorganisms implying that soil microbes and plants compete strongly for

nutrients. This also implies that under conditions of declining microbial populations, microbial biomass is a potential source of nutrients.

The seasonality of nutrient mineralization often differs from the seasonality of plant nitrogen uptake. In these ecosystems where plants are dormant for most of the year, soil microbes may continue to mineralize nitrogen in unfrozen soil water during the dormant season (Bowman 1992; Giblin *et al.* 1991); this may lead to an accumulation of available nitrogen that plants use when they become active (Bilbrough *et al.* 2000). Mineralization during winter (even beneath a snowpack) may create a substantial pool of available nitrogen that is not absorbed by plants until the following spring. This asynchrony between microbial activity and plant uptake is particularly important in low-nutrient environments, where microbes may immobilize nitrogen during the season of most active plant growth, effectively competing with plants for nitrogen (Jaeger *et al.* 1999). In arctic soils that freeze or dry, the death of microbial cells provides additional labile substrates for mineralization when conditions again become suitable for microbial activity.

The extent of this plant-microbe competition is poorly unexplored, and it is uncertain whether plants primarily take up nutrients continuously during the summer when the sink strength is presumably strong, or whether the main nutrient uptake occurs during pulses of nutrient release when the sink strength declines. Plant storage of nutrients to support spring growth is particularly

important in these low-fertility ecosystems because nutrients are not dependably available from the soil at times when the environment favors plant growth (Chapin *et al.* 1990).

Due to these conditions, arctic tundra productivity is generally nutrient limited, primarily by phosphorus and nitrogen (Haag 1974; Ulrich and Gersper 1978; Chapin 1987). This nutrient limitation favors a community dominated by plant species with low nutrient requirements or high nutrient use efficiencies (Jonasson and Chapin 1985; Berendse and Jonasson 1992; Chapin *et al.* 1995a).

Comparisons of elemental concentrations among tundra ecosystems indicate that weathering rates are highly individualistic, depending critically on soil parent material (Marion 1996). Furthermore, tundra ecosystems are leaky with respect to nutrients, which may have ramifications well beyond the disturbance both with respect to time and space, and bears attention in assessing the future response of tundra ecosystems.

Plant Responses to Change in the Arctic

The adaptations of the dominant plants to low nutrient availability make the system vulnerable to changes. Across the Arctic, numerous studies of plant community responses to experimental addition of nutrients, or changes in nutrient availability associated with human activity, have shown that both community productivity and plant species composition are sensitive to changes in

the soil pools of plant available nutrients, mostly nitrogen (N) and phosphorus (P) (e.g. Shaver and Chapin 1980; Shaver and Chapin 1986; Jonasson 1992; Parsons *et al.* 1994; Forbes 1995). Thus, any changes in the input or cycling of these nutrients, as from airborne pollutants or increased rate of nutrient mineralization caused by a predicted future warming of the Arctic, if sufficiently large, will change species composition and, most likely, increase plant productivity (Cattle and Crossley 1995; Rastetter *et al.* 1996).

Individual species will change rather than groups of species (Chapin *et al.* 1997; Callaghan and Jonasson 1998). Some responses to increased nutrient supply are specific to particular growth forms (Jonasson 1992; Chapin *et al.* 1995b; Chapin and Shaver 1996; Callaghan and Jonasson 1998; Shaver and Jonasson 1999). The direct growth responses of evergreen dwarf shrubs to increased temperatures are small (Havström *et al.* 1993; Wookey *et al.* 1993; Chapin *et al.* 1995b; Chapin and Shaver 1996), in contrast to the increased growth rates of graminoids, forbs, and deciduous dwarf shrubs (Wookey *et al.* 1994; Henry and Molau 1997; Arft *et al.* 1999). In the Arctic, where these growth forms are abundant, there is a significant increase in plant biomass in response to increased temperatures in summer (Henry and Molau 1997). The response of reproductive and vegetative structures to warming will vary, depending on abiotic constraints (Wookey *et al.* 1994; Arft *et al.* 1999). Warming in the winter and spring may encourage premature growth, so subsequent frost could damage plants (Gorsuch and Oberbauer 2002).

Nutrients, Climate Change, and Ecosystem Carbon Balance in the Arctic

Arctic ecosystems have low biomass compared with most other biomes, and vast areas are poorly vegetated or even lack vegetation. Consequently, the Arctic has the potential to act as a large sink for CO₂ in the future. However, because arctic soils contain 14% of the world's stores of soil C (Post *et al.* 1982), the Arctic can also act as a large source of atmospheric CO₂. Presumably, the changes in C balance are likely to be different both at local and regional scales (Callaghan and Jonasson 1995a,b).

With climate warming, high decomposition of soil organic matter paired with high nutrient immobilization, i.e. low microbial release of plant-available nutrients, may lead to a loss of carbon from the soil to the atmosphere that may not be compensated fully by increased plant C fixation through increased photosynthetic rates. Hence, the system will be a net source of atmospheric C. Conversely, if plants are able to sequester extra nutrients efficiently, their productivity will increase and the system may accumulate more C and turn into a C sink, particularly if nutrients are allocated to woody tissues of low nutrient concentrations. However, the predictions are complicated by numerous possible interactions and feedbacks between the soil and plant components. For instance, the low Arctic and sub Arctic with much higher proportions of soil C, are likely to act as sources for CO₂ if changes in the environment lead to increased rate of decomposition, e.g. by warming of the soil or changed soil moisture

conditions. At the same time, increased rates of decomposition and mineralization will probably lead to increased CO₂ uptake because plant growth generally is stimulated by increases in soil organic nutrient pools. Hence, carbon will be redistributed from the soil to the plant biomass. Because the C-to-nutrient ratio generally is higher in the plants than the soil, such redistribution would increase the ecosystem sink strength for carbon as the nutrients, particularly N, when moved from the soil to the vegetation, enhance the ecosystem C fixation (Rastetter *et al.* 1996).

Predicted global changes in temperature and moisture regime (Kane *et al.* 1992), in association with indirect abiotic and biotic changes in snow cover, growing season length, nutrient availability, litter quality and community change, may strongly affect the carbon balance of arctic ecosystems (Jonasson 1995; Chapin *et al.* 1995b; Hobbie 1996). The processes in arctic ecosystems can also feed back to the global climate through increased decomposition of the large stock of terrestrial soil carbon (Callaghan and Jonasson 1995b), enhanced carbon uptake by increased plant production (Rastetter *et al.* 1996), and changes in regional energy balance resulting from changes in vegetation structural characteristics. All of these changes will depend ultimately on the ecosystem nutrient balance.

Chapter 2.

Nutrient cycling in Alaskan tundra in response to experimental manipulation of growing season length and soil temperature

Introduction

As a result of increasing atmospheric greenhouse gases, General Circulation Models (GCMs) project that the global-average surface temperature will increase by 1.4 to 5.8°C over the period from 1990 to 2100 (IPCC 2001). Land areas are expected to warm more rapidly than the global average, particularly those at high latitudes during the cold season. Simulations suggest that the warming in these regions of North America will exceed global mean warming by more than 40% (IPCC 2001). Changes in season length are expected to accompany this warming, and will be especially pronounced in the Arctic, where the short growing season is currently only 8-12 wk (Maxwell 1992, 1996). Hypothesized scenarios for the Arctic include an extended season with higher temperatures, increased decomposition rates, a deepening of the active (thawed) layer from melting of permafrost, and a lowering of the water table (Rommanovsky and Osterkamp 1997, Serreze and Hurst 2000, IPCC 2001). Indeed, such changes have already been documented (Serreze *et al.* 2000). These changes may increase net primary productivity as a consequence of increased nutrient availability (IPCC 2001). Whether such an increase is sustainable for long periods, however, will depend on the capacity of the system to maintain elevated levels of nutrients.

In the Arctic, the limiting nutrients in tundra are nitrogen and phosphorus. Most nutrients are bound in the soil organic matter and litter while only a small proportion is in plant biomass (Hobbie *et al.* 1999). In tundra ecosystems with high accumulations of organic matter, such as in dwarf shrub tundra and *Betula* and *Salix* dominated shrub tundra, the percentage of nitrogen in the soil plus litter is between 90 - 95% (Jonasson 1982; Jonasson 1983; Jonasson and Michelsen 1996). These ecosystems often contain large pools of nutrients, but because of low annual temperatures, net mineralization is limited, leading to high residence times. Of the nutrients within plants, a high proportion is locked into tissues with slow turnover (Jonasson 1983; Shaver *et al.* 1996; Eckstein and Karlsson 2001). As a result, plant growth and ecosystem productivity in arctic tundra are generally nutrient limited (Haag 1974; Ulrich and Gersper, 1978; Chapin 1987, Chapin and Shaver 1996). Under these low nutrient conditions, the community is dominated by plant species with low nutrient requirements or high nutrient use efficiencies (Jonasson and Chapin, 1985; Berendse and Jonasson, 1992; Chapin *et al.* 1995a).

Soil temperature along with soil moisture, aeration, and litter quality control the rates of decomposition and nutrient mineralization in the Arctic. The short growing season length and generally low temperatures in the Arctic, snow cover, and topographic position largely determine soil temperature, soil moisture, and soil aeration (Sturm *et al.* 2001), which in turn have strong effects on plant community composition. Although vegetation characteristics can affect all of the

factors above (Sturm *et al.* 2001, McGuire *et al.* 2002), the primary effect of community characteristics on ecosystem nutrient cycling is through litter quality, turnover rates, and their effect on nutrient availability (Hobbie *et al.* 1999). Consequently, changes in season length and/or soil temperatures, active layer depth and mean solar radiation will potentially have strong effects on nutrient cycling and the vegetation biomass.

Growing season length in the low Arctic is determined largely by the timing of snowmelt in the spring. As a result, growing season duration can be experimentally modified by manipulation of snow cover. As part of the International Tundra Experiment (ITEX), the SEASON project has used snow removal and soil warming in low Arctic tundra to simulate a longer, warmer growing season as predicted by GCMs. Working within that project, I combined data on litter decomposition, soil nutrient availability, and plant nutrition to understand the changes in the ecosystem nutrient balance in response to this long-term climate-warming scenario. Improved understanding of the distribution of nutrients within this nutrient-limited ecosystem in response to climate change is critical, because the coupling between nutrient dynamics and primary production will determine the long-term carbon balance of this system.

The objective of this work was to assess the response of soil nutrient availability and plant tissue nutrients to a longer growing season plus soil warming. The study species for plant tissue nutrients included members of four growth forms,

graminoids, perennial forbs, and evergreen and deciduous shrubs (Table 1). These vascular species comprise >90% of the vascular ground cover of the Alaska wet tussock tundra and are key in the ecosystem nutrient regimes (McKane *et al.* 1997).

Methods

Site Description

The study was completed over a period of 7 years, from fall 1995 through 2001 at a site near Toolik Field Station (Figure 1), Arctic Alaska in the foothills of the Brooks Range (68°38' N, 149°34' W; elevation 730 m.a.s.l.). The station is operated by the University of Alaska at Fairbanks and designated a Long Term Ecological Research (LTER) and International Tundra Experiment (ITEX) site. The study site was located on an east-facing slope approximately 1.5 km south of the field station. The vegetation is moist tussock tundra, and the area is typical of the North Slope foothills region (Walker *et al.* 1989). The dominant species is *Eriophorum vaginatum*, a sedge that forms tussocks, or raised mounds of the current growth on top of the growth from previous years. Intertussock space is occupied by several other dominant growth forms that include dwarf deciduous and evergreen shrubs with many forms of lichens and mosses (Bliss and Matveyeva 1992). The climate is low Arctic, with a growing season of approximately nine weeks. For characteristics of soil and vegetation, see Walker *et al.* (1994). Nomenclature follows that of Hultén (1968).

Experimental Design

Experimental treatments commenced in spring 1995. The plot layout (Figure 2) consisted of six blocks of three 1.5 x 1.5 m plots each, with 3 m separating each plot. Each block contained one of each of the following treatments randomly located within the block: control (C), extended season (E, snow removed and plots covered to prevent snow accumulation early in the season, and plots covered late season to prevent snow accumulation and light frosts), and six extended season plots as above plus soil warming (H, heating accomplished with installation of cold frame heating cable installed 10 cm below the surface).

To accomplish the extended season treatments (E and H), spring snow was removed from the plots over the course of 1 - 1.5 d from May 1 to May 3. Snow was carefully removed by hand until the plant canopy protruded from the snow at which time melt proceeds very rapidly because of the change in albedo.

Removed snow was deposited uphill from the plots to provide similar water input to the plots as ambient snowmelt. Plots were kept covered with open-ended, A-frame polyethylene tents to prevent snow accumulation after snow removal until complete snowmelt on the controls occurred and danger of snowfall had passed (usually by June 10). The tents allow for approximately 90% of PAR (photosynthetically active radiation) to pass through. The open ends minimized air temperature increases within the tents. The ends of the tents were temporarily closed during snowfall and windstorms. Complete snowmelt on the

control plots ranged from 13 May to 9 June over the study period (median = 29 May). At the end of the season (15 August to 4 September, plots were again covered with the A-frame tents to prevent snow accumulation and light frosts. For the H treatment, heating cable was installed the year before treatments began (1994) to allow recovery time prior to measurements. Cables were heated for 2 hr each day with a 1400-watt generator for a $0.4 \text{ MJ m}^{-2} \text{ d}^{-1}$ of energy input to the soil (equivalent to 20-30% of the daily soil heat flux for this vegetation during summer months) and provided a temperature increase of approximately 2°C over the course of the growing season. This magnitude of increase in the energy of the soil is similar to that predicted with global warming (Maxwell 1992, 1996).

In addition to the 6 treatment blocks described above, used only for nondestructive sampling, a set of 4 blocks with the same treatments was established to be used for tissue nutrient collections (Figure 2). Boardwalks were installed throughout the study site and on 3 sides of the study plots to minimize damage to the tundra during measurements.

Microclimate

Weather and soil temperature data were acquired from the micrometeorological station of the Long Term Ecological Research Project (LTER) located near Toolik Field Station. Average daily temperature, precipitation, wind speed, global

radiation, and soil temperature at 20 cm depth were acquired for each day from 1 May to 30 September for 1995, 1997, 2000, and 2001 field seasons.

Plant Tissue Material

Live leaf tissue was collected each year of the study to assess the concentrations needed for estimating ecosystem nutrient budgets in response to the treatments. Three to five collections of plant tissue material were made each year on the primary study plots ($n = 6$) spread evenly over the growing season (approximately every 3 wk from early June to mid August), beginning as soon as depth of thaw was sufficient. There were three collections in 1995, five in 1997, and four in 2000 and 2001. Live leaf tissue (5-30 mg dry weight) was collected from each of the destructive plots ($n = 4$) by clipping throughout the growing season resulting in at least three collections per year (1995 – 2001). Sampling was haphazardly distributed over the extent of the plots. All samples were collected within a 48 h period. Samples were dried at 68-70 °C. The samples were brought to Florida International University, re-dried and ground using a Thomas Wily Mill (Arthur H. Thomas Co., Philadelphia, PA) or Wig-L-bug homogenizer (model LC-153, Crescent Dental Mfg, Inc). Samples were analyzed for Carbon (C) and Nitrogen (N) ratios using a Carlo Erba 1500-N CHN analyzer. A single modified Kjeldahl digestion was performed for nitrogen (N) and phosphorus (P) determination. The resulting solutions were subsequently analyzed for Nitrogen colorimetrically using a Flow Solution IV Alpkem Colorimetric Analysis (EPA Method 351.2) and Phosphorus using a Spectro

Ciros ICAP-Inductively Coupled Argon Plasma technique (EPA Method 200.7) at the University of Florida Institute of Food and Agricultural Science (IFAS) laboratory.

Litter Decomposition

Decomposition processes represent a major component of carbon and nutrient cycles within arctic ecosystems, and quantifying rates of litter mass and nutrient losses is critical for understanding nutrient cycling. Litter decomposition rates in response to the experimental treatments were evaluated using recently-senesced dwarf birch (*Betula nana*) leaves collected near the study site in the fall of 1999. Only newly fallen leaves or leaves that easily detached from plants (with a well developed abscission layer) were collected. The plant material was dried to constant weight (48 h, 70°C). In total, 120 bags were made from plastic screening (8 x 8 cm) with 1.0 mm mesh size, and fused into small pouches with a hot iron. Each bag contained a preweighed amount of birch leaves (approximately 2g dry weight). The entire sample of senescent birch leaves was well mixed prior to use to insure uniformity of all samples. Subsamples of the litter were taken for chemical analysis of initial litter quality.

On June 21, 2000, litterbags containing *Betula nana* plant material were buried in each destructive plot of the two treatments and the control plots (n = 4) for determination of rates of decomposition. Approximately 1 year later, litterbags were retrieved during early season (7/13/01), once depth of thaw was sufficient

for removal, and late season (8/31/01) prior to soil freezing. After samples were collected, roots growing into the bags were removed and the remaining litter was dried to constant weight and weighed to an accuracy of 0.1 mg. The samples were processed for nutrient analysis following the same procedures used for plant tissue material.

Soil Solutions

Lysimeters were used each year of the study to assess the soil solution nutrient concentrations. Collection of soil solutions was made at approximately the same time periods and frequency as plant tissue material. There were three collections in 1995, five in 1997, and four in 2000 and 2001. Collection of solution began as soon as depth of thaw was sufficient to insert the lysimeters into the soil. Once installed, the lysimeters were left in place for the length of the growing season. The lysimeters (Rhizon Soil Moisture Samplers) were constructed of a length of porous, chemically inert plastic (2.3 mm o.d., 1.4 mm i.d., average pore diameter 0.1 μm) capped with nylon at one end and attached to a 5 cm polyethylene tube at the other end. Suction was provided by a pulled, 10 ml syringe applied to the lysimeter 12 h prior to sample collection. The process was repeated until 10 - 15 ml sample volume was collected. After collection, samples were acidified with 50 μl concentrated HCl and immediately frozen in order to prevent microbial activity. Samples were analyzed colorimetrically for N ($\text{NH}_4^+\text{-N}$) with a Flow Solution IV (EPA Method 350.1) method, and PO_4^- , K^+ , and Ca^{+2} were analyzed with Spectro Ciros ICAP-Inductively Coupled Argon Plasma technique (EPA Method

200.7) technique at University of Florida's Institute of Food and Agricultural Science laboratory.

Exchangeable Ions

A large percentage of nutrients that plants and microbes assimilate from the soil solution are in ionic form, and nutrients in this form are interpreted as available or labile for uptake. Cations of interest include NH_4^+ , K^+ , Mg^{+2} , Ca^{+2} , and Al^{+3} , and anions include NO_3^- and PO_4^{3-} . To measure bioavailability of ions *in situ*, I used anion (AEM) and cation (CEM)-exchange resin impregnated membranes (Ionics 1987). Ion-exchange membranes (IEMs) provide a well-defined planar ion-sink surface in direct contact with soil particles (Saunders 1964, Huang and Schoenau 1996). This configuration minimizes disturbance of the flow of water through soil and disturbances during placement and removal of membranes. The anion exchange membranes (AEM) and cation exchange membranes (CEM) used are polystyrene sheets with quarternary ammonium (AEM) or sulphonic acid (CEM) groups attached. Nitrate specific sensitive membranes are also available. The amount of nutrients sorbed on IEMs is not a quantitative measure of a pool size, but rather is an index of the ion supply (Saggar *et al.* 1990, Schoenau and Huang 1991a, Abrams and Jarrell 1992).

IEMs were installed in all 18 experimental nondestructive primary study plots during peak growing season (July 19) in 2000 and twice (July 24 and August 1) during the growing season in 2001. Both anion and cation membranes were cut

into 5 x 5 cm squares, a monofilament line was attached for easy retrieval, and rinsed with deionized water (DI-H₂O). Before transport and installation, chloride-saturated AEMs were converted to bicarbonate form (Weih 1998). Three consecutive washes of 0.5 M NaHCO₃ with alternating rinses of DI-H₂O were applied. This method is preferred for determining P availability (Weih 1998). After transport to the field in Nalgene 30 ml bottles, one AEM and one CEM were placed back-to-back and inserted into the soil at a slight angle with a serrated edged knife from a vertical slope ($20^{\circ} \pm 10^{\circ}$), because this created better soil to membrane contact. After insertion, the soil opening was firmly pressed back to undisturbed state to ensure proper soil-membrane contact. In each plot, one pair of IEMS was placed in intertussock spaces and one pair in tussocks per plot. Membranes were not left in soil longer than 100 h, because after this time the membranes no longer maintain a near-zero concentration of phosphate or nitrate at the surface (Weih 1998). Gilblin *et al.* (1994), using resin bags, noted that long deployment times gave lower estimates of nutrient availability than did a series of shorter deployments. Soil particles adhering to the surface were gently removed from membrane before rinsing with DI-H₂O. AEMs and CEMs were placed in 25 ml of 0.5 M HCl in Nalgene 30 ml bottles and gently shaken for approximately 30 h. The resulting solutions were subsequently analyzed for PO₄⁻, K⁺, Mg²⁺, Mn²⁺, Fe²⁺ and NO₃⁻ colorimetrically using a Flow Solution IV Alpkem Colorimetric Analysis (EPA Method 351.2) and Phosphorus with a Spectro Ciros ICAP-Inductively Coupled Argon Plasma technique (EPA Method

200.7) at University of Florida's Institute of Food and Agricultural Science laboratory.

Statistical Analysis

The daily means of temperature ($^{\circ}\text{C}$), precipitation (mm), wind speed (ms^{-1}), global radiation (J cm^{-2}), and soil temperature ($^{\circ}\text{C}$) at 20 cm depth from May to September for the study years were tested for monthly and yearly differences using two-way analysis of variance (ANOVA). Variables were first checked for normality and heterogeneity of variances and transformed when necessary.

Plant tissue nutrients, Carbon to Nitrogen ratio (C:N) and phosphorus concentration (nutrient content in plant tissue material measured as percent of total mass), were analyzed for each species using a three-way randomized complete block ANOVA with three treatments, two, three or four years depending on component, and four or five collections depending on year of analysis. Soil nutrient solutions were analyzed in the same manner as the plant tissue nutrients.

Mass and nutrient changes of the litter decomposition bags were evaluated using one-way ANOVA. Soil exchangeable ions were analyzed for treatment, location, and collection effects with three-way ANOVA.

Statistical analyses were carried out using SPSS 11.5 for Windows (SPSS 2002) software. Based on these findings, the results reported are the differences among treatments, years of study, and the collection during the year. In cases where significant differences were found, Fisher's least significance difference (LSD) post hoc tests were used to compare appropriate means. Tests were considered significant if $p < 0.05$.

Results

Microclimate properties

I restricted all comparisons to weather data from 1 May to 30 September, which encompasses the entire growing season and shoulder seasons when tangible plant growth activity occurs.

Solar radiation peaked in May in all four years even though peak sun angles occur in late June. Cloud cover typically increased during the growing season, and combined with declining sun angles, was the basis for the decline in monthly solar radiation starting in June (Figure 3). Temperatures during the growing season were fairly consistent among years in June, July, and August, but considerable variation among years occurred in May and September (Figure 3). May was particularly variable among years. These monthly differences translated into significant differences in average growing season temperature. Mean daily air temperature 1.0 m above the surface ranged from 3.0 to 6.3 °C with an average of 4.7 °C for the 1995, 1997, 2000, and 2001 growing seasons

(Table 2). During these same years, the seasonal mean daily maximum temperature ranged from 7.7 to 10.9 and seasonal mean daily minimum ranged from -2.3 to 1.2 °C (Table 2). Overall, 1997 was the warmest and 2000 was the coolest of the four study years. Soil temperature showed a similar pattern as that of air temperature (Figure 3). Precipitation was usually highest in July and August, but overall was highly variable among years (Figure 3).

Statistical analysis of microclimate data revealed differences for all recorded weather factors among years: air temperature, precipitation, wind speed, global radiation and soil temperature (Table 3). Air temperature, global radiation and soil temperature at 20 cm depth were also significantly different among years, and all daily averages except precipitation were significant for year x month interactions (Table 3).

Experimental manipulations resulted in an approximately 30% extension in the normal growing season length. The variability of spring weather conditions (snow load, temperature, and global solar radiation) affected the length of the early season manipulation. During the 1995 field season, warm spring temperatures led to 95% of the surface area of the control plots becoming snow-free by May 13th whereas complete snow melt on the manipulation plots occurred by May 6th, thus providing only a one week early season difference between the manipulations and the controls. Over the course of the study (1995, 1997, 2000, and 2001), manipulated plots became snow-free on average by May 3rd to May

7th. The control plots became snow free on May 13th, June 3rd, June 9th, and June 8th for 1995, 1997, 2000, and 2001, respectively (Table 4). These extensions coupled with the late season extension from August 14th to September 4th at the end of the growing season accounted for a 28, 49, 60, and 59 day extension of the growing season for each year, respectively.

Plant Tissue N and C:N Ratios

The overall patterns of carbon to nitrogen (C:N) ratios were similar among the treatments, with a general increasing trend of C:N as the season progressed (see for example *Betula nana*, Figure 4). The increase in C:N ratio was largely due to decreases in nitrogen concentration rather than increases in carbon concentration. The differences in seasonal pattern among years was due in part to differences in timing of the snowmelt which resulted in different collection times for the plants. In 1997 and 2000, plant tissue material was collected prior to plants fully senescing, so the C:N ratios were not as high as years 1995 and 2001 when plant tissue was collected as senescence occurred (Figure 4).

The C:N of four of the seven species differed significantly in response to treatment (Table 5). There were significant main effects of collection and year for all seven species, $p < 0.05$ (Table 5). Treatment x year was significantly different for *Lp* and *Vvi*. The year x collection interaction for C:N ratio was significant for all species except *Cb* and *Pb* (Table 5).

Plant Tissue P content

Phosphorus levels also decreased throughout the growing season for most species. Mean tissue phosphorus concentrations on the treatment plots were typically higher than those of the controls for most growth forms with the differences greatest early in the season (Figure 5). There were significant main effects of treatment for *Bn* and *Lp*, time for *Bn*, *Sp*, *Ev*, and *Lp*, and year for all species, $p < 0.05$ (Table 6). Mean phosphorus levels were significantly different across years for all species and collections except *Cb*, *Vvi*, and *Pb* (Table 6). Means were compared based on collections across years and were significantly different for all of the species (Table 6). Phosphorus concentration for treatment x year was significantly different for *Bn* (Table 6). The year x collection interaction was significant for phosphorus concentration in *Bn*, *Sp*, *Cb* and *Lp* (Table 6).

Litter Decomposition

Decomposition was very slow and the amount of mass loss was small (< 30% in 15 months, Table 7). With such slow rates, treatment differences were not apparent, although the tendency was for greatest loss on treatment plots. Litter weights were converted to percent dry mass remaining, which was then used to calculate a standard decomposition constant (k) using the formula:

$$X/X_0 = e^{(-kt)} \quad (1)$$

Where X_0 is the initial weight, X is the final weight and t = time since installation in days. Differences in k values among treatments were not significant, but again the tendency was for higher values on the treatment plots (Table 7).

After fifteen months of incubation, C:N ratios of both control and treatments were significantly higher compared to those of the control and treatments at the final collection. However, means compared across collections were not significantly different for treatments for any of the nutrient variables. For both experimental manipulations the tendency was for increased N and P concentrations, probably due to lower C relative to that of the controls (Table 7).

Soil Solutions

The seasonal patterns of ions from the soil solutions were distinct (Table 9, Figure 6). Potassium, $\text{NH}_4\text{-N}$, and Ca were higher at the end of the growing season than earlier (Table 9, Figure 6). Phosphorus and calcium concentrations were generally higher in the treatments than the controls. Although there were significant main effects of collection and year for P, K, NH_4 and Ca for nutrient concentration ($p < 0.05$), the main effect for treatment was not significant (Table 8). Mean nutrient concentration levels were significantly different across collection for all elements except Ca (Table 8). Nutrient concentrations for treatment x collection and treatment x year were not significantly different for any of the elements (Table 8). The year x collection interaction was significant for all elements except Ca (Table 8). There was a significant three-way interaction for treatment x year x collection for NH_4 (Table 8).

Exchangeable Ions

Exchangeable ions were sampled with ion exchange membranes once in 2000 and twice in 2001. The response of ion exchange membranes (IEMs) differed between tussock and intertussock locations. Manganese and iron concentrations were higher in intertussock locations (Figure 7). Potassium concentrations were higher in the tussock locations (Figure 7). Calcium and magnesium concentrations were variable for both location and treatments (Figure 7). There were significant main effects of treatment for P and K, location (tussock versus intertussock) for P, K and Fe, type of membrane for P, and collection (collection 1 or 2 in 2001) for P for nutrient solution concentration, $p < 0.05$ (Table 10). As expected, values for the heated and extended season plots were greater than those of the controls for both P and K in both years, with the exception of lower K on the heated plots than on the controls in 2001 (Table 11).

Interaction effects were significant for mean nutrient solution concentration levels across treatment x location (Table 10). Means were compared based on collection frequencies between types and collections for 2001 only and were significantly different for P (Tables 10 and 11). Treatment x location and location x type were also significantly different for P (Table 10).

Discussion

Treatments and microclimate

The treatments used in this study produced relatively small changes in the physical environment. Although the treatments lengthened the growing season approximately 30% on the study plots, about half of that was at the end of the growing season when plants are senescing in response to shortening daylengths (Shaver and Kummerow 1992, Oberbauer *et al.* 1998). The early season extension of approximately of 2-3 weeks is well within the range of variability of the natural timing of snowmelt at this site (Table 4, Hobbie *et al.* 2002).

Nevertheless, important effects on microclimate occurred in response to the snow removal treatment. Peak radiation at the site occurs in May; snow removal effectively shifts the growing season in the direction of higher solar inputs. Higher solar inputs over a longer period increase soil temperatures leading to increased depth of thaw. Soil temperatures at 5 cm on the snow removal treatments average about 1 °C warmer than temperatures in the controls (Oberbauer *et al.* 1998). The snow-removal plus soil warming treatment increases soil temperature about 2 °C (Oberbauer *et al.* 1998). A consequence of increased thaw depth is a lowering of the level of water perched above the frozen soil, decreasing soil moisture in the upper soil layers.

These microclimate changes have led to notable ecosystem effects. Bud break and green up occur earlier on the snow removal plots (Oberbauer *et al.* 1998,

Pop *et al.* 2000). Green biomass at peak season increases as indicated by increased Normalized Difference Vegetative Index (NDVI) and leaf area index (LAI, Oberbauer *et al.* 1998; Parker 2003). As a result of the increased biomass, ecosystem gross primary production increases (Oberbauer *et al.* 1998; Parker 2003).

The effect size of these treatments is strongly determined by the variability among years in terms of snow load, timing of snowmelt, cold temperatures in early season, and timing of the arrival of snow and cold temperatures-frost freeze events near the end of the season. Consequently, differences in plant and soil nutrients among the treatments must be interpreted within the context of this variability (Figure 4).

Plant Nutrient Response

Nutrient responses were relatively moderate among treatments and species, an expected finding given the mild treatment effects on the physical environment (McGraw 1987). These modest responses may also be attributed to the adaptation of tundra plants to chronically low nutrient environments, where having a high uptake capacity or growth rate is no advantage (Chapin 1980). Tundra plants are adapted to a wide range of seasonal and interannual climatic variation. Starr *et al.* (2000) in a detailed study of the forb, *Polygonum bistorta*, found no effect of the same snow removal treatments on leaf tissue nutrients.

When nutrient availability is increased, leaf tissue nutrients may respond in two ways: 1) the concentration of nutrients may increase, increasing the physiological activity of that tissue, or 2) the concentration of nutrients in leaves may remain the same, but the amount of tissue produced increases. Some combination of the two is possible, which likely occurred in this study, where biomass clearly increased with relatively small changes in tissue concentrations.

Evaluation of plant responses to changes in nutrient availability is also complicated in the Arctic by carryover and lag effects from previous years due to adaptations to the short growing season. Leaf and flower primordia for a given year's growth are typically preformed the previous year. Consequently, a plant may not be able to respond to additional nutrients by increasing growth the year that they become available. Bowman and Conant (1994), working at Niwot Ridge, Colorado, showed that in response to fertilization a deciduous alpine tundra species had higher leaf tissue nutrients concentrations in the first year (when the number of leaves was predetermined) than the following years when leaf tissue concentrations fell back to original levels, but leaf production was greatly increased.

Superimposed on the plant responses and their lags are the differences in treatment strength as a result of the year-to-year seasonal temperature variation. The interannual variability also affected the tissue concentrations through its effect on plant phenology. Sampling was initiated based on when snow-melt

occurred. Consequently, samples were not taken at the exact same time of year, and because of interannual temperature differences and their effects on rates of phenological change, samples were not necessarily at the same phenological stage at sampling each year. This difference explains the large variation in C:N ratios at the end of the season because in some years senescence was more advanced than in others at the time of collection. The tissue nutrients for the different growth forms were most strongly influenced by collection (time of season), then by year, and lastly by treatment.

Litter decomposition

Decomposition was slow (<30%) during the fifteen months. Low soil temperature may have contributed to the low rate; years 2000 and 2001 were the coldest years (see averages in Table 2) of the study. Drying of soil surface may also have lowered the rate of decomposition on the treatment plots. Liski *et al.* (2003) were able to explain the decomposition rates of various litter types tested in a range of environments over large geographical using a simple model based on temperature and drought effects.

The tissue from birch leaves is relatively recalcitrant and requires a long incubation period to break down (Hobbie 1996). At the rates found in this study, it would have taken 6 y for 50% of the litter to decompose. Mary *et al.* (1996) have shown that for incubations carried out at low mineral N concentrations, the

decomposition rate of plant residues is decreased but not stopped. The immobilization intensity, expressed per unit of mineralized C, is reduced and N remineralization is delayed. Nitrogen availability in soil can therefore strongly modify the mineralization-immobilization turnover kinetics by a feed-back effect (Mary *et al.* 1996). The trend observed in my study was indicative of increased decomposition with treatments. Given more time, the trend is likely to show significant differences among the treatments, although the drying effect of treatments on decomposition may dampen the response.

Soil solutions

No significant differences in soil solution nutrients were found among treatments in this study. This finding suggests a strong competition of roots with microbes and consequently, maintenance of soil solution nutrients at very low concentrations. An intriguing result was the increase of NH_4 across years. However, it is unclear if this is an artifact of the sampling methodology or a real phenomenon. Likewise, there was a higher concentration of NH_4 in 1997. However, there was a late collection in September that was not conducted the other years in the study that may have skewed the values higher. Otherwise, we see a general decreasing trend in nutrient concentration throughout the season. I should also note that uptake of organic nitrogen components have been shown to be an important component of nitrogen balance of tundra plants (Kielland 1994; Chapin 1995), but were not addressed in this study. However, these

components would have likely responded similarly to the treatments as the inorganic forms of nitrogen.

Ion exchange membranes

Ion exchange resins provide a more realistic estimate of what is bioavailable to the plants than soil solutions. The exchange membranes did indicate significant treatment effects for phosphorus and potassium. Gibling *et al.* (1994) observed that landscape differences in N vs. P availability ascertained from resins corresponded well with N/P ratios in soils and soil solutions and with results from factorial fertilizer experiments. Seasonal patterns of nutrient availability determined by resins were also consistent with plant uptake data (Gibling *et al.* 1994).

Where the membranes were located in my study also had a significant effect on the results. Tussock locations were higher in concentrations for P, K, and Mg. This finding has important implications for nutrient partitioning among vascular species. Tussocks are occupied predominantly by *Eriophorum vaginatum*, which send annual roots vertically to exploit decomposing tissue. Other species largely are only able to exploit intertussock areas.

Nutrient dynamics in response to snow removal and soil warming

All of the available evidence suggests that snow removal and soil warming increases the nutrients available for plants. These plots have undergone

community changes and species abundance shifts, as well as exhibiting higher NDVI, LAI and gross primary productivity (Oberbauer *et al.* 1998; Parker 2003, Walker *et al.*, unpublished data). My results support these observations and point to the overall mechanism behind them. I found higher N and P concentrations in several of the species in response to the experimental treatments. Given the higher nutrient concentrations and higher leaf area production, there is a substantial elevation of aboveground nutrient pools in treatment plots. Decomposition rates tend to be faster on the treatment plots. As more nutrient rich leaves from treatments decompose, there may be further increases in cycling rates. Soil solutions tended to be higher on treatment plots, and ion exchange membranes revealed significantly higher nutrient availability in response to snow removal. These results point to faster nutrient cycling in response to the snow removal and warming treatments.

My objectives were to evaluate the effects of season extension and soil warming, on nutrient availability within tussock tundra. My results clearly showed that nutrient availability in the system increased. However, a larger issue is whether this increase is sustainable or a transient phenomenon that is a result of lags in the system on its way to a new steady-state. Changes in primary production depend mainly upon the response of soil microbial decomposer activity to changes in soil temperature, moisture and plant litter quality (Callaghan and Jonasson 1995b). Assumptions that climate warming will lead to warmer soils

and increased nutrient availability to sustain higher productivity are uncertain as greater biomass may lead to reduced soil temperatures through insulation effects, and additional nutrients released may be immobilized by soil microorganisms (Callaghan and Jonasson 1995b).

Arctic ecosystems have limited productivity due to low air and soil temperatures (Jonasson and Shaver 1999). Inorganic nutrient pools are small, limiting plant growth (Jonasson and Shaver 1999). Nutrient inputs from external sources are typically minimal, and pools in the vegetation also are small (Jonasson and Shaver 1999). In contrast, organically-bound nutrient stocks are large but mostly unavailable for plant uptake (Hobbie and Chapin 1998). If released slowly with increased decomposition, they could sustain increased growth for some time (Grogan and Chapin 2000). Arctic vegetation is very efficient in acquiring nutrients. By minimizing the seasonal nutrient losses and reducing the demand for nutrient uptake, tissue production and growth can continue for an extended period (Grogan and Chapin 2000).

Higher productivity is also sustainable with higher turnover rates (Grogan and Jonasson 2003). With higher productivity, more nutrients become available and leaf turnover increases with faster cycling of nutrients. In this ecosystem, more than 90% of the nitrogen and phosphorus absorbed by plants each year comes from the recycling of nutrients that were returned from vegetation to soils the previous year (Vitousek 1982). Tissue senescence is the major mechanism of

nutrient loss from arctic vascular species. All else being equivalent, a reduction in tissue turnover causes a corresponding reduction in the turnover of the associated tissue nutrients. Plants compensate by reducing senescence loss of nutrients predominantly by reducing tissue turnover (Gifford *et al.* 2000). Tissue turnover is strongly reduced in low-resource environments such as the Arctic (Chapin *et al.* 1993). Low tissue turnover is probably the single most important adaptation for nutrient retention within this low-nutrient habitat (Gifford *et al.* 2000).

I did not address retranslocation of nutrients, but changes in retranslocation could accelerate nutrient cycling (Shaver and Laundre 1997). Nutrient resorption plays a crucial, but not completely understood, role in nutrient retention by plants. On average, plants in the Arctic resorb about half of their nitrogen, phosphorus and potassium from leaves before leaves are shed at senescence, so nutrient resorption is quantitatively important to plant nutrient budgets (Tolvanen and Henry 2001). Under field conditions, nutrient resorption may be influenced by so many factors that no single environmental factor has been identified as the primary control (Eckstein *et al.* 1999). Alternatively, nutrient resorption may be such an important trait that it is equally expressed in all arctic vascular plants.

Turnover times of the bulk soil organic matter in the Arctic can range from a few decades in the most productive systems to several centuries in the most nutrient-deficient ecosystem types (Jonasson and Shaver 1999). Decomposition rates of

the soils are controlled by the varying environmental conditions (temperature, snow load, and soil-moisture) and nutrients can be strongly immobilized within the soil-microbial ecosystem compartment if the soil is nutrient poor (Zepp *et al.* 2003). The composition of the vegetation regulates the turnover of plants and plant nutrients but plays a less important role for the function of the entire plant-soil system (Jonasson and Shaver 1999). Characteristics of nutrient cycling at the larger scale level are less important for the function of the overall soil-plant system and characteristics of the plants in general (such as nutrient resorption, tissue type, and leaf longevity, etc.). These processes reflect the function of the system rather than play a major role in regulating ecosystem function (Jonasson and Shaver 1999).

The primary effects of my experimental treatments were warmer soils and deeper thaw depth, both of which increased nutrient availability for plants. Greater thaw depth both increases volume of soil available for rooting and lowers the water table thereby increasing the aerated zone in the soil. However, warmer soils may increase evaporation and lower soil moisture at the surface, a result that would tend to reduce decomposition rates (Hobbie 1996). The consequences of this drying may partially counteract the warming effects on a long-term basis.

Increased season length is only one of several possible scenarios for arctic-region season length predicted by GCMs. While the evidence is overwhelming that climate is warming in Alaska (Rabus and Echelmeyer 2002; Walker *et al.*

2003), 3 of the last 4 y at the study site have had very late snowmelt, providing a shorter than normal growing season. Climate variability among the study years was very large. Virtually, all nutrient parameters differed significantly among years with significant interactions with collection date, suggesting that interannual variability in weather is driving many of the responses seen in this study. The season length signal of the treatments may have been overwhelmed by the noise of large interannual variability and its effects on seasonality.

Of all the components of environmental change (radiation inputs, CO₂ concentration, nutrient availability, temperature, snow load, and soil-moisture), the ultimate driver for future change in arctic vegetation is likely to be increased nutrient availability (Gifford *et al.* 2000). Minor changes in precipitation, increases in radiation and increased atmospheric CO₂ concentration alone will have little effect on arctic plants in the short term without an increase in nutrients to support additional growth. Any factors that change nutrient availability, such as temperature elevation or external nutrient inputs, however, will cause immediate plant-growth responses and alter nutrient cycling. In the case of increased nutrient and/or temperature, the effects on nutrient cycling may create positive feedbacks on plant biomass (Hobbie 1996). Thus, interactions among species, growth forms, resources, and climate may result in dramatic alterations in arctic communities and ecosystems on a long-term basis (Wolters *et al.* 2000).

Table 1. The selected study species and their growth forms. The abbreviations used throughout the text are indicated below for each species.

Forb	Graminoid	Deciduous shrub	Evergreen shrub
<i>Polygonum bistorta</i> (Pb)	<i>Eriophorum vaginatum</i> (Ev) <i>Carex bigelowii</i> (Cb)	<i>Betula nana</i> (Bn) <i>Salix pulchra</i> (Sp)	<i>Ledum palustre</i> (Lp) <i>Vaccinium vitis-idaea</i> (Vvi)

Table 2. Estimated means by Year for Daily Mean, Maximum, and Minimum Air Temperature (°C) May - September 1995, 1997, 2000, and 2001.

Year	Mean air temperature (°C)	Maximum air temperature (°C)	Minimum air temperature (°C)
1995	5.9	10.4	1.2
1997	6.3	10.9	1.3
2000	3.0	7.7	-2.3
2001	3.7	7.7	-2.0

Table 3. Summary of microclimate properties for Toolik Field Station (May - September) for years 1995, 1997, 2000, and 2001. Values are all daily averages and * indicates significance at $p < 0.05$.

Month 5-9	Air Temper- ature Mean °C	Precipitation Total mm	Wind Speed m/s	Global Radiation J/cm ²	Soil Temperature °C at 20 cm
Year	*			*	*
Month	*	*	*	*	*
Year x Month	*		*	*	*

Table 4. Dates of snowmelt and snow depth at the study site for 1995, 1997, 2000, and 2001.

Year	Date of Snowmelt	Snow Depth on May 2
1995	5/13	52.8
1997	6/3	65.4
2000	6/9	62.2
2001	6/8	65.0

Table 5. Summary of ANOVA for plant tissue Carbon:Nitrogen ratio (Treatments C, E, H for 1995, 1997, 2000, and 2001). See Table 1 for species abbreviations.

Main Effects	Species						
Treatment	Bn	Sp	Ev			Vvi	
Collection	Bn	Sp	Ev	Cb	Lp	Vvi	Pb
Year	Bn	Sp	Ev	Cb	Lp	Vvi	Pb
Treatment x Collection							
Treatment x Year					Lp	Vvi	
Year x Collection	Bn	Sp	Ev		Lp	Vvi	
Treatment x Year x Collection							

Table 6. Summary of ANOVA for plant tissue Phosphorus (Treatments C, E, H for 1997, 2000, and 2001). See Table 1 for species abbreviations.

Main Effects			Species					
Treatment	Bn			Lp				
Collection	Bn	Sp	Ev	Lp				
Year	Bn	Sp	Ev	Cb	Lp	Vvi	Pb	
Treatment x Collection								
Treatment x Year	Bn							
Year x Collection	Bn	Sp	Cb		Lp			
Treatment x Collection x Year								

Table 7. Litter decomposition summary for final weight, decomposition constant (k), % N, % P, C:N and C:P ratios for 2000 and 2001. P-values are for tests of all treatments including initial. No significant effects were found for comparisons of control versus treatments alone.

	Final Weight	k	% N	% P	C:N ratio	C:P ratio
Initial	~2.000		0.91	0.200	62.50	249.09
C	1.539	7.77×10^{-4}	1.13	0.244	49.61	207.69
E	1.430	9.31×10^{-4}	1.16	0.208	45.50	221.90
H	1.321	8.67×10^{-4}	1.20	0.229	45.78	219.09
p-value		0.166			<0.001	

Table 8. Summary of ANOVA for soil solutions (Treatments C, E, H for 1995, 1997, 2000, and 2001). * indicates significance at $p < 0.05$

Main Effect	P	K	Ca	NH ₄
Treatment				
Collection	*	*		*
Year	*	*		*
Treatment x Collection				
Treatment x Year				
Year x Collection	*	*		*
Treatment x Year x Collection				*

Table 9. Estimated mean concentrations (mg/L) of soil solution nutrients by collection and year for Phosphorus (P), Potassium (K), Ammonium (NH₄), and Calcium (Ca). Symbols:n/a = not available, n/m= not measurable

Collection	Year	Mean (P)	Mean (K)	Mean (NH ₄)	Mean (Ca)
1	1995	0.078	0.693	0.110	1.459
	1997	0.072	0.872	0.150	1.672
	2000	0.080	0.574	0.228	1.562
	2001	0.011	0.041	0.254	1.470
2	1995	0.099	0.678	0.072	1.884
	1997	0.061	0.497	0.028	1.407
	2000	0.027	0.721	0.152	1.946
	2001	0.006	0.091	0.213	1.897
3	1995	n/m	0.568	0.034	1.436
	1997	0.012	0.617	0.117	1.444
	2000	0.015	0.898	0.193	2.056
	2001	0.039	0.697	0.155	1.425
4	1995	n/a	n/a	n/a	n/a
	1997	0.016	0.538	0.056	1.368
	2000	0.017	0.570	0.183	2.012
	2001	n/m	1.219	0.208	1.444

Table 10. Summary of ANOVA for labile ions from ion exchange membrane results (Treatments C, E, H for 2000 and 2001). Only one collection was made in 2000; italicized effects indicate those effects that were only relevant to tests for 2001.

Main Effects Year	Ions (P, K, Ca, Mg, Mn, Fe, NO ₃)	
	2000	2001
Treatment	K	P
Location	K	P Fe
<i>Collection</i>		P
Treatment x Location	Mn	
<i>Treatment x Collection</i>		
<i>Location x Collection</i>		

Table 11. Potassium (K) and Phosphorus (P) concentrations (mg/L) from ion exchange membranes for 2000 and 2001.

Treatment	2000		2001 (Mean of two collections)	
	K (mg/L)	P (mg/L)	K (mg/L)	P (mg/L)
C	24.02	0.207	16.29	0.718
E	43.57	0.390	17.77	1.083
H	32.86	0.268	14.24	0.896

Figure 1. Alaska map with Toolik Field Station (TFS). (Map courtesy of Institute of Arctic Biology (IAB) at University of Alaska Fairbanks).

Figure 2. Plot layout of the study site.

Figure 3. Means of daily global radiation, air temperature, soil temperature at 20 cm, and precipitation from May to September for 1995, 1997, 2000, and 2001.

Figure 4. Carbon:Nitrogen ratio for *Betula nana* for four collections in 1995, 1997, 2000, and 2001.

Figure 5. Mean concentrations (mg/g) of tissue phosphorus for four collections and three treatments for a representative species from each growth form. Means are averages of values from 1997, 2000, and 2001.

Figure 6. Mean concentrations of nutrients from soil solutions (mg/L) for four collections and the three treatments. Means are averages of values from 1995, 1997, 2000, and 2001.

Figure 7. Mean concentrations of labile ions from ion exchange membranes (mg/L) for location (tussock and intertussock) collections.

Chapter 3.

Conclusions

The objective of this work was to assess the effects of experimental soil warming and lengthening of growing season on the nutrient dynamics of tussock tundra in Northern Alaska. The results of this study indicate that snow removal and soil warming increase the nutrients available for plants and accelerate the rate of nutrient cycling in tussock tundra. This conclusion is based in part on higher N and P concentrations in plant tissue nutrients in response to the experimental treatments. Given the higher nutrient concentrations found in my study and higher leaf area production observed by others, there must be a substantial elevation of aboveground nutrient pools in response to the experimental manipulation. I also found indications of increased decomposition rates on the treatment plots. Soil solution nutrient contents tended to be higher on treatment plots, and ion exchange membranes revealed significantly higher nutrient availability in response to snow removal and soil warming. This increase in nutrient availability is likely a result of the soil environmental changes induced by snow removal, increased soil temperatures and increased soil depth of thaw. These changes in soil environment presumably increased mineralization rates of limiting nutrients for plants as well as increased the soil volume available for root exploitation.

At the ecosystem level, the observed increase in nutrient availability has important implications for tundra carbon balance. Greater aboveground nutrients

should lead to increased gross primary production, and such increases have been observed. Additionally, warmer soil environments and increased aboveground biomass should also increase ecosystem respiration, which also has been observed on the study plots. The overall carbon balance of these ecosystems will depend on the magnitude of these processes and how long changes in nutrient availability persist.

These treatment effects on nutrient dynamics, although significant in many instances, were superimposed on a background of large year-to-year variability, probably a result of large inter-annual differences in weather and timing of snowmelt. Plants of arctic environments are specifically adapted to low nutrient availability and possess traits that help reduce nutrient losses such as slow growth, low tissue concentrations, and low tissue turnover. These traits, while allowing plants to persist in highly variable environments, ultimately result in relatively subtle responses to environmental change such as those imposed by this experiment.

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