EFFECTS OF A TEN-YEAR CLIMATE WARMING EXPERIMENT ON NITROGEN CYCLING IN HIGH ARCTIC TUNDRA

by

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THE UNIVERSITY OF BRITISH COLUMBIA

March, 2003

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Date 11 March 2003
ABSTRACT

The effects of a 10-year climate warming experiment on nitrogen (N) cycling in high arctic tundra ecosystems were examined along a soil moisture gradient at Alexandra Fiord, Ellesmere Island, Canada (78°53'N, 75°55'W). Open top chambers were established in 1992 to passively warm five tundra plant communities within the range predicted for a doubling of atmospheric CO₂. Inorganic N availability, measured using ion exchange membranes, was consistently higher in the warmed plots throughout the growing season in three plant communities. Soluble organic N availability increased significantly with warming in a wet sedge meadow. Net N mineralization in buried bag incubations was not significantly affected by the warming treatments; however, net N immobilization was four-times higher in the warmed plots compared to the controls in the sedge meadow. Reciprocal transplantation of buried bags between temperature treatments indicated that the increase in net N immobilization was a result of changes in soil properties during the nine-year experiment, in conjunction with continued temperature enhancement.

Significant reductions in litter quality, measured as C:N ratios, were observed for woody and herbaceous growth forms in the warmed treatments at the end of the growing season. Reproductive parts had higher C:N than vegetative parts, and C:N increased with warming. Therefore, previously observed increases in reproductive effort with warming have likely reduced litter quality. Despite this potential for negative litter quality feedbacks to N availability with warming, soil organic matter was not significantly affected by the ninth year of the experiment.

We hypothesize that the short-term changes in soil N transformations and increased N availability have contributed to the increases in plant growth observed in the warmed plots, and that shifts in the relative availabilities of NO₃, NH₄, and SON may have contributed to changes in the species composition of the tundra plant communities. However, this negative feedback to greenhouse warming may be strongly constrained by longer-term litter quality feedbacks to soil organic matter quality and N availability in high arctic tundra ecosystems.
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CHAPTER 1: INTRODUCTION & RESEARCH OBJECTIVES

1.1. INTRODUCTION

The effects of a 10-year climate warming experiment on N cycling were studied at five sites along a soil moisture gradient at Alexandra Fiord, Ellesmere Island, Canada. This thesis has been divided into two main chapters; Chapters two and three examine the effects of the warming experiment on:

II. Soil N processes and bioavailability, and
III. Plant litter and soil quality.

The chapters have been separated according to the temporal scales at which climate warming may affect plant N availability. Daily and seasonal changes in temperature affect soil processes of microbial N mineralization and immobilization, which directly affect N bioavailability over short time scales. Conversely, changes in plant litter chemistry, with changes in plant nutrient use efficiency, allocation, and species composition, will affect soil organic matter quality, thereby affecting soil N processes and bioavailability at longer time scales (Shaver et al. 2000). The triangular relationship between climate, litter chemistry and decomposition illustrates the rationale for the division between Chapters 2 and 3 in this thesis (Figure 1) (Aerts, 1997).

![Figure 1: The triangular relationship between climate, litter chemistry, and decomposition modified from Aerts (1997). The three ways in which changing climate may impact litter chemistry are also shown in the bottom right corner. The distinction between the main chapters of this thesis is illustrated.](image)
1.2. RESEARCH OBJECTIVES

During the tenth year of temperature manipulations at Alexandra Fiord, Ellesmere Island, Canada, the main objectives of this study were to:

1. Investigate the impacts of 10 years of temperature manipulations on soil N availability in five plant communities of the high arctic;

2. Evaluate net N mineralization and immobilization processes between the control and experimentally warmed treatments;

3. Determine if changes in net N mineralization and/or immobilization between the temperature treatments were a result of direct, short-term temperature influences on soil N processes, and/or indirect, longer-term temperature effects through changes in soil properties;

4. Examine changes in litter and soil organic matter quality in response to the warming manipulations to evaluate potential feedbacks to N availability.

5. Compare the sensitivity of different arctic tundra plant communities and soil types to the climate warming manipulations.
CHAPTER 2: THE EFFECTS OF A TEN-YEAR CLIMATE WARMING EXPERIMENT ON NITROGEN MINERALIZATION AND AVAILABILITY IN HIGH ARCTIC TUNDRA

ABSTRACT
The effects of a 10-year climate warming experiment on nitrogen (N) availability and processes of mineralization and immobilization were examined along a soil moisture gradient at Alexandra Fiord, Ellesmere Island, Canada (78°53'N, 75°55'W). Open top chambers were used to passively warm five tundra plant communities within the range predicted for a doubling of atmospheric CO₂. Inorganic N availability, measured using ion exchange membranes, was consistently higher in the warmed plots throughout the growing season in three plant communities. Soluble organic N (SON) availability increased significantly with warming in a wet sedge meadow. Net N mineralization in buried bag incubations was not significantly affected by the warming treatments; however, net N immobilization was four-times higher in the warmed plots compared to the control treatments in the wet sedge meadow. Reciprocal transplantation of the buried bags between temperature treatments indicated that the observed increase in net N immobilization was a result of longer-term changes in soil properties during the ten-year experiment, in conjunction with continued temperature enhancement. We hypothesize that changes in soil N transformations and increased N availability under warmer climate conditions have contributed to the increases in biomass observed at the study site, and shifts in the relative availabilities of NO₃⁻, NH₄⁺, and SON have contributed to changes in the species composition of the tundra plant communities. These findings indicate that responses of high arctic tundra systems to warming may not be strongly constrained by nutrient limitations.

2.1. INTRODUCTION

2.1.1. The International Tundra Experiment

In response to predictions that climate change will be most pronounced in high latitude regions (Maxwell 1992, Houghton et al. 1996, Hagen et al. 2001), the International Tundra Experiment (ITEX) was established to examine variability in tundra plant species response to climate warming during long-term manipulations of growing season temperature and duration (Henry and Molau 1997). A meta-analysis of the first four years of data from 13 ITEX sites indicated a shift from a primary growth response to a secondary reproductive response, that may be due to decreases in nutrient availability (Arft et al. 1999). The focus of this research, therefore, was to evaluate the effect of warming on plant N availability and soil N transformations at a study site in the high arctic. The goal was to help explain plant community responses to the 10-year warming experiment at this site.
2.1.2. The Nitrogen Economy of Arctic Ecosystems

Fertilizer addition experiments have shown that N is the primary limiting resource to plant growth in arctic tundra ecosystems (Shaver and Chapin 1980, 1986, Henry et al. 1986). Although substantial amounts of organic N are held within tundra soils, low temperatures and anaerobic soil conditions in some wetland systems reduce rates of N mineralization. Chapin et al. (1980a) refer to this as the “bottleneck in the N cycle of arctic ecosystems.”

There is abundant evidence that soil microbial communities elicit strong controls on N availability in tundra soils. Low, or negative, net N mineralization rates are common during the growing season (Giblin et al. 1991, Jonasson et al. 1993). Stimulation of plant productivity in fertilization experiments often requires additions of N that far exceed the annual plant requirement (Shaver and Chapin 1980). Jonasson et al. (1996) found that microbial biomass doubled within four weeks of fertilizer addition. Because a large proportion of nutrients are fixed in the soil microbial pool of arctic ecosystems, fluctuations in the microbial N pool will have significant impacts on N availability to plants (Jonasson et al. 1999). Increased microbial activity and N immobilization under warmer growing conditions may reduce N availability and constrain plant productivity. It is important, therefore, to include evaluations of microbial N immobilization in climate manipulation experiments.

Nitrogen that is immobilized during the growing season may be released in the winter as microbial populations decline, leading to annual positive N mineralization rates (Giblin et al. 1991, Hobbie and Chapin 1996). Chapin et al. (1978) hypothesized that repeated freezing and thawing of soils lyses the cells of dying microbes, and releases the mineralized nutrients within. This flush of available N is absorbed by perennial tundra plants, and utilized during the following growing season (Chapin, 1980b, Marion and Kummerow 1990). Investigations of soil N processes should be conducted on annual time scales because of the strong seasonal cycles of immobilization and mineralization.

2.1.3. Effects of Climate Warming on the Nitrogen Economy of Arctic Ecosystems

Predicted climate change in high latitudes, leading to longer and warmer growing seasons, deeper active layers, drier soils, and increased N mineralization rates, will initially increase plant available N (Maxwell 1992, Nadelhoffer et al. 1992). This has potential to increase plant growth, net primary productivity, and net ecosystem carbon (C) storage, providing a negative feedback to greenhouse gas induced climate warming (Rastetter et al. 1991).
Small increases in growing season net N mineralization have been observed in some high latitude warming experiments (Jonasson et al. 1993, Robinson et al. 1995, Schmidt et al. 2002), however, significant increases have only been observed when experimental warming exceeded 5°C above ambient conditions (Shaver et al. 1998, Hartley et al. 1999) (Table 1). This is within the upper limit of growing season air temperature increase predicted for high latitudes with a doubling of atmospheric carbon dioxide (CO₂) (Maxwell 1992). Schmidt et al. (2002) examined net N immobilization in response to warming at two sites in Abisko, Sweden and two sites in Alaska, USA. Average N immobilization generally increased under warmer growing season conditions, although the differences between temperature treatments were not statistically significant. In a meta-analysis, Rustad et al. (2001) found a positive effect of warming on net N mineralization across 12 sites; however, seven of the sites were from Abisko, Sweden. There were no significant effects within any biome (high arctic tundra, subarctic tundra, or temperate forest). This illustrates the need for more studies that include evaluations of both N mineralization and N immobilization in response to predicted climate change. In order to examine variability in ecosystem responses to climate change, these studies should span broader climatic and geographic gradients.

2.1.4. Long-term Feedbacks to Nitrogen Availability with Changing Climate

Climate change could affect decomposition and N mineralization rates directly through short-term influences on soil microbial activity (discussed above), and indirectly by affecting litter production, litter chemistry, and soil organic matter quality at longer time scales (Aerts 1997, Shaver et al. 2000). Soil temperature, water content, and organic matter quality elicit the strongest controls on decomposition rates and N mineralization rates in arctic tundra systems (Heal and French 1974). After comparing litter decomposition rates, litter chemistry and climate from 44 locations, Aerts (1997) agreed with the hierarchically organized model of decomposition control following the order of: climate > litter chemistry > soil organisms (Swift et al. 1979), at the global scale. At regional and local scales, however, litter quality was the best predictor of decomposition rate.

Hobbie (1996) found that the variability in decomposition rate and N release between litter types was as great as the variability for the same litter type at different temperatures in a microcosm experiment. Furthermore, species and growth form sometimes had a greater effect on decomposition and N release than incubation temperature. Similar findings have been observed
Table 1: Summary of similar high latitude warming experiments and the general effects on net N mineralization (MIN) and immobilization (IMMOB).

<table>
<thead>
<tr>
<th>Reference</th>
<th>Treatment &amp; Location</th>
<th>Site Description(s)</th>
<th>Temperature Increase</th>
<th>Year of Exp.</th>
<th>Effect on Soil N Processes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jonasson et al. 1993</td>
<td>Warming with greenhouses - Abisko, Sweden</td>
<td>subarctic dwarf shrub heath</td>
<td>air: +5°C, soil +1-2°C</td>
<td>2</td>
<td>No significant effect on growing season MIN.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high altitude fellfield</td>
<td>air: +5°C, soil +1-2°C</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Robinson et al. 1995</td>
<td>Warming with polyethylene tents - Abisko, Sweden.</td>
<td>high arctic polar semi desert</td>
<td>air: +3.5°C, soil +0.7°C</td>
<td>3</td>
<td>No significant effect on growing season MIN. Means were higher in warmed treatments for both sites</td>
</tr>
<tr>
<td></td>
<td></td>
<td>subarctic dwarf shrub heath</td>
<td>air: +2.8°C, soil -0.3°C</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>* Effects after 2 and 5 years.</td>
<td></td>
<td>5</td>
<td>No significant effect in year 5.</td>
</tr>
<tr>
<td>Schmidt et al. 2002</td>
<td>Warming with greenhouses - Abisko, Sweden &amp; Toolik Lake, Alaska, USA.</td>
<td>low altitude heath (Sweden)</td>
<td>air: +4 to +5°C</td>
<td>5</td>
<td>No significant effect. MIN and IMM30B means were higher in warmed plots on all sites with one exception.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high altitude fellfield (Sweden)</td>
<td>soil: +1 to +2°C</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>tussock tundra (USA)</td>
<td>(avg. for all sites)</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>wet sedge tundra (USA)</td>
<td></td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Nadelhoffer et al. 1991</td>
<td>Lab incubations of six arctic soils at 3 temperatures - Alaska, USA.</td>
<td>Soils from a toposequence, from tussock tundra (high)</td>
<td>treatment a: 3 - 9°C</td>
<td>1</td>
<td>MIN Insensitive to temperature from 3 - 9°C. Significant differences between 9 - 15°C.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>to riverside willow (low.)</td>
<td>treatment b: 9 - 15°C</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(air)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shafer et al. 1998</td>
<td>Warming with greenhouses - Toolik Lake, Alaska, USA.</td>
<td>Wet sedge tundra</td>
<td>air: +5.6°C</td>
<td>8</td>
<td>MIN increased significantly by 40-200%</td>
</tr>
</tbody>
</table>
in the field (Giblin et al. 1991), and other lab experiments (Nadelhoffer et al. 1991, Binkley et al. 1994). Nutrient addition affects allocation patterns in tundra species more than manipulations of other resources; therefore, warming will likely affect allocation patterns in tundra species indirectly through changes in N availability (Chapin and Shaver 1996). Changes in allocation, and species composition with climate change will have significant impacts on nutrient cycling in tundra ecosystems (Hobbie 1996). Ecosystem feedbacks to CO₂-induced greenhouse warming will be constrained by carbon/nutrient interactions (Shaver et al. 1992).

Changes in litter quality can also occur through changes in litter chemistry at the individual plant level. Increased growth and nutrient use efficiency under warmer growing conditions increase plant tissue C:N ratios (Shaver et al. 1992). Furthermore, C:N ratios increase as photosynthates are stored, rather than being allocated to plant tissue construction if nutrient uptake is insufficient for increased growth (Bryant et al. 1983). During the 5th year of experimental warming at Alexandra Fiord, Tolvanen and Henry (2001) observed significant increases in C:N ratios of woody growth forms in the warmed plots. Following seven years of warming, Welker (2000, personal communication) observed consistent decreases in plant tissue N concentrations for shrub, forb, and sedge growth forms in the warmed plots of three plant communities in the Alexandra Fiord lowland. These findings indicate potential for individual species to affect soil organic matter quality and soil N processes in this warming experiment.

The effects of warming on soil N transformations and N availability will help to explain plant community responses to climate change in this experiment. Because microbial communities elicit strong, seasonal controls on soil N availability, evaluations of both of the opposing processes of N mineralization and N immobilization were conducted on annual time scales. In order to examine variability in ecosystem responses to climate change, manipulations that attempt to simulate climate changes should span broad climatic and geographic gradients. Feedbacks to initial ecosystem responses, including changes in soil N transformations and N availability, should continue to be evaluated in long-term climate manipulation experiments (Shaver et al. 2000).

2.1.5. Research Objectives

This study was conducted during the tenth year of temperature manipulations along a soil moisture gradient in the high arctic. The main objectives were to:
1. Investigate the impacts of 10 years of temperature manipulations on soil N availability in five plant communities of the high arctic;

2. Evaluate net N mineralization and immobilization processes between control and experimentally warmed treatments;

3. Determine if changes in net N mineralization and/or immobilization between the temperature treatments were a result of direct, short-term temperature influences on soil N processes, and/or indirect, long-term temperature effects through changes in litter chemistry and soil properties;

4. Compare the sensitivity of different arctic tundra plant communities and soil types to experimental warming.

2.2. METHODOLOGY

2.2.1. Site Description

This research was conducted at the Alexandra Fiord lowland (78°53'N, 75°55'W), on the eastern side of Ellesmere Island, Nunavut, Canada (Figure 2). The 8-km² lowland is situated on a relatively flat, triangular glacial outwash plain and has been ice-free for approximately 7000 years (Freedman et al. 1994). The valley is bordered to the south by glacial ice and to the north by the fiord. Precambrian bedrock cliffs, 500 to 700 m high, surround east and west sides of the valley. A glacier-fed river and three smaller streams drain the lowland to the northern ocean shore.

The climate of this high arctic oasis is warmer than the surrounding polar desert as a result of relatively clear sky conditions and radiation of long-wave energy from the surrounding bedrock cliffs and dark soils (Labine 1994). The prevailing winds are from the south, which are frequently accompanied with warm weather Chinooks (Labine 1994). Average annual and growing season air temperatures for the period from 1980 to 1988 were -12.3°C and +5.1°C, respectively (Labine 1994). Precipitation at Alexandra Fiord is minimal, with usually less than 1.0 cm falling during the growing season.

The Alexandra Fiord lowland has well-developed, stable soils that are characteristic of polar oases (Muc et al. 1994a), and provide habitats for diverse plant communities relative to the upland polar desert (Muc et al. 1989). The Alexandra Fiord lowland oasis is 90% covered by closed or semi-closed vegetation (Muc et al. 1994b), which is substantially greater than the 5% cover in the surrounding polar deserts (Bliss et al. 1994).

Nitrogen availability was examined in five plant communities along a soil moisture gradient. Table 2 outlines the dominant plant communities in the Alexandra Fiord lowland. Three of these
Figure 2: The study site at Alexandra Fiord on the East coast of Ellesmere Island, Nunavut, Canada. 78°53'N, 75°55'W. Map by D. Bean, Department of Geography, UBC.
Table 2: The five dominant plant communities at Alexandra Fiord as described by Muc et al. (1989). Shaded cells indicate the plant communities in the lowland that are included in this study.

<table>
<thead>
<tr>
<th>Plant Community &amp; % Lowland Cover</th>
<th>Most Prominent Vascular Species</th>
<th>Soil Moisture Class, Type</th>
</tr>
</thead>
</table>
| **Sedge, Cushion Plant, Dwarf Shrub**  
(S-CP-DS) 28.4% | Monocots: *E. angustifolium*, *C. stans*, *C. membranacea*  
Dicot Forbs: *S. oppositifolia*, *P. viviparum*, *O. digyna*  
Dicot Woody: *D. integrifolia*, *C. tetragona*, *S. arctica*, *V. uliginosum* | hydric  
organic |
| **Cushion Plant, Plant, Dwarf Shrub**  
(CP-DS)* 18.7% | Monocots: *L. nivalis*  
Dicot Forbs: *S. oppositifolia*  
Dicot Woody: *D. integrifolia*, *C. tetragona*, *S. arctica*, *V. uliginosum* | hydric-mesic  
organic (3-5cm)  
mineral |
| **Lichen, Cushion Dwarf Shrub**  
(L-CP-DS) 37.0% | Monocots: *C. niranda*  
Dicot Forbs: *S. oppositifolia*  
Dicot Woody: *D. integrifolia*, *C. tetragona*, *S. arctica* | xeric-mesic  
organic (3-5cm)  
mineral |
| **Deciduous Dwarf Shrub, Graminoid**  
(DDS-G)* 3.8% | Monocots: *L. confusa*, *P. arctica*, *F. brachyphylla*  
Dicot Forbs: *P. lapponicum*, *S. longipes*  
Dicot Woody: *S. arctica* | xeric  
mineral |
| **Herb Dominated**  
(HERB) 5.3% | Monocots: *L. confusa*  
Dicot Forbs: *E. latifolium*  
Dicot Woody: *D. integrifolia*, *S. arctica* | xeric  
mineral |
were included in this study. The Sedge Meadow site is dominated by sedge, cushion plant, and dwarf shrub functional groups (S-CP-DS). The top 12 cm of soil is organic peat, which has the highest soil water content (SWC) in the lowland. The Heath site is dominated by cushion plant and dwarf shrub functional groups (CP-DS). The mesic soils at this site consist of 2 to 3 cm of organic soil underlain by coarse mineral soil. The Riverside Willow site is dominated by deciduous dwarf shrub and graminoid functional groups (DDS-G), and has the highest plant diversity of all the sites. The sandy mineral soils at this site are well drained, with a xeric soil moisture regime.

Two polar semi-desert sites were also examined in this study. They were located in the uplands to the west of the Alexandra Fiord lowland, at 550 m above sea level. The first Polar Semi-desert site was located on mineral soil that is granite in origin (PSD-G). The second Polar Semi-desert site was located on dolomite substrate (PSD-D). Deciduous dwarf shrubs (Salix arctica) and semi-evergreen shrubs (Dryas integrifolia) dominated both of the PSD sites.

2.2.2. Experimental Design

Hexagonal open top chambers (OTCs), made of transparent SunLite™ HP fiberglass (Solar Components Corp., Manchester, NH, USA) were used to passively warm the tundra air and soils by an average of 2°C and 1.3°C, respectively (Marion et al. 1997). The inclined sides of the chambers are 0.5 m high and cover a surface area 1.8 m². Dr. G.H.R. Henry installed the OTCs in the lowland and upland plant communities in 1992 and 1993, respectively.

2.2.3. Microclimate and Soil Water Content

Soil and air temperatures were monitored throughout the 2001 growing season at the Riverside Willow and Heath sites at +10, -2, and -10 cm, relative to the surface, with thermocouples connected to data loggers (CR-10, Campbell Scientific Inc. Utah, USA). At the Sedge Meadow site, Hobo® Pro Temperature loggers (H8, Onset Computer Corp. MA, USA), and thermistors connected to Pocket Data Loggers (XR220, Pace Scientific, NC, USA) were used to monitor air temperature (+10 cm) and soil temperature (-10 cm), respectively.

A Hydrosense™ SWC measurement system (Campbell Scientific Inc. Utah, USA) was used to measure volumetric SWC to a depth of 12 cm. Measurements were taken throughout the growing season in the lowland communities. Three replicates were taken in each plot during each sampling period. Gravimetric SWC was evaluated in soil cores from the PSD sites, as rocky
soil prevented adequate insertion of the Hydrosense™ probes. SWC between treatments was compared only once at the PSD sites to minimize plot disturbance.

### 2.2.4. Soluble Inorganic Nitrogen

Soil cores (10 cm deep × 2 cm diameter) were removed from the control plots and OTCs at the Sedge Meadow and Riverside Willow sites three times during the growing season. The cores were kept frozen prior to analysis in order to minimize N transformations. The following methods for extraction of soluble inorganic N (SIN) follow those described by Lajtha et al. (1999). The cores were sieved through a 4 mm-mesh screen to homogenize the soil and remove roots and pebbles. Approximately 15 g of soil were weighed and dried (to a constant mass) for analysis of SWC, while the remainder of the sample was mixed with 0.5M K2SO4 in sterile Whirl-packs™. The soil sample to extract solution ratio was 1g to 4 ml. The extract solutions were shaken at high speed on a shaker table for one hour before they were filtered through Whatman 42 filter paper into acid-washed polyethylene vials. Blanks were also shaken and filtered. The sample solutions were kept frozen until the concentrations of ammonium (NH4) and nitrate (NO3) were measured with a Lachat QuikChem Ae Autoanalyzer at the Soil Science Laboratory at the University of British Columbia (UBC).

### 2.2.5. Soluble Organic Nitrogen

The soil sample extracts analyzed for SIN (above) were also analyzed for soluble organic N (SON) using alkaline persulphate digestion. A persulphate reagent was used to oxidize SON and NH4 in the extract solutions to NO3. This method was adopted from methods used to measure total N in sea and freshwater samples (Grasshoff et al. 1976, D’Elia et al. 1977). It is safer, has a lower detection limit, and produces less waste than the conventional Kjeldahl digestion method (Ameel et al. 1993, Cabrera and Beare 1993, Yu et al. 1994).

To prepare the persulphate reagent, 25 g of low N K2S2O8 and 15 g of H3BO4 were dissolved in 50 mL of 3.75M NaOH in a dark bottle. The solution was then diluted to 500 mL with de-ionized water, and stored at room temperature for no longer than 1 week. A subsample of soil extracts (described in section 2.2.4.) was vacuum-filtered through a 0.45 µm Durapore™ PVDF membrane filter. The sample and the persulphate reagent were pipetted into a 40 mL borosilicate glass vial in a 1:1 ratio. The vial was sealed with a teflon-lined cap, weighed, and autoclaved at 121°C for 45 minutes. After the vial had cooled it was re-weighed to determine evaporation loss. The sample solutions were analyzed for NO3 as previously described for SIN.
The digestion efficiency was evaluated for each set of samples by mixing a standard solution (i.e. having a known concentration of NO₃, NH₄, or H₂NCONH₂ (urea)), with a field sample. This aliquot was then digested with the persulphate reagent as described above. Sample sets with digestion efficiencies less than 80% of the expected N concentration were discarded, and fresh samples were re-analyzed using a new batch of persulphate reagent. If the digestion was successful, the following equation was used to determine the Sample SON concentration:

\[ \text{SON} = (\text{TN}_D + D_{\text{eff}}) - \text{SIN} \]

Where:
- SON is the soluble organic N concentration of the soil extract solution.
- TN_D is the total NO₃-N concentration in the digested sample.
- D_eff is the digestion efficiency as determined by the oxidation of the inorganic and organic sample:standard aliquots.
- SIN is the combined NO₃ and NH₄ concentration of the extract solution.

2.2.6. Soluble Inorganic and Organic Nitrogen Availability

Ion exchange membranes (IEMs) were used to evaluate the nutrient bioavailability between warming treatments. IEMs are thin plastic strips coated with ion exchange resin. The ions adsorbed onto the membrane surface area during the IEM incubation period yield a flux measurement of ion from the soil to the membrane (i.e. µgN/cm²/h) (Lajtha et al. 1999).

Ion exchange resin bags have long been used to measure nutrient availability in situ, however the use of resin-impregnated membranes is relatively new (Abrams and Jarrell 1992, Cooperband and Logan 1994). IEMs mimic ion uptake by plant roots, and thus provide a measure of nutrient supply in soils (Huang and Schoenau 1996). Ziadi et al. (1999) found that IEM fluxes of NO₃ were significantly related to water soluble NO₃ in soil samples and plant N uptake. SWC is also positively correlated with IEM NO₃ adsorption (Lajtha et al. 1999).

There are several advantages to using IEMs for comparing nutrient bioavailability in long-term ecosystem manipulation studies. Soil disturbance is minimal, thereby preserving long-term plots. IEMs determine dynamic fluxes of nutrients through soils, as opposed to static pool measurement in soil cores. The two-dimensional nature of the IEMs allows for good soil-membrane contact, while having relatively little impact on the diffusion rate of soil solution, compared to the resin bag method.

The cation and anion exchange membranes (CEMs, AEMs), typically used for water purification, were purchased in large sheets from Ionics Inc. (Watertown, MA, USA). They were cut into 5 × 5 cm squares and soaked in a 1M solution of HPLC-grade sodium bicarbonate.
(NaHCO₃) for 24 h. The CEMs and AEMs, saturated with Na⁺ and OH⁻ ions, respectively, were used in the field within 6 days. The IEMs were incubated in the OTCs and control plots at the five sites during early growth, peak growth, and senescence of the vegetation. There were 8 OTC-control plot pairs at the Sedge Meadow and Riverside Willow sites, 5 at each of the Polar Semi-desert sites, and 4 at the Heath site. Three replicates were incubated in each plot. A 45° slit in the soil was made with a putty knife, and a CEM and AEM pair was inserted side by side with tweezers. After four days the IEMs were removed, rinsed with de-ionized water, and placed in a Whirlpack™. Four days is the maximum recommended incubation period in order to maintain a near zero concentration of NH₄ and NO₃ at the IEM surface. Under these conditions the IEM is a sink for ions, and the integrated ion flux to the IEM may be calculated. Otherwise the IEMs become dynamic ion exchangers, making interpretation more complicated (Lajtha et al. 1999, Dr.W.M. Jarrell personal communication, 2001). IEMs that were not incubated in the soil were placed in Whirlpacks™ as blanks. The IEMs were then frozen until they were extracted and analyzed at UBC.

To extract the NH₄ and NO₃ ions from the membranes, 25 mL of 0.5M HCl was added to the Whirlpack™, and the samples were shaken for 24 h. During this time they were kept on ice to minimize N transformations. The solution was filtered through Whatman #1 filter paper to ensure that any remaining soil particles were removed. The sample solution was analyzed for NH₄ and NO₃ as described in section 2.2.4.

IEMs from the Sedge Meadow and Riverside Willow sites were also analyzed for SON flux. A preliminary test, using standard solutions of NH₄, NO₃, urea, and glycine, confirmed that the persulphate digestion method was not suitable for oxidation of SON in 0.5M HCl. For this reason, a separate set of IEMs from the peak growth phenological period was extracted in 0.5M K₂SO₄. Part of this solution was analyzed for SIN, while the other was oxidized for SON (described in section 2.2.5.). A second preliminary test indicated that the IEMs extracted with 0.5M K₂SO₄ yielded significantly more NH₄ than those extracted with 0.5M HCl. Similar types of inconsistencies have been noted for soil extracts (Shepard et al. 2001). For this reason, the results from the IEMs extracted with 0.5M K₂SO₄ were analyzed independently.

2.2.7. Microbial Nitrogen

To determine the amount of NO₃ and NH₄ immobilized by the soil microbes, soil samples were fumigated with chloroform to lyse the microbial cell walls. The procedures for chloroform fumigation and extraction (CFE) follow Horwath et al. (1994). Soil was sieved through a 4 mm
mesh to homogenize the samples and remove small pebbles. A subsample was dried and weighed (105°C, constant mass) for SWC, and another was extracted for SIN as described above. Approximately 20 g of the remaining soil was added to a clean 50 mL glass beaker, which was then placed in a vacuum dessicator. The dessicator was lined with damp paper towels to prevent drying of the soil. Under a fume hood, a 50 mL beaker containing boiling chips and ethanol-free chloroform (CHCl₃) was added to the dessicator, which was then sealed and evacuated until the chloroform boiled for 1 min. The vacuum was then released and re-evacuated. During the second evacuation, the dessicator was sealed and kept in the dark for 5 days. Following the incubation the SIN was extracted and analyzed. Microbial inorganic N (MIN) was determined by subtracting the SIN in soil (unfumigated) from the SIN in the fumigated samples.

2.2.8. Net Nitrogen Mineralization and Immobilization

Buried bag incubations were conducted during the growing season and winter to measure net SIN mineralization and net MIN immobilization (Eno 1960). Two intact cores (10 cm deep × 4 cm diameter) were removed from the OTCs and control plots at the Riverside Willow and Sedge Meadow sites at the start of the growing season when the thaw depth reached 10 cm (June 20 and 27, 2001). The cores were sealed in polyethylene bags that were 0.0254 mm thick. Polyethylene bags between 0.015 and 0.032 mm thick are permeable to gasses and impermeable to water, and are therefore adequate for soil incubations (Gordon et al. 1987).

The two cores were returned to the ground and covered with natural vegetation. In order to determine the initial amounts of SIN and MIN in each plot, another set of cores were taken at the same time and frozen for analysis at UBC. These cores were removed as close as possible to the buried bags.

The bags were removed at the end of the growing season (August 14-15, 2001) and frozen for analysis of the final SIN and MIN concentrations. Net SIN mineralization and MIN immobilization were calculated as the difference between the initial and final SIN and MIN concentrations. The winter incubation period was initiated at the same time that the growing season bags were removed. The winter cores were removed in spring 2002 when the thaw depth reached 10 cm (June 15 and 17 at the Riverside Willow and Sedge Meadow sites, respectively). They were analyzed for SIN and MIN as described above.

During the 2001 growing season, one core from each temperature treatment was incubated in its original plot, and the other was transplanted to the other temperature treatment. If there was a
significant difference in the N transformations between the cores from the OTCs and control plots (incubated in their original location), the transplanted cores were analyzed to determine if the difference was a result of direct, short-term temperature influences on soil N processes, and/or indirect, long-term temperature effects through changes in soil properties (i.e. initial nutrient availability, changes in the structure of the soil microbial community, and litter and soil organic matter quality). The three hypotheses tested in this experiment are outlined in Table 3.

Table 3: Null Hypotheses tested in the buried bag transplant experiment. The top section of the table indicates the comparisons between soil origin/incubation treatments (where shaded cells meet) that address the hypotheses outlined in the bottom section of the table.

<table>
<thead>
<tr>
<th>Soil Origin (top)</th>
<th>Control Location</th>
<th>Incubation Location</th>
<th>Control Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Short-term (H2)</td>
<td>OTC</td>
<td>Short-term (H2)</td>
</tr>
<tr>
<td>OTC</td>
<td>Short + Long-term (H1)</td>
<td>Long-term (H3)</td>
<td>OTC</td>
</tr>
<tr>
<td>OTC</td>
<td>Long-term (H3)</td>
<td>Control</td>
<td>Short-term (H2)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Effect Tested</th>
<th>Null Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-term + Long-term</td>
<td>H1$_0$: There are no combined short-term or long-term effects of the temperature treatment on soil processes or properties, respectively, affecting net N mineralization or immobilization.</td>
</tr>
<tr>
<td>Short-term</td>
<td>H2$_0$: There is no short-term effect of the temperature treatment directly on soil processes affecting net N mineralization or immobilization.</td>
</tr>
<tr>
<td>Long-term</td>
<td>H3$_0$: There is no long-term effect of the temperature treatment indirectly on litter quality/soil properties affecting net N mineralization or immobilization.</td>
</tr>
</tbody>
</table>
2.2.9. Data Analysis

To evaluate N availability to plant roots in a given volume of soil, SIN and SON concentrations were expressed on a volumetric basis (gN/cm³). The nutrient bioavailability from the IEMs is given as N flux to the IEM per unit IEM area and incubation time (gN/cm²/h).

Statistical analyses were conducted using JMP IN™ statistical software (Version 4.0.3. SAS Institute Inc. 2000. Pacific Grove, California: Duxbury Press). Significant differences between temperature treatments were determined with the appropriate ANOVA/Kruskal Wallis test. We chose a significance level of p < 0.1 due to the high spatial heterogeneity of the treatment plots. Table 4 summarizes the measurements conducted in each plant community, and lists the number of plots and replicates included in the analyses.

Table 4: Measurements of soil N pools, fluxes and processes conducted at each site. The number of plots (N) and replicates per plot are also given. Sampling periods are based on vegetation phenological events, and are abbreviated as: BB = Bud Break, PG = Peak Growth, SN = Senescence. Summer and winter buried bag incubation periods were from June 2001 to August 2001 and from August 2001 to June 2002, respectively.

<table>
<thead>
<tr>
<th>Site and Plant Community Description</th>
<th>Measurement</th>
<th>Sampling Period(s)</th>
<th>N</th>
<th># Reps per plot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polar Semi-desert: PSD-G</td>
<td>SIN IEMs - Flux</td>
<td>BB, PG, SN</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Polar Semi-desert: PSD-D</td>
<td>SIN IEM - Flux</td>
<td>BB, PG, SN</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Heath: CP-DS</td>
<td>SIN IEM - Flux</td>
<td>BB, PG, SN</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Riverside Willow: DDS-G</td>
<td>SIN IEM - Flux</td>
<td>BB, PG, SN</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>SON IEMs - Flux</td>
<td>PG</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>SIN cores - Pool</td>
<td>BB, PG, SN</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bag Incubations</td>
<td>summer, winter</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Sedge Meadow: S-CP-DS</td>
<td>SIN IEM - Flux</td>
<td>BB, PG, SN</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>SON IEMs - Flux</td>
<td>PG</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>SIN cores - Pool</td>
<td>BB, PG, SN</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bag Incubations</td>
<td>summer, winter</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Transplanted Bags</td>
<td>summer</td>
<td>8</td>
<td>1</td>
</tr>
</tbody>
</table>
2.3. RESULTS

2.3.1. Microclimate and Soil Water Content

The growing season air and soil temperatures at each site and treatment are summarized in Table 5 and Figures 3a-h. The Sedge Meadow Site (S-CP-DS) OTCs had the largest air temperature increase, relative to the controls, with a difference of 1.5°C between treatments. The warming effect of the OTCs decreased with depth, however, the soils in the OTCs at the Sedge Meadow were consistently warmer than the control plots at -2 and -10 cm. The OTCs at the Heath (CP-DS) and Riverside Willow (DDS-G) sites were warmer than the control plots at +10 and -2 cm, and cooler than the controls at -10 cm.

There were no significant differences in volumetric SWC between the control plots and OTCs in the three lowland sites (Riverside Willow, Heath, Sedge Meadow), with the exception of the Sedge Meadow site on July 25 where the control plots were significantly drier than the OTCs (p = 0.0053) (Figure 4a-c). At the Riverside Willow site, the SWC decreased from 50% to 35% during the growing season. There was no consistent seasonal trend at the Heath or Sedge Meadow sites. In the upland sites (PDS-D and PSD-G), the gravimetric SWC generally decreased during the growing season (Figure 4d,e). The OTCs on the PSD-D site had a significantly higher SWC compared to the control plots at the end of the growing season (p= 0.0328).

Table 5: Air and soil temperatures of the OTCs and Control plots at each site averaged over the growing season. The temperature data coincides with the buried bag incubations (indicated at bottom of the table), from bud break to senescence of the vegetation.

<table>
<thead>
<tr>
<th>Site Name &amp; Plant Community</th>
<th>Height cm</th>
<th>Warmed °C</th>
<th>Ambient °C</th>
<th>Difference °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riverside Willow (DDS-G)</td>
<td>+10 cm</td>
<td>9.55</td>
<td>8.48</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>-2 cm</td>
<td>9.66</td>
<td>9.19</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>-10 cm</td>
<td>5.81</td>
<td>7.59</td>
<td>-1.78</td>
</tr>
<tr>
<td>Heath (CP-DS)</td>
<td>+10 cm</td>
<td>8.90</td>
<td>8.61</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>-2 cm</td>
<td>9.36</td>
<td>9.16</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>-10 cm</td>
<td>3.89</td>
<td>4.98</td>
<td>-1.09</td>
</tr>
<tr>
<td>Sedge Meadow (S-CP-DS)</td>
<td>+10 cm</td>
<td>9.81</td>
<td>8.35</td>
<td>1.46</td>
</tr>
<tr>
<td></td>
<td>-10 cm</td>
<td>7.05</td>
<td>6.40</td>
<td>0.65</td>
</tr>
</tbody>
</table>

Figure 3a-c: Air and soil temperatures (daily averages) in the control plots and OTCs during the 2001 growing season at the Dry Riverside Willow Site (DDS-G).
Figure 3d-e: Air and soil temperatures (daily averages) in the OTCs and control plots during the 2001 growing season at the Heath Site (CP-DS).
Figure 3g,h: Air and soil temperatures (daily averages) in the OTCs and control plots during the 2001 growing season at the Sedge Meadow Site (S-CP-DS).
Figure 4: Soil water content (SWC) at the lowland sites (a-c), and at the upland polar semi-desert sites (d,e). Volumetric SWC was measured with a Hydrosense™ sensor at a depth of 12 cm in the lowland sites, and gravimetric SWC was measured in soil cores (10cm x 2cm dia.) in the polar semi desert. Significant differences between temperature treatments (p ≤ 0.1) are indicated with an asterisk. Error bars are +/- 1SE of the mean.
2.3.2. Soil Nitrogen Pools

A significant increase in the SIN pool was observed in the OTCs compared to the controls at senescence in the Riverside Willow site (p = 0.0613) (Table 6, Figure 5). SIN and SON in the OTC soils were consistently higher than in the control soils at the Sedge Meadow site. The SON pool was significantly different between the treatments at bud break and senescence (p = 0.0157 and 0.0351, respectively).

There was a significant increase in SIN between bud break and peak growth in both temperature treatments at the Riverside Willow site (p = 0.0017 and 0.0510, respectively). There were no seasonal trends in the SON pool. At the Sedge Meadow site, SIN and SON concentrations were generally lowest during peak growth.

The SON pool was substantially larger than the SIN pool at both sites. The dominant form of available SIN was NH₄, as NO₃ was less than 5% of the total SIN pool at both sites throughout the growing season (Table 6).

Table 6: Nitrate, Ammonium, Total SIN, and Total SON measured in soil core extracts. The percentage of the total SIN as nitrate is also given. Significant differences between temperature treatments (p ≤ 0.1) are bolded. Refer to Table 4 for a key of phenological period abbreviations.

<table>
<thead>
<tr>
<th>Plant Community and Description</th>
<th>Treatment</th>
<th>Phenological Period &amp; Date</th>
<th>μg N/cm³</th>
<th>% SIN as NO₃</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDS-G Riverside Willow</td>
<td>ambient</td>
<td>BB: June 20</td>
<td>0.00 1.05 1.05 17.31 0%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 24</td>
<td>0.39 10.09 10.48 21.22 4%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD: Aug 13</td>
<td>0.10 3.48 3.58 15.24 3%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: June 20</td>
<td>0.05 2.80 2.85 20.41 2%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 24</td>
<td>0.00 7.42 7.42 15.67 0%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD: Aug 13</td>
<td>0.00 5.90 5.90 16.69 0%</td>
<td></td>
</tr>
<tr>
<td>S-CP-DS Sedge meadow</td>
<td>ambient</td>
<td>BB: June 27</td>
<td>0.00 1.96 1.97 4.91 0%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 25</td>
<td>0.04 2.21 2.24 8.46 2%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD: Aug 12</td>
<td>0.12 6.29 6.42 11.78 2%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: June 27</td>
<td>0.10 6.83 6.94 18.39 2%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 25</td>
<td>0.02 3.50 3.52 10.52 1%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD: Aug 12</td>
<td>0.20 8.44 8.64 27.58 2%</td>
<td></td>
</tr>
</tbody>
</table>
Figure 5: SIN and SON at the Riverside Willow (DDS-G) (a,b) and Sedge Meadow (S-CP-DS) (c,d) sites. Soil cores were removed and analyzed three times during the growing season according to phenological events (BB = bud break, PG = peak growth, SD = seed dispersal). NO₃-N was less than 4% of the total SIN measured in all cases. Significant differences between temperature treatments (p ≤ 0.1) are indicated with an asterisk. Error bars are +/-1 SE of the mean.
2.3.3. Soil Nitrogen Availability

In the OTCs, soluble inorganic nitrogen (SIN) availability was higher than in the controls throughout the growing season in the lowland plant communities, except at the Riverside Willow site early in the growing season (Figure 6c-e). This trend was statistically significant during senescence for total SIN in the Sedge Meadow site (p = 0.0535), and for NH$_4$ in the Riverside Willow site (p = 0.0676). The NO$_3$ fluxes were significantly lower in the OTCs than the control plots during early growth and senescence in the upland PSD-D community (p = 0.0993 and 0.0251, respectively) (Figure 6a,b). Total SIN availability was significantly lower in the OTCs at senescence (p = 0.0170).

There were no significant differences in SON or SIN availability between the temperature treatments during peak growth at the Riverside Willow site (Figure 7). Nitrate and SON fluxes to the IEMs were significantly higher in the OTCs than the controls at the Sedge Meadow site, (p = 0.0437, 0.1000, respectively). Similar to the soil pool data, SON exceeded SIN availability at both sites.

Throughout the growing season, SIN availability remained relatively constant at the Sedge Meadow site. At the Riverside Willow and Heath sites N availabilities were lowest at peak growth, with a recovery by the senescence period. There was a weak, positive correlation between NO$_3$ flux and SWC among all communities and sampling periods (r = 0.2252, p < 0.0001). There was also a positive correlation between soil NO$_3$ concentrations from soil cores and IEM NO$_3$ fluxes (r = 0.2188, p = 0.0322) for the Sedge Meadow and Riverside Willow sites. Nitrate was often the dominant form of available SIN adsorbed on the IEMs (Table 7). There were no significant correlations between IEM NH$_4$ flux and SWC or soil NH$_4$ concentration.
Figure 6: Total SIN Flux to the IEMs during phenological periods of Bud Break (BB), Peak Growth (PG), and Senescence (SN). The sites are ordered from driest to wettest along a soil moisture gradient. Lines within the bars indicate proportions of NO$_3$ (bottom) and NH$_4$ (top). Significant differences between temperature treatments ($p \leq 0.1$) are indicated with an asterisk either over the bar for SIN, or within the bar for NO$_3$/NH$_4$ independently. Error bars are +/- 1 SE of the mean.
Figure 7: Flux of SIN and SON to IEMs in the Riverside Willow (a) and Sedge Meadow (b) communities during peak growth. SIN bars include a division between NO$_3$ (bottom) and NH$_4$ (top). Due to differences in methodology, these data were analyzed separately from the seasonal IEM data shown in Figure 6. Significant differences between temperature treatments (p \leq 0.1) are indicated with an asterisk. Error bars are +/-1 SE of the mean.
Table 7: Flux of NO$_3$, NH$_4$, and Total SIN to IEMs. The percentage of the total SIN as NO$_3$ is also given. Phenological periods are abbreviated as: bud break = BB; peak growth = PG, senescence = SN. Significant differences between temperature treatments (p ≤ 0.1) are bolded.

<table>
<thead>
<tr>
<th>Plant Community and Site Name</th>
<th>Treatment</th>
<th>Phenological Period &amp; Date</th>
<th>$\mu$g N/cm$^2$/hr (x10$^{-3}$)</th>
<th>% as NO$_3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSD-G Polar Semi-desert (granite)</td>
<td>ambient</td>
<td>BB: July 5-11</td>
<td>0.92 0.20 1.11</td>
<td>82%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 23-29</td>
<td>0.92 0.29 1.21</td>
<td>76%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 1-7</td>
<td>0.93 0.45 1.38</td>
<td>68%</td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: July 5-11</td>
<td>0.88 0.22 1.11</td>
<td>80%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 23-29</td>
<td>0.93 0.39 1.32</td>
<td>71%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 1-7</td>
<td>0.86 0.45 1.31</td>
<td>66%</td>
</tr>
<tr>
<td>PSD-D Polar Semi-desert (dolomite)</td>
<td>ambient</td>
<td>BB: July 5-11</td>
<td>1.14 0.26 1.40</td>
<td>82%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 23-29</td>
<td>2.10 0.23 2.33</td>
<td>90%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 1-7</td>
<td>1.43 0.38 1.80</td>
<td>79%</td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: July 5-11</td>
<td>0.93 0.18 1.11</td>
<td>83%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 23-29</td>
<td>1.30 0.25 1.55</td>
<td>84%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 1-7</td>
<td>0.91 0.30 1.21</td>
<td>75%</td>
</tr>
<tr>
<td>DDS-G Riverside Willow</td>
<td>ambient</td>
<td>BB: June 23-27</td>
<td>2.45 3.44 5.90</td>
<td>42%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 20-24</td>
<td>1.94 1.35 3.29</td>
<td>59%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 7-11</td>
<td>2.94 2.38 5.32</td>
<td>55%</td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: June 23-27</td>
<td>1.77 3.43 5.20</td>
<td>34%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 20-24</td>
<td>1.76 2.00 3.76</td>
<td>47%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 7-11</td>
<td>3.36 3.40 6.76</td>
<td>50%</td>
</tr>
<tr>
<td>CP-DS Heath Tundra</td>
<td>ambient</td>
<td>BB: June 26-30</td>
<td>1.30 1.36 2.66</td>
<td>49%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 22-26</td>
<td>1.10 2.30 3.39</td>
<td>32%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 9-13</td>
<td>2.03 3.84 5.87</td>
<td>35%</td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: June 26-30</td>
<td>1.36 2.05 3.41</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 22-26</td>
<td>1.07 2.28 3.35</td>
<td>32%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 9-13</td>
<td>1.57 6.28 7.86</td>
<td>20%</td>
</tr>
<tr>
<td>S-CP-DS Sedge Meadow</td>
<td>ambient</td>
<td>BB: June 24-28</td>
<td>3.07 2.03 5.11</td>
<td>60%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 21-25</td>
<td>2.64 2.79 5.43</td>
<td>49%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 8-12</td>
<td>2.99 2.01 5.01</td>
<td>60%</td>
</tr>
<tr>
<td></td>
<td>warmed</td>
<td>BB: June 24-28</td>
<td>3.95 2.17 6.12</td>
<td>65%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PG: July 21-25</td>
<td>3.68 1.97 5.65</td>
<td>65%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SN: Aug 8-12</td>
<td>4.61 2.05 6.66</td>
<td>69%</td>
</tr>
</tbody>
</table>
2.3.4. Microbial Nitrogen Transformations

a) Growing Season Incubations

There were no significant differences in SIN or MIN pools between the temperature treatments at the start of the buried bag incubations (Figure 8a,c). SON was significantly higher in the OTCs at the Sedge Meadow site (p = 0.0157). At the end of the incubations the SIN and MIN pools had increased in all treatments at both sites (Figure 8b,d). MIN increased by a factor of 3.2 during the incubation in the OTCs, and by a factor of 1.7 in the controls at the Sedge Meadow. As a result, net N immobilization in the OTCs was significantly greater than in the control plots at the Sedge Meadow site over the growing season (p = 0.0971) (Figure 9). Consequently, the first null hypothesis (H1o) in the buried bag experiment was rejected (Table 1). The 10-year warming treatments have affected soil N processes at the Sedge Meadow site. There was no statistically significant effect of warming on net N mineralization or immobilization at the Riverside Willow site (Figure 9).

b) Transplant Experiment

In order to test the second and third null hypotheses outlined in Table 3, the transplanted samples from the Sedge Meadow site were analyzed (Figure 10). The increase in net N immobilization between temperature treatments, leading to a rejection of H1o, is illustrated (p = 0.0971). Net N mineralization was more than five times greater in soil from the OTCs than soil from the controls when both cores were incubated in the control plots (p = 0.0460). Net N immobilization was 4 times greater in the OTCs soils than in the control soils, when both core were incubated in the OTCs (p = 0.1103). When OTC soil was transplanted to the control plots, net N mineralization increased by a factor of 4, and net N immobilization decreased by a factor of 2, compared to the incubations in their original location (p = 0.0920, 0.4116, respectively). Net N mineralization in the control soil cores doubled when they were transplanted to the OTCs (p = 0.1152). Incubation location (temperature) and soil origin (soil properties) significantly affected soil processes in at least one comparison, leading to the rejection of H2o and H3o (Table 3). Therefore, changes in soil properties over the 10-year warming experiment and continued temperature enhancement both contributed to the observed changes in soil N processes at the wet sedge meadow site.

c) Wintertime Net N Mineralization and Immobilization

Unfortunately, the soil cores that were incubated over the winter season thawed to room temperature for longer than 24 hours during transport to UBC. This likely had severe impacts on soil N processes given that winter net N mineralization and immobilization in Sedge Meadow
soils was two to five times higher than for the growing season incubation (Figure 11). For this reason, interpretation is restricted to comparisons between the experimental and control soils. There were no differences in net N mineralization or immobilization between the control and OTC soils at the Riverside Willow site. Net N mineralization and immobilization were higher in the OTC soils than in the control soils from the Sedge Meadow, although the differences were not statistically significant.

**Riverside Willow (DDS-G)**

![Graph showing soil N pools for Riverside Willow site](image)

**Sedge Meadow (S-CP-DS)**

![Graph showing soil N pools for Sedge Meadow site](image)

**Figure 8:** The initial and final soil N pools (microbial, organic, and inorganic) at the Riverside Willow site (a,b), and the Sedge Meadow Site (c,d) in the buried bags that were incubated in their original plots over the growing season. Significant differences between the temperature treatments \((p \leq 0.1)\) are indicated with an asterisk. Error bars are +/-1 SE of the mean.
Figure 9: SIN mineralization and MIN Immobilization in the Riverside Willow (a) and Sedge Meadow (b) communities during the 2001 growing season. The cores were incubated in polyethylene bags from late June to mid-August 2001. Significant differences between temperature treatments (p ≤ 0.1) are indicated with an asterisk. Error bars are +/-1 SE of the mean.
Figure 10: Growing season net N mineralization (a) and immobilization (b) at the Sedge Meadow Site (S-CP-DS) in buried bags incubated within their original temperature treatment (solid bars) and transplanted to the opposite temperature treatment (shaded bars - center shade indicates soil core origin). Significant differences between origin-incubation treatments ($p \leq 0.1$) are indicated with different letters.
Figure 11: SIN mineralization and MIN Immobilization in the Riverside Willow (a) and Sedge Meadow (b) communities during the 2001-2002 winter. There were no significant differences between the temperature treatments. Error bars are +/-1 SE of the mean.
2.4. DISCUSSION

2.4.1 Nitrogen Availability Under Experimentally Warmed Conditions

SIN availability increased in the OTCs compared to the control plots in the lowland plant communities, particularly at the end of the growing season during senescence of the vegetation. Therefore, warmer growing conditions in the OTCs, and an increase in N availability have both contributed to the observed increases in productivity in this long-term warming experiment. A slight decrease in SIN availability was observed in the OTCs at the upland polar semi desert site on the dolomitic substrate; however, the low variability in the PSD compared to the lowland may have contributed to the significant differences observed between treatments. Investigations of soil N transformations and plant productivity may help to support these results in future studies.

The effect of warming on NH₄, NO₃, and SON availabilities was not consistent between the vegetation communities in the lowland. Ammonium increased in the mineral soils of the Riverside Willow and Heath sites, whereas NO₃ and SON increased in the organic soils of the Sedge Meadow site. In a previous study at Alexandra Fiord, graminoids and forbs showed a strong, positive response to inorganic fertilizer addition, affecting the species composition in three plant communities (Henry et al. 1986). McKane et al. (2002) examined plant uptake of NO₃, NH₄, and amino acid-N, and concluded that niche differentiation for the same limiting resource (N) drives plant diversity and species composition in arctic plant communities. It is likely that the increases in SIN and SON, leading to changes in the relative availability of the different chemical forms of available N in each plant community, have contributed to the observed changes in species composition in the OTCs in this 10-year warming experiment.

Integrated fluxes of soil nutrients to IEMs are a better indicator of nutrient bioavailability than soil pool concentration. Although NO₃ concentrations in soils were positively correlated to IEM fluxes, pool measurements do not account for cycling rates and mobility of ions through the soil. For example, NO₃ was less than 4% of the total SIN pool, yet it was often more than 50% of the total SIN flux.

Table 8 gives SIN fluxes to IEMs from this study compared to others from subarctic, boreal, and temperate regions. Fluxes of NO₃ increased by one order of magnitude from the high arctic polar semi-desert to the temperate grasslands. The NH₄ fluxes in this study were similar to those measured by Weih (1998) for subarctic heath and meadow communities. However, due to the variability in methodologies between studies (i.e. incubation time, watering, and extract solution), comparisons between different studies should be interpreted with caution.
To our knowledge, this is first study that employed IEMs to measure SON availability. Similar to SIN fluxes, SON flux to the IEMs was correlated to the relatively high SON measured in soil pools, indicating that IEMs effectively measure both SIN and SON bioavailability. Due to the advantages of minimizing plot disturbance (relative to buried resin bags), and measuring both SIN and SON fluxes, IEMs are effective tools for evaluating nutrient bioavailability between treatments in long-term ecosystem manipulation studies.

Table 8: Summary of IEM studies from high to low latitudes. Results were obtained from text or estimated from graphs in published articles. Measurement units were converted to \( \mu g/cm^2/hr \) for comparison to this study.

<table>
<thead>
<tr>
<th>Reference and Location of Study</th>
<th>Incubation Period</th>
<th>Extract solution</th>
<th>( \text{NO}_3^- ) ( \mu g/cm^2/hr )</th>
<th>( \text{NH}_4^+ ) ( \mu g/cm^2/hr )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>This Study</strong>: High Arctic ITEX site. Ellesmere Is. Nunavut, Canada.</td>
<td>4 days</td>
<td>0.5M HCl</td>
<td>0.0009 - 0.0021 0.0002 - 0.0004</td>
<td>0.0011 - 0.0020 0.0014 - 0.0038</td>
</tr>
<tr>
<td>Polar Semi-desert (PSD) and lowland oasis.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PSD</td>
<td>4 days</td>
<td>0.5M HCl</td>
<td>0.00026 - 0.0031 0.0020 - 0.0028</td>
<td></td>
</tr>
<tr>
<td>heath</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>meadow</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Weih 1998</strong>: Subarctic birch heath and meadow communities near Abisko, Sweden</td>
<td>1 month</td>
<td>2M NaCl in</td>
<td>&lt; 0.0001 0.0013</td>
<td></td>
</tr>
<tr>
<td>dry heath</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>moist heath</td>
<td></td>
<td>1M HCl</td>
<td>0.0054 0.0023</td>
<td></td>
</tr>
<tr>
<td>meadow</td>
<td></td>
<td></td>
<td>0.0189 0.0015</td>
<td></td>
</tr>
<tr>
<td><strong>Huang et al. 1996</strong>: Aspen boreal forest in Saskatchewan, Canada</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Note: plots were watered during experiment.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 hours*</td>
<td></td>
<td>0.5M HCl</td>
<td>0.3650 - 0.4250 0.2300 - 0.3000</td>
<td></td>
</tr>
<tr>
<td><strong>Zandi et al. 1999</strong>: Grasslands in western Quebec, Canada (fertilization experiment)</td>
<td>2 weeks</td>
<td>1M NaCl</td>
<td>0.0092 - 0.0875 na</td>
<td></td>
</tr>
<tr>
<td>control</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fertilized</td>
<td></td>
<td>0.0096 - 0.6250</td>
<td>na</td>
<td></td>
</tr>
<tr>
<td><strong>Turrion et al. 1997</strong>: Deciduous forests in Spain (warm Mediterranean climate, summer data)</td>
<td>1 month</td>
<td>0.3M HCl</td>
<td>0.0015 - 0.0109 na</td>
<td></td>
</tr>
</tbody>
</table>
2.4.2. The Importance of Soluble Organic Nitrogen in Arctic Ecosystems

Mycorrhizal fungi hydrolyze simple proteins and amino acids and transfer the N to the host plant in exchange for energy-rich C from the host plant (Ricklefs 1993). Some plant species, including arctic tundra sedges, can absorb and assimilate amino acids directly from the soil (Chapin et al. 1993, Kielland 1994). The Riverside Willow community is dominated by woody growth forms (e.g. Salix arctica, Dryas integrifolia), in which mycorrhizae are ubiquitous (Ricklefs 1993), and sedges that have been shown to directly absorb amino acids (e.g. Eriophorum angustifolium, Carex stans) (Chapin et al. 1993, Kielland 1994), dominate the Sedge Meadow community. Therefore, SON is potentially an important N resource for plants at both of these lowland sites.

SON measured using persulfate oxidation includes mainly large polyphenolics, and small amounts of proteins and amino acids that may be used by plants (Qualls et al. 1991). The total SON pools and fluxes measured in the Riverside Willow and Sedge Meadow sites far exceeded SIN pools and fluxes. These results are similar to previous studies in arctic soils (Keilland 1995, 1997). Studies from tundra and taiga ecosystems indicate that the free amino acid portion of SON is between 10 and 20% (Kielland 1995, 1997, Kielland and Jones 2002). If this is representative of amino acid portion of SON at our study sites, amino acid availability (measured on IEMs at peak growth) is as much as 49% and 42% of the SIN availability at the Riverside Willow and Sedge Meadow sites, respectively. For plant species that use organic forms of N, either through mycorrhizial symbiosis or direct uptake, this is a substantial source of N.

SON availability increased significantly in the OTCs at the Sedge Meadow site. Compounded with the observed increase in SIN availability, soil N limitation may therefore be substantially reduced in Sedge Meadow communities under warmer growing season conditions. As discussed above, the partitioning of different chemical forms of N (NO₃, NH₄, amino acid-N), affects niche differentiation for plant species in tundra soils (McKane et al. 2002). In the Sedge Meadow communities at this study site, this has likely contributed to the observed changes in species composition and productivity over the 10-year warming experiment.

2.4.3. Short-term versus Long-term Effects of Warming on Soil Nitrogen Processes

Variation in nutrient pool sizes is a poor indicator of bioavailability, however, changes in pool sizes may indicate fluctuations in nutrient cycling processes (Robertson et al. 1999). At the Sedge Meadow site, the differences in SIN and SON pools between the controls and OTCs were paralleled with substantial differences in the soil N transformations between the temperature
treatments. The 10-year warming treatments have significantly affected soil N processes at the Sedge Meadow site.

Incubation of the control soils in both temperature treatments is similar to an evaluation of soil processes during the first year of experimental warming. Although net N mineralization was higher in the control soils when transplanted to the OTCs, there was no significant difference between the two temperature treatments. This result is similar to the findings of other studies that evaluated N mineralization in the first few years of experimental warming (e.g. Jonasson et al. 1993, Robinson et al. 1995, Table 1) Therefore, experimental warming, within the range of temperatures predicted for a doubling of CO₂ in the atmosphere, has little effect on soil N processes at short time scales.

Conversely, soil from the OTCs was sensitive to the incubation treatment. The cooler temperatures of the control plots, relative to the OTCs, caused a significant increase in net N mineralization and a decrease in immobilization. Thus, temperature (independent of soil properties) does contribute to significant differences in soil N processes between treatments after ten years of experimental warming.

There were large differences in net N mineralization and immobilization between the soils from the OTCs versus the soils from the controls when they were incubated in the same temperature treatment (in both cases). This shows that changes in soil properties (independent of temperature) over the ten-year experiment significantly affected soil N processes in the OTCs. Changes in soil properties over the 10 years of warming may include changes in nutrient availability. For example, more SON was observed in the OTC buried bags at the start of the incubation at the Sedge Meadow site. Changes in litter quality have also been observed for several tundra species at this study site during the 5th and 7th years of experimental warming (Welker Pers. Comm. 2000, Tolvanen and Henry 2001). These changes have likely affected the soil organic matter, in terms of C quality and N content. Moreover, changes in microbial species composition and abundance between the temperature treatments may also have taken place, although this was not examined in this study. These three factors, therefore, likely affected soil properties, contributing to the observed effects of the 10-year experiment on soil N transformations.

The transplant experiment in this study, and other short-term experimental warming experiments in high latitudes (Jonasson et al. 1993, Robinson et al. 1995), have shown that initial changes in temperature have little effect on soil N processes. However, the ten-year warming treatments in this experiment, and in at least one other long-term (8 a.) study in high
latitudes (Shaver et al. 1998), where warming was within the range predicted for a doubling of atmospheric CO₂, significantly affected soil N processes. We hypothesize that these findings are a result of changes in litter chemistry and soil properties following long-term experimental warming in conjunction with continued temperature enhancement in Sedge Meadow soils.

2.4.4. Soil Nitrogen Processes versus Nitrogen Availability: Temporal Considerations

Despite higher net N immobilization in the Sedge Meadow OTCs during the growing season, the IEM data indicate that N availability to plants was also higher in the OTCs throughout the growing season. This is inconsistent with the knowledge that high nutrient immobilization limits N availability when microbial activity is high (Aber and Melillo 1991); however, the buried bag technique is used to measures soil nutrient transformations in the absence of competition with plants. In four arctic ecosystems, Schmidt et al. (2002) observed high nutrient immobilization in buried bags, yet low immobilization in the surrounding soils. They hypothesized that plants compete well with soil microbes for nutrients when competition is not prevented (i.e. not within buried bags). Therefore, the high N immobilization in the buried bags observed in this study may indicate a large pool of N that is potentially available to plants in the surrounding soil. This is supported by the observed increase in N availability measured by the IEMs, which mimic plant N uptake (Huang and Schoenau 1996).

Although interpretation of our wintertime incubation is limited, due to the thawing of the samples, increases in N mineralization over the winter period have been observed in some studies (Giblin et al. 1991, Hobbie and Chapin 1996). Declining microbial activity with cooler temperatures and repeated freeze-thaw cycles may cause release of nutrients to the soil (Chapin et al. 1978, DeLuca et al. 1992). Higher N immobilization in the Sedge Meadow OTCs compared to the control plots, potentially leading to a greater release of N when the soils cooled, may explain why the largest differences in N availability between the temperature treatments were observed at the end of the growing season. This flush of nutrients is absorbed by plants and stored for growth during the following growing season (Chapin et al. 1980b, Marion and Kummerow 1990). However, not all studies support the hypothesis that soil microbes release nutrients during the winter. In soils of a subarctic heath, Schmidt et al. (1999) did not observe any increases in N mineralization during the winter. Larsen et al. (2002) found that microbial N remained constant and microbial C declined in tundra heath soils during 18 diurnal freeze-thaw cycles in laboratory mesocosms. More research is required, therefore, to determine if seasonal changes in soil N processes affect N availability on annual time scales. Inclusion of winter data
and investigations of microbial N are needed to determine the effects of experimental warming on plant N availability.

2.4.5. Site Sensitivity to Climate Warming

The Sedge Meadow site showed the strongest increases in SIN and SON availability with warming compared to the other lowland and upland sites. We hypothesize that this is a combined result of the observed short and long-term effects of warming on microbial activity and soil properties, respectively. Soil microorganisms compete with plants for available N, particularly when N is limited in C-rich soils (Kaye and Hart 1997). Furthermore, relatively large amounts of N were immobilized in the soil microbial biomass during the growing season. Small changes in microbial populations, therefore, may have a potentially large impact on soil available N (Jonasson et al. 1999). This may explain why the effects of warming on soil N process and availability were pronounced in the organic soils at the Sedge Meadow site.

At the Riverside Willow site, net N mineralization and immobilization were not significantly affected by the warming treatment. The temperature data indicate that although the air temperature increased in the OTCs relative to the control plots, the OTC soils at a depth of 10 cm were consistently cooler compared to the control plots. This is likely a result of increased shading with increases in plant growth in the OTCs (Marion et al. 1997). Increased plant growth and shading under warmer growing conditions may, therefore, feedback negatively to soil temperature, soil N processes, and N availability in some tundra plant communities.

2.4.6. Methodological Considerations

a) Temperature Manipulation with Open-top Chambers

Marion et al. (1997) evaluated methods of experimental warming in arctic ecosystems, and concluded that OTCs efficiently manipulate temperature while minimizing unwanted ecological effects compared to other field designs. However, some unwanted effects included temperature extremes, altered light, moisture, gas concentrations, wind, and site disturbance. Soil compaction and water flow disturbance was also observed around the edges of the OTCs as a result of sampling and observations at the Sedge Meadow site. The average SWC in the OTCs was higher than the control plots, and the difference was statistically significant on the July 25 sampling date (Figure 4). It is unlikely that an 8% increase in SWC would have an important effect in soils that are saturated (+90%). Nonetheless, this experiment may have evaluated the effects of both increased temperature and soil moisture on the N economy in the Sedge Meadow site. General
circulation models predict that under warmer climatic conditions soil moisture in the high arctic may either increase, with the predicted increases in spring and summer precipitation, or it may decrease, with longer summer thaw seasons, deeper active layers, and increased evaporation (Maxwell 1992).

b) Soil N Processes in Buried Bags

While the buried bag method (Eno 1960) prevents uptake of nutrients by plant roots during soil incubations, it also inhibits the supply of C from root exudates (Schmidt et al. 2002). The polyethylene bags are impermeable to water, preventing a supply of dissolved organic C over the incubation period. The microorganisms may therefore become C limited and mineralize more N than in the surrounding soil. Conversely, damaging roots during the initial coring process may add a large C source to the incubated core, which may lead to increased immobilization of nutrients (Adams et al. 1989). The SWC remained constant in the bags during the incubations, however, the SWC declined over the growing season on the Riverside Willow site. Because the chemical and physical properties of the soil are affected by the incubation, interpretation of soil N processes within the bags should not be extended the surrounding soil; however, comparisons between experimental treatments are useful as both treatments are subjected to the same physical and chemical constraints of the buried bag incubation.

2.5. CONCLUSIONS

1. Under warmer growing conditions, N availability will likely increase in the dominant plant communities at the Alexandra Fiord lowland. The reverse trend was observed in the upland polar semi-desert dolomitic site, where SIN availability was lower on the warmed plots compared to the controls.

2. The 10-year warming treatments caused an increase in net N immobilization in the Sedge Meadow community over the 2001 growing season. This N may usually be accessible to plants when plant-microbe competition is not prevented in buried bags.
3. The transplant experiment at the Sedge Meadow site demonstrated that changes in soil properties over the ten-year experiment, combined with continued temperature enhancement caused the observed changes in soil N transformations between the experimental and control treatments.

4. As found in other high latitude studies, short-term temperature manipulations had no significant effect on soil N transformations. Therefore, long-term warming experiments that are within the range predicted for a doubling of atmospheric CO₂ have elicited changes in soil properties leading to changes in soil N transformations.

5. Increases in plant growth and shading associated with climate warming will likely feedback negatively to soil temperatures, soil N transformations, and N availability in some tundra plant communities.

6. The soil N economy was most affected by the warming experiment at the Sedge Meadow site. We hypothesize that increased N availability, and shifts in the relative availabilities of NO₃, NH₄, and SON have contributed to the observed increases in plant growth and changes in species composition of tundra plant communities in this 10-year experiment.
CHAPTER 3: THE EFFECTS OF A TEN-YEAR CLIMATE WARMING EXPERIMENT ON LITTER AND SOIL CARBON AND NITROGEN IN HIGH ARCTIC PLANT COMMUNITIES: Potential Feedbacks to Nitrogen Cycling and Plant Growth

ABSTRACT
This study examined the effects of a ten-year climate warming experiment on litter and soil carbon (C) and nitrogen (N) concentrations in five high arctic tundra ecosystems along a soil moisture gradient at Alexandra Fiord, Ellesmere Island, Canada. Open top chambers (OTCs) were used to passively warm five tundra plant communities within the range predicted for a doubling of atmospheric CO₂. Senesced litter and soil was collected at the end of the 2001 growing season and C and N concentrations were analyzed. Litter C:N ratio was consistently higher in the OTCs relative to the controls in the lowland plant communities. Significant increases in C:N ratio were observed in some woody and herbaceous growth forms, indicating a decline in litter quality. Litter from reproductive parts had higher C:N ratio in the OTCs than in the controls, which may be due to increases in reproductive effort with warming. Furthermore, the reproductive parts had higher C:N than the vegetative parts within each species, indicating that increased reproductive effort with warming increases litter C:N regardless of changes in litter chemistry. These findings indicate potential for negative litter quality feedbacks to decomposition and N availability. Soil C and N concentrations were not significantly affected by the warming treatments.

3.1. INTRODUCTION and RESEARCH OBJECTIVES

3.1.1. Introduction
In order to better understand ecological responses to predicted climate changes in high latitudes, it is necessary to consider how biogeochemical processes affect tundra ecosystems. Despite substantial stores of organic N held within tundra soils, low temperatures and anaerobic soil conditions reduce rates of N mineralization (Chapin et al. 1980a). Consequently, N is the primary limiting resource to plant growth in arctic tundra ecosystems (Shaver and Chapin, 1980; Henry et al. 1986). Climate warming, resulting in longer and warmer growing seasons, deeper active layers, drier soils, and increased mineralization rates, will lead to initial increases in available N (Nadelhoffer et al. 1992). This has potential to increase plant growth, net primary productivity, and net ecosystem C storage, providing a negative feedback to CO₂-induced climate warming (Rastetter et al. 1991). However, increases in nutrient use efficiency and changes in tissue allocation by tundra species under warmer growing conditions may reduce litter quality, thereby inhibiting decomposition and N mineralization over the long-term (Melillo et al. 1982, Shaver et al. 1992). C:N ratios also vary between species and functional groups, therefore changes in species composition will also affect nutrient turnover rates (Hobbie 1996, Shaver et al. 2000). In order to decompose larger amounts of low-N litter, soil microbes require
more N and may therefore compete with plants, thus reducing plant N availability further (Rastetter et al. 1997). Therefore, long-term C and N interactions will constrain changes in terrestrial C cycling under warmer climate conditions (Shaver et al. 1992).

At global scales, climate is the primary factor affecting decomposition rates, however, litter chemistry is the best predictor of decomposition at local scales (Aerts, 1997). Field and lab studies have demonstrated that litter and soil organic matter quality have greater impacts on decomposition and N mineralization than temperature manipulations (Giblin et al. 1991, Nadelhoffer et al. 1991, Binkley et al. 1994, Hobbie et al. 1996). Therefore, the effects of climate change on litter quality will likely have greater long-term impacts on soil quality, N cycling and N availability than the direct short-term effects of warming.

The ratio of lignin:N is often best predictor of decomposability at local scales (Hobbie 1996; Aerts et al 1997; Scott and Binkley 1997); however, N concentration and C:N are often correlated with litter decay rate (Van Cleve 1974; Taylor et al. 1989). In this study we use litter C and N data, in conjunction with observed changes in plant growth, reproductive effort, and species composition to explore the potential for long-term plant litter feedbacks to N availability in this long-term warming experiment.

3.1.2. Research Objectives

This study was conducted during the tenth year of temperature manipulations in five plant communities along a soil moisture gradient in the high arctic. The main objectives were to:

1. Evaluate the effects of the warming treatments on litter C and N concentrations in each of the plant communities;

2. Examine the soil C and N concentrations to determine if the warming treatments have affected soil organic matter quality;

3. Compare these results (1 and 2) with similar data collected during the 5th and 7th years of warming;

4. Compare the sensitivity of different species, plant communities, and soil types to the climate warming manipulations;

5. Evaluate potential feedbacks of litter quality to long-term N availability at this study site.
3.2. METHODOLOGY

3.2.1. Site Description

This research was conducted at the Alexandra Fiord lowland (78°53'N, 75°55'W), on the eastern side of Ellesmere Island, Nunavut, Canada (Figure 2, previous chapter). The 8-km² lowland is situated on a relatively flat, triangular glacial outwash plain and has been ice-free for approximately 7000 years (Freedman et al. 1994). The valley is bordered to the south by glacial ice and to the north by the fiord. Precambrian bedrock cliffs, 500 to 700 m high, surround east and west sides of the valley. A glacier-fed river and three smaller streams drain the lowland to the northern ocean shore.

The climate of this high arctic oasis is warmer than the surrounding polar desert as a result of relatively clear sky conditions and radiation of long-wave energy from the surrounding bedrock cliffs and dark soils (Labine 1994). The prevailing winds are from the south, which are frequently accompanied by warm weather Chinooks (Labine 1994). Average annual and growing season air temperatures at Alexandra Fiord, for the period from 1980 to 1988 were −12.3°C and +5.1°C, respectively (Labine 1994). Precipitation at Alexandra Fiord is minimal, with less than 1.0 cm falling during the growing season.

The Alexandra Fiord lowland has well-developed, stable soils that are characteristic of polar oases (Muc et al. 1994a), and provide habitats for diverse plant communities relative to the upland polar desert (Muc et al. 1989). The Alexandra Fiord lowland oasis is 90% covered by closed or semi-closed vegetation (Muc et al. 1994b), which is substantially greater than the 5% cover in the surrounding polar deserts (Bliss et al. 1994).

Litter C and N concentrations were examined in five plant communities along a soil moisture gradient. Table 2 (previous chapter) outlines the dominant plant communities in the Alexandra Fiord lowland. Three of these were included in this study. The Sedge Meadow site is dominated by sedge, cushion plant, and dwarf shrub functional groups (S-CP-DS). The top 12 cm of soil is organic peat, which has the highest soil water content (SWC) in the lowland. The Heath site is dominated by cushion plant and dwarf shrub functional groups (CP-DS). The mesic soils at this site consist of 2 to 3 cm of organic soil underlain by coarse mineral soil. The Riverside Willow site is dominated by deciduous dwarf shrub and graminoid functional groups (DDS-G), and has the highest plant diversity of all the sites. The sandy mineral soils at this site are well drained, with a xeric soil moisture regime.

Two polar semi-desert sites were also examined in this study. They are located in the uplands to the west of the Alexandra Fiord lowland, at 550 m above sea level. The first Polar Semi-
The desert site is located on mineral soil that is granite in origin (PSD-G). The second Polar Semi-desert site is located on dolomite substrate (PSD-D). Deciduous dwarf shrubs (*Salix arctica*) and semi-evergreen shrubs (*Dryas integrifolia*) dominate both of the PSD sites.

### 3.2.2. Experimental Design

Hexagonal open top chambers (OTCs), made of transparent SunLite™ HP fiberglass (Solar Components Corp., Manchester, NH, USA) were used to passively warm the tundra air and soils. The inclined sides of the chambers are 0.5 m high and cover a surface area 1.8 m$^2$. Dr. G.H.R. Henry installed the OTCs in the lowland and upland plant communities in 1992 and 1993, respectively.

The OTCs increased the 2001 average growing season air temperatures (+10 cm) by 1.1 °C, 0.3 °C and 0.5 °C relative to the controls in the Riverside Willow, Heath, and Sedge Meadow sites, respectively (Table 5, previous chapter). The soil temperatures in the OTCs decreased by 1.8 °C and 1.1 °C in the Riverside Willow and Heath sites, and increased by 0.7 °C in the Sedge Meadow site relative to the controls.

### 3.2.3. Litter Collection & Analysis

Litter samples were harvested from the OTCs and control plots in each of the plant communities following senescence. Vegetative and reproductive parts were separated during sample collection. Vegetative samples include current-year fascicles and leaves, and inflorescences included the stem and cauline leaves or bracts. The samples were dried at 40°C for 48 hours and stored at room temperature. They were ground to a powder using a Wiley Mill™ in the Department of Forest Sciences, UBC. Carbon and N concentrations were determined by combustion with a LECO™ CHN analyzer at the Soil Science Laboratory at UBC.

### 3.2.4. Soil Collection & Analysis

Soil cores (3 cm diameter, 10 cm depth) were removed at the end of the growing season from the Riverside Willow, Sedge Meadow, and Polar Semi-desert sites. One core was removed from each of the eight OTCs and control plots from the Sedge Meadow and Riverside Willow sites, and from the five plot pairs in the Polar Semi-desert site. They were kept frozen prior to analysis. The soils were thawed and dried at 60°C for 48 hours and then sieved through a 2 cm mesh to
remove roots and rocks, homogenize the samples, and ensure complete combustion during analysis. Carbon and N concentrations were determined as described above.

3.2.5. Data Analysis

Data were analyzed with JMP IN™ statistical software (Version 4.0.3. SAS Institute Inc. 2000. Pacific Grove, California: Duxbury Press). Some samples were discarded because they did not meet the minimum 0.1 g required for analysis on the LECO™ analyzer. Differences between temperature treatments, species and sites were evaluated using Kruskall Wallis tests. We chose a significance level of p ≤ 0.1 due to the high spatial heterogeneity of the treatment plots.

3.3. RESULTS

3.3.1. Litter Carbon and Nitrogen

Table 9 gives the percent difference in litter C concentration, N concentration, and C:N ratio between temperature treatments. Variation in the N concentration in each species was usually greater than that of C, such that differences in C:N ratio were largely the result of changes in leaf N concentration. ANOVA for all sites, species, and parts together yielded no significant differences in C:N ratio between temperature treatments, and there were no consistent trends between sites for the same species or between species within the same site. Higher N concentration and lower C:N were observed in S. arctica in the OTCs in the upland Polar Semi-desert sites (Figure 12a). Conversely, litter C:N was higher in the OTCs in most of the species and parts sampled in the lowland (Figure 12b-d). This trend was significant for S. arctica (V) and L. confusa (V) at the Riverside Willow site (p = 0.0472 and 0.1000, respectively), and for E. triste (V) and D. integrifolia (R) at the Sedge Meadow site (p = 0.0472 and 0.1000, respectively). However, lower C:N were observed in the vegetative parts of four species in the lowland OTCs, and this was significant for O. digyna (p = 0.0285). When the C:N was averaged for each species (vegetative and reproductive parts together) at each site, C:N was consistently higher in the litter from the OTCs in the lowland, with the exception of D. integrifolia at the Sedge Meadow site (Table 9); however, the differences between treatments were not significant.

In the OTCs, C:N increased in the vegetative parts of the woody growth forms (shrubs) at the Riverside Willow site, and decreased at the Sedge Meadow site. Similarly, the C:N ratios in the vegetative parts of the herbaceous growth forms (forb and graminoids) increased in the OTCs in the Sedge Meadow site and decreased at the Riverside Willow site. Furthermore, in the four species that had lower vegetative C:N ratios, the reproductive C:N ratios consistently increased
Differences in C and N concentration, and C:N ratio were greater between species within each site (in the control plots) than between temperature treatments. The differences in C:N ratio between species were significant at the Heath, Riverside Willow, and Sedge Meadow sites ($p = 0.0218$, $0.0001$ and $0.0026$, respectively). The highest C:N ratios were generally found in the woody semi-evergreen shrubs ($C. tetragona$, $D. integrifolia$), and the reproductive parts of the woody deciduous shrub ($S. arctica$) followed by the herbaceous forb ($O. digyna$), and graminoids ($L. arctica$, $L. confusa$, $C. stans$, $E. triste$). Furthermore, the differences in C:N ratio for the same species between sites (in the control plots) were often greater than the differences between temperature treatments. The vegetative parts of $S. arctica$ and $D. integrifolia$ were significantly different between the sites from which they were sampled ($p = 0.0101$ and $0.0283$, respectively). The differences in C:N ratio between vegetative and reproductive parts within a species at each site were also usually greater than the treatment differences. The C:N ratio of the reproductive (female) parts of $S. arctica$ was significantly higher than the vegetative parts at the Heath, Riverside Willow, and Sedge Meadow sites ($p = 0.0209$, $0.0140$ and $0.1016$, respectively). Similarly, the reproductive parts of $C. stans$, and $E. triste$ had higher C:N ratios than the vegetative parts at the Sedge Meadow site ($p = 0.0143$ and $0.0283$, respectively). The reproductive parts of $D. integrifolia$ had a significantly lower C:N ratio than the vegetative parts at the Sedge Meadow site ($p = 0.0283$).

3.3.2. Soil Carbon and Nitrogen

There were no significant differences between temperature treatments in soil C concentration, N concentration, or C:N ratio at any of the sites sampled (Figure 13). The average soil C:N increased in the OTCs in the two lowland sites, and decreased in the OTCs at the upland Polar Semi-desert site. This follows the same general trends observed for the litter C:N ratios between the temperature treatments. Total C and N concentrations were greater in the mineral soils at the Riverside Willow and Polar Semi-desert sites within the OTCs. Conversely, C and N concentrations were approximately 25% lower in the OTCs compared to the controls at the Sedge Meadow site, although the differences were not statistically significant.
Table 9: Percent difference for C, N, and C:N ratios between the Control plots and OTCs for litter collected at the end of the 2001 growing season. Positive values indicate increases in the OTCs. For each species, the reproductive and vegetative parts are abbreviated as "R" and "V", and the average of all parts sampled is indicated as "avg". R-f and R-m distinguish the male and female reproductive parts for *S. arctica*. The growth forms are abbreviated as DDS: deciduous dwarf shrub, EDS: evergreen dwarf shrub, F: forb, GR: graminoid rush, GS: graminoid sedge. Significant differences between temperature treatments for each species and part (p \leq 0.1) are bolded.

<table>
<thead>
<tr>
<th>Plant Community and Description</th>
<th>Species (Part), Functional Group</th>
<th>n</th>
<th>% Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>C</td>
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<tr>
<td><strong>Polar Semi-desert (D)</strong></td>
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<td>3</td>
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<td><em>S. arctica</em> (V) DDS</td>
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<td>-1.2</td>
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</tr>
<tr>
<td></td>
<td><em>S. arctica</em> (R-m) DDS</td>
<td>5</td>
<td>-0.7</td>
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<tr>
<td></td>
<td><em>S. arctica</em> (V) DDS</td>
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<td>2.0</td>
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<tr>
<td></td>
<td><em>S. arctica</em> (avg) DDS</td>
<td>-</td>
<td>-0.1</td>
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<tr>
<td></td>
<td><em>D. integrifolia</em> (R) EDS</td>
<td>5</td>
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<td><em>O. dignya</em> (R) F</td>
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<td><em>L. arctica</em> (V) GR</td>
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<td><strong>Sedge Meadow</strong></td>
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<tr>
<td></td>
<td><em>C. stans</em> (R) GS</td>
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<td>0.7</td>
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<td></td>
<td><em>C. stans</em> (V) GS</td>
<td>5</td>
<td>-1.0</td>
</tr>
<tr>
<td></td>
<td><em>C. stans</em> (avg) GS</td>
<td>-</td>
<td>-0.1</td>
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<tr>
<td></td>
<td><em>E. triste</em> (R) GS</td>
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<td>-0.1</td>
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<tr>
<td></td>
<td><em>E. triste</em> (V) GS</td>
<td>5</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td><em>E. triste</em> (avg) GS</td>
<td>0.04</td>
<td>7.81</td>
</tr>
</tbody>
</table>
Figure 12: C:N ratios of litter collected at the end of the 2001 growing season. The X-axis labels include the species and part sampled: vegetative = V, reproductive = R, and R-f or R-m represent female and male reproductive parts. V-dolo and V-gran distinguish the samples collected from the dolomite and granite substrates in the Polar Semi-desert communities. OTC bars shown in black versus white illustrate where C:N increased or decreased relative to the controls, respectively. Significant differences between the Control and OTC plots (p ≤ 0.1) are indicated with asterisks. Error bars are +/-1 SE of the mean.
Figure 13: a) %C, b) %N, c) C:N of soils at the end of 2001 growing season. All cores were 2 cm in diameter. The depth of the cores from the lowland Riverside Willow and Sedge Meadow communities was 10 cm. The depth of the cores from upland Polar Semi-Desert (granite substrate) was 5 cm. There were no significant differences between temperature treatments.
3.4. DISCUSSION

3.4.1. The Effects of Warming on Litter Carbon and Nitrogen

Although the effects of warming on litter N concentration and C:N ratio were not significant for all sites, species and parts analyzed together, at least one species from each growth form was significantly affected by the warming treatment. This is contrary to the findings during the fifth year of warming, where only the woody growth forms had higher C:N ratios in the OTCs, and there were no differences between temperature treatments for the herbaceous growth forms (Tolvanen and Henry, 2001). Welker (2000, pers. comm.) observed consistent decreases in plant N concentration in both woody and herbaceous growth forms in the OTCs, and this trend was significant for two species (*O. dignya* and *S. arctica*). In this study, however, the effect of warming on the C:N ratio of each species was in some cases positive or negative depending on the site. This may be related to the different effects of warming on NO₃, NH₄ and SON availability in each plant community (Chapter 2). At the Sedge Meadow site, significant increases in NO₃ and SON availability in the OTCs may have caused an increase in N uptake by the shrubs (vegetative samples), leading to lower C:N ratios. Similarly, increases in NH₄ availability in the OTCs at the Riverside Willow site may have increased N uptake and reduced C:N ratios in the herbaceous species. The effect of warming on litter C:N ratio in the Polar Semi-desert sites was opposite to the trend observed in the lowland plant communities. The observed increase in litter N content and plant growth in the OTCs in the upland Polar semi-desert sites indicates greater overall plant N uptake. This may help to explain the significant decrease in N availability observed in soils at the PSD-D site, discussed in Chapter 2.

Changes in allocation between the reproductive and vegetative parts in the OTCs have also affected litter C:N ratios within each species. For each of the four species that had lower vegetative C:N ratios in the OTCs, the C:N ratios of the reproductive parts increased. This may be due to increased growth and C accumulation in the reproductive parts, causing dilution of leaf N (Shaver et al. 1992). This hypothesis is supported by the findings of a meta-analysis of 13 ITEX sites, where reproductive effort increased in the warmed treatments, particularly in the high arctic sites (Arft et al. 1999).

3.4.2. The Effects of Warming on Soil Carbon and Nitrogen

Changes in soil C and N concentrations reflect the observed changes in litter C and N concentrations, quantity of litter input, and decomposition in the OTCs. Although the soil C:N ratios followed the same general trends as the litter C:N ratios, there was no significant effect on
soil C:N ratio. The slight increases in the soil C and N concentrations in the OTCs at the Riverside Willow site was similar to the trend observed during the 7th year of warming, however the difference between the treatments was much less than that observed by Welker (2000, pers. comm.). Higher soil C and N concentrations may be due to the increases in litter input each year with the significant increases in plant growth observed in the OTCs at this site (Jones, 1995, G.H.R. Henry pers. comm. 2002). Plant growth has also increased in the OTCs at the Sedge Meadow site, however, the decrease in C and N concentrations may be a result of increased decomposition of the soil organic matter over the ten-year experiment. This is supported by the observed increase in N immobilization in the OTCs at the Sedge meadow site (Chapter 2). Furthermore, the buried bag transplant experiment demonstrated that changes in soil properties, independent of temperature, affected soil N processes during the 2001 growing season (Chapter 2). The observed reduction in soil C and N concentrations, although not significant, provides further support for the foregoing conclusion.

3.4.3. Litter Quality Feedbacks to Nitrogen Availability and Plant Growth

The results of this study demonstrate the potential for negative litter quality feedbacks to N availability in the lowland plant communities under warmer growing conditions. Firstly, higher litter C:N ratios were measured in nearly all species in the warmed treatments at the lowland sites, and significant increases were observed for four species. Secondly, the trend of increasing reproductive effort with warming (Arft et al. 1999) has also significantly affected litter C and N concentrations. Reproductive parts of each species had higher C:N ratios, and furthermore, warming increased the C:N of reproductive parts consistently in this study.

The large differences in C:N between species and growth forms, compared to treatment differences indicate that changes in species composition with warming will have the greatest potential for litter quality feedback to N availability. Hobbie (1996) reached a similar conclusion after observing greater differences in decomposition and N release between species than between temperature treatments in a laboratory microcosm experiment. Furthermore, nutrient addition affects allocation patterns in tundra species more than manipulations of other resources; therefore, warming affects allocation indirectly through changes in N availability (Chapin and Shaver 1996). The observed changes in N availability (Chapter 2) have likely affected allocation patterns of vegetation in the OTCs, although this has not yet been examined at this study site because of the need to minimize plot disturbance and continue the long-term experiment. In the same microcosm experiment discussed above, Hobbie (1996) also found that the variability in
decomposition rate and N release between litter types (leaves, shoots, and roots) was as great as the variability for the same litter type at different temperatures. Therefore, changes in allocation will likely have significant impacts on nutrient cycling at this study site under warmer climate conditions.

The above conclusions support the hypothesis that ecosystem feedbacks to CO₂-induced climate warming will be constrained by carbon/nutrient interactions (Shaver et al 1992). Increases in C:N ratio demonstrate the potential for negative litter quality feedback to N availability, plant growth, and C fixation. However, the soil C:N was not significantly different between treatments. This may be due to opposing effects of warming on litter quality, quantity, and decomposition rates combined. During the 2001 growing season increases in N availability were observed in the OTCs despite the evidence of higher litter C:N ratios for some of the dominant species at each site. This has contributed to increases in plant growth in the warmed plots. If this response holds across high arctic tundra types, then this would provide a negative feedback to CO₂-induced climate warming.

3.5. CONCLUSIONS

1. Litter had a higher C:N ratio in all functional groups and dominant species at each of the lowland sites during the tenth year of experimental warming. This indicates potential for negative feedbacks to N availability with long-term warming.

2. The C:N ratio increased in the reproductive parts of each species with warming. This is likely a result of increased reproductive effort. Furthermore, increases in allocation to reproductive parts also affects litter quality, as the reproductive parts of most tundra species had higher C:N ratios than the vegetative parts.

3. Soil C:N ratios followed the same decreasing trend as litter C:N in the lowland study sites; however, there were no significant differences between temperature treatments.

4. Soil C and N concentrations declined in the organic soils at the Sedge Meadow, possibly due to increased microbial activity and decomposition of soil organic matter in the OTCs.
CHAPTER FOUR: SUMMARY AND CONCLUSIONS

4.1. PURPOSE OF STUDY

The purpose of this study was to examine the effects of a 10-year warming experiment on N cycling in high arctic plant communities. Several aspects of the plant-soil N cycle were examined, firstly to identify short-term (current) effects of warming of soil N processes and availability (Chapter 2), and secondly to evaluate the potential for long-term (future) feedbacks to soil N processes/availability through changes in litter and soil quality (Chapter 3). This study was conducted in five plant communities along a soil moisture gradient. The effects of warming in the lowland sites may be extrapolated to other high arctic oases and similar sub arctic locations, while the upland polar semi-desert sites provide contrasting information that may be more representative of broad areas in the high arctic. Furthermore, it is assumed that site differences along the gradient reflect longer-term responses to changing environmental conditions (decades to centuries), while the warming experiment within each site reflects the short-term responses (years to decades) (Shaver et al. 2000).

4.2. SIGNIFICANT FINDINGS

Short-term climate warming is likely to increase N availability in the lowland plant communities as a result of increased microbial activity, decomposition, and annual N mineralization, particularly in organic soils of wet sedge meadows. These findings indicate the growth responses of high arctic tundra ecosystems to warming may not be constrained by nutrient limitations. As a result, plant growth, net primary productivity, and net ecosystem carbon (C) storage, will likely increase, providing a negative feedback to CO₂-induced climate warming (Rastetter et al. 1991).

Increases in plant growth and shading with warmer growing season temperatures may reduce to soil temperatures. This might offset the positive effects of warming on soil N transformations and N availability. Furthermore, changes in litter C and N concentrations will feedback to soil C and N concentrations and N transformations, which may also constrain initial increases in N availability under long-term conditions of climate warming.
4.3. FUTURE RESEARCH

Sampling methods that minimize site disturbance should be employed to preserve long-term study plots. Ion exchange membranes (IEMs) are easy to use and require minimal plot disturbance, making them ideal tools for assessing changes in nutrient availability. The results of this study indicated that IEMs are effective at measuring SON availability, which should be included in nutrient assessments as plants can absorb SON either directly from the soil or through mycorrhizal symbiosis. The index of ion availability indicated by IEMs was affected by duration of incubation and extract solution. Standardized methods should be adopted to compare the results between study sites. Inclusion of such methods into the ITEX Manual (Molau and Molgaard 1996) will help to facilitate this.

Continuation of long-term experiments is needed to determine the time scales at which ecosystems initially respond to environmental manipulations, and eventually feed back to ecosystem processes. In this study, short-term (first season) temperature manipulations had no significant effect on soil N transformations (Chapter 2); however, longer-term (10 year) changes in soil properties elicited changes in soil N transformations. This highlights the importance of long-term ecosystem manipulation experiments, even on decadal time scales. Furthermore, continuation of this experiment will allow us to test the hypothesis that litter quality feedbacks will adversely soil organic matter quality, N availability, and plant growth under long-term conditions of climate warming. If this hypothesis is supported, a more precise time scale for litter quality feedbacks to N availability and plant growth may be identified for arctic ecosystems in response to climate warming.
REFERENCES


