# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page #</th>
</tr>
</thead>
<tbody>
<tr>
<td>List of Project Investigators, Cooperators and Graduate Students</td>
<td></td>
</tr>
<tr>
<td>Overview of Arctic LTER Research</td>
<td>1</td>
</tr>
<tr>
<td>Terrestrial Research in the Arctic LTER Project</td>
<td>3</td>
</tr>
<tr>
<td>Land-Water Interactions</td>
<td>5</td>
</tr>
<tr>
<td>River Studies</td>
<td>6</td>
</tr>
<tr>
<td>Lakes</td>
<td>3</td>
</tr>
<tr>
<td>References</td>
<td></td>
</tr>
<tr>
<td>Data Access Information</td>
<td></td>
</tr>
<tr>
<td>List of Publications</td>
<td></td>
</tr>
<tr>
<td>Biographical Information</td>
<td></td>
</tr>
</tbody>
</table>
The Arctic LTER Project, 1995 Site Review
see also the Arctic LTER Home Page for more information

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OVERVIEW OF ARCTIC LTER RESEARCH

Objectives

The overall objectives of the Arctic LTER project are to gain an understanding of the arctic ecosystem near Toolik Lake, Alaska. There are three approaches used:

1. Measure the long-term changes in ecosystem structure and function that might occur;
2a. Determine the extent of control by resources (bottom up control);
2b. Determine the extent of control by predation and grazing (top-down control);
3. Determine the land-water interactions of flux of water, gases, nutrients, and organic matter.

History

Pleistocene mountain glaciers covered the foothills region; the most recent, which formed Toolik Lake, retreated some 12,000 years ago. A 350,000 year-old surface occurs near the Kuparuk River. Pollen analysis shows that birch (*Betula*) dominated the region (12,000-9,500 B.P.) after the last glacial retreat but that present vegetation has been unchanged for the past 9,500 years (*Alnus* and *Picea* pollen).

In 1970 a major pipe-line construction camp was built near the lake and in 1975 the road from Prudhoe Bay to the Yukon River (and Fairbanks) was completed. Scientists immediately took advantage of the opportunity: aquatic research began in 1975 and terrestrial studies soon after. In 1987 the LTER project began and was renewed in 1992. It encompasses the upper watersheds of several rivers near Toolik Lake (Fig. 1 and Cover). Within LTERs, the project is unusual in that both aquatic and terrestrial systems, and their interaction, are studied. This breadth is possible only because of several closely-allied NSF projects (funded by DEB and OPP). Currently, the LTER project funds monitoring, the database support, and maintenance of large-scale experiments. The other projects fund process studies and subcontract P.I.s.

Location and Climate

The Arctic LTER site is located at 69°N 149°W at 720 m above sea level in the northern foothills of the Brooks Range, Alaska. In northern Alaska (Fig. 1) the foothills province covers 100,800 km² (the size of New York State), the mountain province 136,200 km², and the coastal plain to the north 70,900 km². The continuous cover of the tussock tundra is typical of the low arctic. Permafrost, which lies just a meter or so beneath the surface, extends to 700 m depth and acts as a seal to water percolation so that even the small amounts of rainfall (total precipitation is 20-30 cm) create a moist tundra. The annual temperature is around -7°C and the ground is unfrozen from mid-May until mid-September (Fig. 2).

Monitoring Studies

This approach of the LTER research (Fig. 3) has the goal of determining the amount of long-term change and natural variability in these ecosystems (Objective 1) and in the driving variables of climate, insolation, soil and water physics, and soil and water chemistry (for Objective 2). In the terrestrial system, monitoring includes vegetation distribution and production, annual flowering rates along a northern Alaska transect, climate (insolation, air temperatures, soil temperatures, windspeed and direction), and thaw depth. For land-water interactions, monitoring includes water movement in a research watershed, nutrients in soil and surface water, and gas (CO₂, CH₄) concentrations in streams and lakes. In streams, the monitoring includes water flow, conductivity, concentrations of nutrients, chlorophyll amounts on the stream rocks, distribution of mussels, insect populations, and fish (grayling) numbers and production. In lakes, monitoring includes physics (light penetration, temperature stratification), chemistry (oxygen, pH, nutrients, conductivity), and biology (primary productivity, chlorophyll, zooplankton species and abundance, and fish abundance).

Process Studies

These are designed to investigate controls of ecosystem processes as well as the bottom-up and the top-down controls (Fig. 3). In the terrestrial system, process studies include litter bag measures of decomposition, CO₂ flux measures of production, small chamber measures of CH₄ production, and ¹⁵N studies of the incorporation of nitrate, ammonia, and glycine into different plants (variables of type of nitrogen, season of uptake, depth of uptake). For land-water, process studies include measuring the effect of land-derived organic matter on planktonic microbial food webs in 5 m³ enclosures, measuring soil water movement with the gas SF₆, and determining the evasion coefficient of CO₂ from stream and lake
Figure 1. The location of the study site of the Arctic LTER project. The field station is at Toolik Lake where most of the terrestrial research takes place. Stream research takes place in Blueberry Creek, the Kuparuk River south of the haul road, and Osrukuyik Creek.
Figure 2. Monthly air temperatures (4-6 year average) and summer rainfall (1989-1994) at Toolik Lake. Daily solar radiation for 1993 is also shown.
GOALS AND RESEARCH APPROACHES OF THE ARCTIC LTER

Arctic LTER Goals

<table>
<thead>
<tr>
<th>Land-water interactions</th>
<th>Long-term change in ecosystems</th>
<th>Control by resources</th>
<th>Control by predation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluxes of: H₂O gases, nutrients, organic matter</td>
<td>∆ vegetation production, GEM</td>
<td>N &amp; P addition, ¹⁵N tracer</td>
<td>exclude grazers, experimental browsing, defoliation</td>
</tr>
<tr>
<td>Fluxes of: H₂O gases, nutrients, organic matter</td>
<td>∆ hydrology, temperature, chemistry, chlorophyll, insects</td>
<td>N &amp; P addition, ¹⁵N tracer, N flux model</td>
<td>add fish, remove insects</td>
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<tr>
<td>DOC addition, gas emission</td>
<td>nutrients, physics, primary production, chlorophyll, zooplankton, benthic invertebrates, fish</td>
<td>N &amp; P addition, ¹⁵N tracer, mesocosm experiments, bioenergetic model</td>
<td>add, eliminate fish, bioenergetic model, planktonic fish, feeding model</td>
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Figure 3.
Table 1. The five research areas common to LTER sites and the corresponding measurements being carried out at the Arctic LTER site.

1. **Primary production, pattern and control**
   - Tundra: biomass production control by nutrients, light, temperature; enclosures to test effects of herbivores; annual and regional variation
   - Streams: production control by nutrients, grazers; natural variations, seasonal, yearly, and between streams
   - Lakes: primary production natural variation measured seasonally, yearly, and between lakes; control of production by nutrients, grazers

2. **Populations representing trophic structure, spatial and temporal distribution**
   - Streams: algae (chlorophyll), insects, fish; $^{15}$N gives trophic level, $^{13}$C gives food resources; isotope comparisons with other LTER's
   - Lakes: phytoplankton and benthic algae (species, chlorophyll); zooplankton, insects, molluscs, fish; $^{15}$N distribution gives trophic level, $^{13}$C gives food resources; isotope comparisons with other LTER's

3. **Organic matter accumulation in soils and sediments, pattern and control**
   - Tundra: long term accumulation by $^{14}$C dating; decomposition in lab and field; comparative decomposition with other LTER's; effects of fertilizer and greenhouse treatments
   - Lakes: sediment accumulation by $^{14}$C; sediment trap studies; benthic respiration in chambers; nutrient addition effects on sedimentation and sediment nutrient flux and respiration; controls of sulfur accumulation, sediment cores

4. **Nutrients, inorganic inputs and movement through soils, groundwater, and surface waters**
   - Tundra: nutrient budgets of contrasting ecosystems; water and nutrient transport between systems on a toposquence; exchange of gases between tundra and atmosphere; export of nutrients and dissolved organic matter from experimental watersheds
   - Streams and Lakes: output budget for Kuparuk River and for Toolik feeder stream; input budget for Toolik Lake; seasonal and yearly variations in nutrients; nutrient transformations in riparian and hyporheic zone; flux of CO$_2$ and CH$_4$ from surface waters to atmosphere; 160 nutrient analyses for snow, springs, surface water

5. **Disturbance at site, pattern and frequency**
   - Tundra: measurement of long-term change of communities due to climate change; amount of disturbance by road dust; population dynamics of native and exotic plant species; short and long term effects of nutrient addition
   - Streams: chemical and biotic response to eutrophication; measurement of fishing pressure and effects of removal of fish on trophic structure; extreme natural variations in snowmelt, discharge
   - Lakes: chemical and biotic response to eutrophication; disturbance of trophic structure caused by removal of top predator, the lake trout; variations in primary production caused by natural changes in discharge and resulting changes in nutrient input
surfaces. For stream studies, process studies include the determining the effect of insect grazing on algae with inhibitor diffusion chambers, determining the effect of fish predation by an increase in fish numbers, measuring primary productivity with oxygen techniques, and determining the importance of hyporheic flow with bromide as the conservative tracer. For lake studies, process studies include measurements of nutrient limitations in plankton, the grazing rate of microflagellates and ciliates on bacteria, measuring the flux of nutrients and oxygen between sediment and water, and measuring the feeding behavior of fish in a large chamber.

Long-term and Large-scale Experiments

The short growing season and cool temperatures determine that processes and ecosystems are slow to reach a new equilibrium of changed production and changed species dominance after disturbance. Terrestrial manipulations of light, temperature, and nutrients have been carried out for ten years on 4 m x 4 m replicated plots. Other plots have been fertilized for decades. Stream fertilization with phosphate (continuous addition) began in 1983 in the Kuparuk River and in 1991 in Oksrukuyik Creek. Whole lake fertilization continued for 5 years in a divided lake and recovery studies have extended from 1991 to the present. Lake trout, grayling, and sculpin have been added or removed from several lakes to determine the top-down controls of lake biotic structure.

Other Tools (data base, Mosaic, GIS, protocols)

The data collected in the monitoring and the long-term studies, as well as other information, are placed into the Arctic LTER data base, maintained at the MBL in Woods Hole. Most of the data are accessible to all through a Gopher and Mosaic (http://www.mbl.edu/html/ECOSYSTEMS/Iterhtml). Some of the data are available only with the permission of individual P.I.'s; the document file for this material is always available. Method descriptions (protocols) have been assembled for each section and will eventually be put on Mosaic.

Stable Isotopes

The use of the stable isotopes $^{15}$N and $^{13}$C are an important research tool of the project. The natural abundance of these isotopes was first used to determine the food-web relationships (trophic level) of stream and lake animals. In tundra plants on the same plot, $^{15}$N natural abundance showed a large but consistent difference in the source of nitrogen for plants on the same plot. The project pioneered in the approach of adding $^{15}$N to large systems. It was added as ammonia to one lake and has now been added in a continuous mode to two streams. As already mentioned, $^{15}$N in various forms (nitrate, ammonia, and glycine) was added to tundra soil to help understand the reason for the differential use.

Mathematical Modeling

The biogeochemical model GEM (General Ecosystem Model) has been parameterized for the tussock tundra at Toolik Lake and the carbon stored (net ecosystem production) was estimated over the past 150 years. A stream model of the distribution of $^{15}$N was constructed, based on many years of process studies of the nitrogen cycle, and then validated against the actual distribution found after the addition. Lake models of greyling feeding strategy were developed and a model of fish bioenergetics was adapted for tundra lake trout. A model of stream discharge based upon TOPMODEL is under construction with NOAA funding. Models of drift feeding Arctic grayling and food web dynamics of Toolik Lake are also under development.

Comparisons with Other Systems

The Arctic LTER is taking part in the LTER-wide comparison of decomposition rates using standard litters to separate out the influence of the litter quality from the temperature and moisture effects. Brian Fry of the Arctic LTER project also conducted a stable isotope workshop in which foodwebs for streams and lakes from a number of long-term sites were compared (Fry, 1993). GEM is also being used to compare effects of climate change on net ecosystem production across tundra, deciduous forest, coniferous forest, and grassland ecosystems (McKane et al., in review).

Within the LTER research network, five types of research have been identified that are carried out at each site. At the Arctic LTER site, all of these areas are under study anyway as described in Table 1.
Figure 4. A vegetation map of the intensive study site of the Arctic LTER project at Toolik Lake, showing the watershed being studied intensively as part of the land-water interactions research and the main experimental area in moist tussock tundra.
TERRESTRIAL RESEARCH IN THE ARCTIC LTER PROJECT

Overview

The landscape near Toolik Lake includes a diverse array of tundra types, ranging from relatively unproductive dry heath and wet sedge communities to highly productive riparian shrub vegetation (Fig. 4). The most common tundra, both at Toolik Lake and over the whole North Slope of Alaska, is moist tussock tundra dominated by the sedge, Eriophorum vaginatum. Terrestrial research of the Arctic LTER project began in 1978 (funding began in 1987) and involves long-term monitoring and experimentation in all of these tundra types. Most of the intensively studied sites are located within walking distance of the Toolik Field Station. An additional 20-25 sites, located along the ecological transect opened up by the Dalton Highway from Fairbanks to Prudhoe Bay, are monitored every 1-3 years.

Over the past 20 years, our hypotheses and the overall design of our research have evolved considerably, from an early focus on response to construction-related disturbances through studies of (1) plant growth rates in relation to internal C, N, and P status, (2) nutrient limitation of whole-community productivity, (3) nutrient transport and linkages between communities in the landscape, and (4) carbon-nutrient interactions at the whole-ecosystem level. The current focus is on comparisons among ecosystem types in terms of the regulation of overall carbon balance by carbon-nutrient interactions.

The conceptual model that has guided our recent research is called the Simple Arctic Model, or SAM (Fig. 5; Shaver et al. 1992). In this model the carbon balance of arctic tundras is viewed as interacting with other nutrients (e.g., N, P) in three major ways: (1) through controls on C:nutrient ratios within major organic matter pools such as plants and soils; (2) through controls on the distribution of nutrients among pools with different C:nutrient ratios, and (3) through controls on the balance of nutrient inputs and outputs from outside the ecosystem. We developed this model on the basis of past research that showed strong nutrient limitation to productivity of essentially all tundra communities (Shaver and Chapin 1986, 1991, Shaver et al. 1986, Nadelhoffer et al. 1991, Gilpin et al. 1991), and other research that showed relatively small long-term change in response to atmospheric CO₂ concentration or changes in temperature alone (Billings et al. 1982, 1983, Oechel et al. 1994). In the past few years we have tested this model in long-term field experiments in which we have manipulated nutrient availability, air temperature, and light intensity (Chapin et al. 1995), in laboratory microcosms (Johnson et al. in review), and using a detailed, ecosystem simulation model (Rastetter et al. 1991, 1992, McKane et al. in review). The majority of this work has been done in moist tussock tundra, where we have found SAM to be quite useful as a heuristic guide to the design and interpretation of our research. One current emphasis of our research is on testing SAM in wet sedge tundra, dry heath tundra, and tall shrub tundra, in order to test the model's generality. A long-term goal is to develop a model like SAM that is useful in developing predictions of how and why different ecosystems should vary in their overall responses to a given climatic change or other disturbance.

We have also identified several priorities for future research. One priority is to increase our understanding of the overall balance of soil respiration:N mineralization in tundra ecosystems (bow tie #2 in Fig. 5). We feel that this balance is critical to the overall C balance because primary production is strongly nutrient-limited, and essentially all of the nutrients taken up by plants are recycled from soil organic matter (Shaver et al. 1992). Thus, the C balance of the ecosystem is essentially equal to the net C gains associated with nutrient uptake, balanced against C losses associated with nutrient mineralization. In preparation for this research we have developed a more detailed conceptual model of C:nutrient interactions in tundra soils, called the Model of Arctic Decomposition (MAD; Fig. 6); we are now seeking additional funding for research based on this model. A second priority is to return to research at the plant species level, with the aim of improving our understanding of how different plant functional types affect ecosystem-level biogeochemistry. This was an early theme of our work in the 1970’s and 1980’s. Our new work on species effects will begin in earnest in 1995, in collaboration with four other NSF-supported projects that are part of the US-ITEX program. To link these first two priorities for future research and guide their overall development, we have developed a new set of three organizing hypotheses about the regulation of primary production on both short and long time scales (Table 2).

A third priority for future research is to increase our understanding of the role of animals in tundra carbon and nutrient cycling. To this end we held a workshop in 1993 and reviewed past research on the role of herbivores in arctic ecosystems (Jeffries et al. 1994). We also have begun two experimental studies on effects of herbivores, one using long-term exclosures and a second on the effects of herbivory on plant C:N balance. In the long term we need to integrate this work more fully with our other research.
**Figure 5.** The Simple Arctic Model (SAM; Shaver et al. 1992) of nutrient interactions in tundras, using C and N as an example. In this model there are two major pools of organic matter in the ecosystem (i.e., plants and soil). Carbon fluxes into and out of these pools are indicated by solid lines and N by dashed lines. The bow ties suggest links between C and N fluxes. Bow tie #1 implies that net C uptake by plants (net primary production, NPP) is constrained by the plant's ability to take up N, and vice versa. We suggest that in many nutrient-limited systems, such as tundras, essentially all of the plant's nutrient supply comes from the mineralization of soil organic matter (including recent litter) and that N mineralization is linked to the loss of C in soil respiration. (Dissolved C losses indicated by the arrow at lower left, are usually small relative to gaseous exchanges.) Thus, at least in a proximate sense, the overall C balance of such ecosystems (i.e., the difference between NPP and soil respiration) is largely determined by C gains associated with N uptake by plants, balanced against C losses associated with N mineralization.
Table 2. Three organising hypotheses for the terrestrial research of the Arctic LTER project.

The first hypothesis deals with short-term adjustments of primary production to climate by tundra vegetation, the second hypothesis deals with long-term adjustments, and the third deals with the rate of long-term adjustment. In the context of this research, "short-term adjustment" means year-to-year variation while "long-term adjustment" refers to changes taking place over 5-10 years or more. Very long-term adjustments, involving migration of new species into the vegetation, are also important but are beyond the scope of this research.

**HYPOTHESIS #1:** Short-term, annual variation in net primary production of tundra vegetation is strongly "buffered" in its adjustment to annual variation in climate. This buffering is the result of mechanisms operating at several levels of ecological organization including:

- **a.) Within-plant storage and reallocation of essential resources,** such that resources (e.g., C, N, P) acquired in one year are reused in support of primary production in subsequent years.

- **b.) Within-community differences in species responses to climate in a given year.** Responses of different species tend to compensate for each other, such that not all species have "good years" at the same time.

- **c.) Lags in the response to annual climate variation on the part of soils relative to plants.** Because productivity is closely tied to nutrient supply (Hypothesis #2) the effect of a "good year" for nutrient mineralization is mainly seen in subsequent years, with different climates.

**HYPOTHESIS #2:** Long-term adjustments of net primary production in tundra vegetation, in response to sustained climate change, are driven primarily by effects of climate on nutrient supply from the soil and by constraints on plant nutrient use efficiency and nutritional balance.

- **a.) Although nutrient use efficiency varies among species and ecotypes, effects of these differences in nutrient use efficiency on community productivity are small relative to the effects of a change in nutrient supply.**

- **b.) Direct effects of climate on physiological uptake processes like photosynthesis cannot overcome these nutritional constraints to productivity.**

**HYPOTHESIS #3:** The rate of adjustment of primary production to a sustained change in climate (and soil nutrient supply) is determined primarily by species and ecotypic differences in potential growth rates, as regulated by flexibility in their allocation patterns, nutrient use efficiency, and vegetative demography.
Figure 6. The Model of Arctic Decomposition (MAD), in which a new level of detail is added to the “Soil Organic Matter” (SOM) box of SAM (Figure 1). Inputs and outputs to SOM are the same as in the SAM model with solid lines representing C fluxes and dashed lines representing N fluxes. The three SOM pools (I, II and III) are operationally defined as extractives, acid soluble and acid insoluble and are hypothesized as having different turnover times and C:N ratios. Inputs to these pools include soluble organic matter, cellulose and lignin from plant litter and microbiologically mediated fluxes of C and N from other SOM pools. Microbial by-products also serve as inputs to all three SOM pools. Respiratory losses of CO₂ and/or CH₄ accompany C transfers among SOM pools. In addition, dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) can be lost as leachate. Mineralized N and dissolved organic N (DON) released from individual pools can be assimilated by microbes, incorporated into other SOM pools, taken up by plants or leached from soils. Small amounts (not shown) can be exported as nitrous oxides formed during nitrification or denitrification.
Figure 7. Net aboveground primary production versus biomass for 6 tundra vegetation types along a riverside toposequence at the Sagavanirktok River, near Toolik Lake. Linear regression of these gives the formula: NPP = 0.126*Biomass + 60.5 (P<0.001, r² = 0.58).
Figure 8. Yearly average number of *Eriophorum* inflorescences in 2x2 m plots along the transect from Fairbanks to Prudhoe Bay (averaged among all sites for which at least 10 years of data are available).
Figure 9. Gross ecosystem production (GEP), or ecosystem photosynthesis, plotted against aboveground biomass in wet sedge tundra at Toolik Lake. Symbols indicate treatments applied over seven growing seasons before the measurements were made in 1994.
Figure 10. Net primary production of moist tussock tundra at Toolik after 3 years (1983) and 9 years (1989) of treatment. C = controls; N = nutrients added (N+P); T = increased air temperature (greenhouse); NT = nutrients + increased temperature; L = reduced light (shading).
Specific Contributions to Overall Project Goals

Land-water Interactions: During the 1980's our work along a riverside toposequence showed dramatic variation in soil nutrient cycling among adjacent ecosystems along the toposequence (Giblin et al. 1991), and suggested that transport of N and P in soil water moving across the top of the permafrost was potentially an important component of landscape nutrient budgets (Shaver et al. 1991). These results, combined with George Kling's discovery that C transport in soil water was likely to be a major landscape-level C flux (Kling et al. 1991), and the need to understand C and nutrient inputs to streams and lakes, led to the development of our program in land-water interactions in the current Arctic LTER project. By locating our primary experimental site immediately adjacent to the experimental watershed where land-water interactions are being studied (Fig. 4), we are contributing to the understanding of land-water interactions through our research on ecosystem C, N, and P budgets including inputs and outputs in soil water (Fig. 5). Most recently, we have also returned to our original toposequence site and shown that, contrary to expectations, primary production and plant biomass are linearly correlated with the lowest production:biomass ratios at the most productive, highest-biomass locations in the toposequence (Fig. 7). This is important because it indicates that element turnover in vegetation is slower in more productive locations in the landscape, thus slowing the movement of these elements from land to water.

Long-term changes: Since 1980 we have monitored the annual variation in flowering by Eriophorum vaginatum at sites ranging from Fairbanks to Prudhoe Bay (at some sites since 1976). Although this annual variation is uniform throughout northern and central Alaska, until recently the climatic drivers were unclear (Fig. 8). Recent collaboration with the Swedish ecologist, Ulf Molau, indicates that similar annual variation occurs in Sweden and perhaps also Siberia as well, suggesting that annual variation in flowering is uniform throughout the Arctic. Using our long-term data base, Molau has also developed a model that uses climate data over the previous four years, combined with assumptions about the multiyear development and mortality of inflorescences, to predict successfully the flowering in a given year. 1995 will be the first year in which these predictions will be tested (it's supposed to be a moderately above-average year for flowering). This is an important breakthrough because in the future it will allow us to integrate our extensive early work on Eriophorum growth, nutrition, vegetative demography, and seedling establishment (Shaver et al. 1986, Chapin et al. 1986, Fetcher and Shaver 1983, Gartner et al. 1986) into a comprehensive model of long-term population dynamics. Eriophorum is a keystone species in moist tussock tundra because its tussock growth form largely determines the fine-scale microtopography and microenvironmental variation that strongly regulates abundance and distribution of other species in the community.

Control by resources: Our research on resource control of tundra ecosystems is focused on long-term field experiments in which we manipulate nutrient availability with fertilizer, air temperature with small greenhouses, and light intensity by shading. These treatments are applied to four major ecosystem types: moist tussock tundra, wet sedge tundra, dry heath tundra, and riparian shrub tundra. Thus far, the majority of our research has focused on moist tussock tundra, where we have shown that nutrient limitation is by far the most important limiting factor to vegetation productivity and biomass accumulation (Fig. 9), both in the short term (1-3 years) and in the medium-to-long term (5-10 years). In the very long term, the primary importance of temperature may be exerted more through its impact on soil nutrient mineralization processes than through its direct effects on plant growth and resource uptake (Chapin et al. 1995, McKane et al. in review). In 1994, we sampled our long-term experiments in wet sedge tundra and found similar responses, but in wet sedge tundra P is most limiting (versus N in moist tundra). One of our more interesting results from wet sedge tundra was the highly significant, linear correlation between canopy N or P content and whole-system photosynthesis in our experiments (Fig. 10), suggesting that the large changes in species composition that we observed had little impact on the overall limitation of production by nutrient availability.

Control by predation/herbivory: Early work by George Batzli and coworkers (Batzli and Lesieutre 1991, 1995, Batzli and Henttonen 1990) described the nutritional controls, community organization, and use of the landscape by microtines at Toolik Lake. Brian Barnes of the University of Alaska has maintained long-term research on arctic ground squirrels at Toolik Lake, and reproduction and energetics of birds are under continuing study by John Wingfield and colleagues. Large mammals (caribou and moose) are not
abundant at Toolik Lake, but are under long-term study by Bob White and colleagues at nearby Happy Valley and Prudhoe Bay. A long-term aim is to develop more explicit collaborations with these investigators, who are now formally part of the Arctic LTER project. Our own research involving long-term herbivore exclusion and effects on plant C:N balance (done with Bob Jefferies of the University of Toronto) is growing slowly but needs more explicit integration into our overall conceptual approaches (Table 2, Fig. 5).

LAND-WATER INTERACTIONS

Introduction and Study Sites

Inputs of materials from land strongly regulate the functioning of lake and river ecosystems. These inputs include water, nutrients, and organic matter, which form the building blocks of aquatic food webs. The amounts, chemical forms, and timing of delivery of materials from land to water are critical, and thus the chemical transformations of material in terrestrial environments can have an important impact on aquatic systems. Although there are many indirect effects of terrestrial inputs, such as the support of grazing fish by algal production that is in turn driven by nutrient availability, it is the direct effects on aquatic systems that are most related to inputs from land. In our research on land-water interactions we consider the controls on production, transformation, and export of materials from land, and how those materials are processed within lakes and streams.

Our original work on land-water interactions was of a survey nature, and involved sampling sites along a transect from Toolik Lake to the Arctic Ocean. Although we have maintained those survey sites, intensive research began in 1991 when we established a small experimental watershed close to Toolik Lake. The watershed has an area of about 1.5 ha, is composed mainly of tussock tundra, and contains a primary stream with a birch and willow riparian zone. There are three transects of wells and lysimeters in the catchment, and an H-flume is installed to gauge water flow at the bottom. The study area has been mapped for vegetation, soils, topography, and landforms at the 1:500 and 1:24,000 scales. We maintain standard monitoring of biological and chemical processes, and are building a GIS database on key parameters such as thaw depth, soil characteristics, and chemical outputs.

Hypotheses

The LTER research on land-water interactions started with our observation that lakes and streams in the Arctic had higher pressures of CO₂ than the ambient pressure found in the atmosphere. This supersaturation was found in all seasons, and showed that surface waters contained excess CO₂ and were a net source of CO₂ to the atmosphere. The first hypothesis for our research was that (1) the excess carbon in surface waters originated in terrestrial environments. Because we knew that much dissolved organic carbon (DOC) is input from land to lakes and streams, and that land-derived DOC is considered to be relatively poor in quality, our second and corollary hypothesis was that (2) processing of land-derived DOC is relatively unimportant for bacterial activity in surface waters.

Below we briefly describe what we have learned about these two hypotheses, and how our ideas have changed in the course of research discoveries.

(1) Arctic carbon balance: For the most part the movement of nutrients and other materials is unidirectional from land to water over geologically short time scales. A notable exception, and perhaps the most important feedback from water to land involves the cycling of carbon gases. The cycle begins by fixation of atmospheric CO₂ by tundra vegetation, and the subsequent respiration of plant organic matter in the soil to produce CO₂ and CH₄. In testing our first hypothesis we have shown that these gases then dissolve in groundwaters and are transported to lakes and streams where they are subsequently released to the atmosphere to complete the cycle (Fig. 11). Thus, as expected, the main source of the excess CO₂ is input from land. In addition, we found that the flux to the atmosphere resulting from excess CO₂ and CH₄ in surface waters is a consistent feature of tundra areas. This feedback of terrestrially produced carbon to the atmosphere from aquatic systems represents an important flux in the global carbon cycling of tundra environments (Kling et al. 1991). What we do not yet understand is what controls the production and transport of these gases in soils under different vegetation and on landscapes of different age.
Figure 11. A conceptual diagram of the arctic carbon balance, showing the exchange of carbon (as CO₂ and CH₄) by terrestrial ecosystems, the transport of carbon in groundwater to rivers and lakes, and the release of carbon from rivers and lakes either by diffusion of dissolved inorganic carbon or following metabolism of dissolved organic carbon (DOC).
Figure 12. Toolik Lake experimental limnocorals. Bacterial production (ng C/l/hr) remained low in both controls (control light and control dark) and in those to which nitrogen and phosphorus had been added (nutrients light and nutrients dark.)
1993 Toolik Inlet Discharge and DOC

Figure 13. Toolik Lake inlet discharge and dissolved organic carbon. Discharge was monitored from the start of spring run-off through the summer 1993. Increases in µM DOC correlate with the increases in discharge.
(2) Processing of terrestrial material in surface waters: Organic matter in particulate and dissolved form dominates the nutrient and carbon budgets of arctic surface waters. While the response of aquatic organisms to dissolved nutrients input from land is well understood, the response to particulate and dissolved material washed in from land is less clear. Despite some debate, it appears that decomposition through the activity of bacteria in aquatic systems is limited by the supply of organic substrate rather than by grazing of bacteria by protozoans in all but the most eutrophic systems. Some of this organic substrate originates in terrestrial environments and some is produced within aquatic environments as exudates from algae and zooplankton. The relative importance of these two sources to bacterial activity varies, in part as a result of the amounts of dissolved organic matter (DOM) available from each source and in part as a result of the quality of the DOM.

Our second hypothesis was that the DOM leached from terrestrial systems is of low quality and unavailable for further bacterial use in surface waters. In experimental limnocorals, we demonstrated that, contrary to our expectation, some fraction of terrestrial DOM leached from surface plant litter contains labile compounds and strongly stimulates bacterial activity in the lake (Fig. 12). Because most arctic lakes are oligotrophic and in-lake sources of DOM are limited, it is probable that bacterial activity and decomposition is regulated by the inputs of terrestrial DOM. In addition we replicated the results of this experiment by measuring DOC inputs to Toolik Lake and the corresponding bacterial activity. During spring runoff DOC concentrations increase (Fig. 13) and strongly stimulate bacterial activity in the lake. However, during storm events later in the summer when DOC inputs to the lake also increase, there is no corresponding increase in bacterial activity. The reasons for this pattern are unclear, although they may involve the changing quality of DOC leached from land at different times of the year, or the changing bacterial composition in the lake as the season progresses. Finally, there is also evidence that in arctic lakes this terrestrial material initially incorporated by bacterial secondary production is made available to higher trophic levels through trophic interactions in the microbial food web (Ruby 1992; Kling 1994), as has been found in other aquatic systems (Azam et al. 1983; Stockner and Porter 1988).

Summary and Future Directions

Given our current knowledge of land-water interactions, it is apparent that three main factors regulate the transfer of land-derived materials to surface waters: (1) water flow, (2) vegetation and soil uptake and release, and (3) landscape heterogeneity. A first direction in future research will be to determine the relative importance of these factors in controlling the material fluxes arising from different vegetation types and landscape units. A second direction is to continue research on what controls the quality of DOM input from land, and how that quality is related to bacterial processing within surface waters. A third direction is to evaluate the increasing evidence that nutrients in the form of dissolved organic nitrogen and phosphorus may be important for phytoplankton nutrition and growth in temperate (Palenik and Morel 1990) and arctic (Kling 1994) systems, especially in nutrient-limited situations; as part of our future plans we will begin detailed studies into the fluxes and processing of dissolved organic nutrients. Finally, this research on material fluxes and transformations is needed to develop models that predict how changing environmental conditions will alter land-water interactions and consequently, the structure and function of tundra terrestrial and aquatic ecosystems.

RIVER STUDIES

Introduction and Study Sites

The rivers of arctic drainages are responsible for the storage, transformation and long-distance transport of materials originating from the tundra landscape. Long-term observations from monitoring and experiments have shown that rivers are responsive to changes in land-water fluxes. One important consequence is that land-derived nutrients and organic matter are transformed such that materials exported to downstream lakes and to the Arctic Ocean bears little resemblance to the materials introduced from land. Well known examples of these roles of rivers are the retention and long-term storage of nutrients and particulates in pool sediments and river flood plains. Another example is the rapid loss of CO₂ and CH₄ to the atmosphere. More subtle changes involve the amounts and ratios of dissolved inorganic nutrients. For example seepage waters entering streams are frequently ten times higher in dissolved ammonium (NH₄) and soluble reactive phosphorus (SRP) than is river water exported.
downstream. River studies at the Toolik LTER site have focused on the biotic responses to nutrient enrichment and, conversely, on the role of the river biota in transforming nutrients and organic matter.

The primary study site for the LTER river research has been the Kuparuk River near the Pipeline Haulroad Crossing. The Kuparuk at this point drains an area of tussock and alpine tundra of 140 km². This 4th order reach has a rocky bottom and meanders widely between tussock tundra banks. The stream averages 15-20 meters in width and consists of the classical alternating pattern of pools and riffles. Study of the Kuparuk was begun in 1978. Initial studies documented the concentrations and export of all forms of carbon, nitrogen and phosphorus. In 1983 we initiated a long-term nutrient fertilization experiment to investigate what would happen to the stream biota if a perturbation such as soil warming on land were to increase nutrient supply to the river. In 1991 after three years of baseline study, we initiated a similar nutrient enrichment experiment on Oksrukuyik Creek in order to compare responses of two rivers to similar levels of enrichment.

These experimental studies have been complemented by surveys of the chemistry and biota of streams along the Dalton Highway north of the Brooks Range (Lock et al. 1989). In recent years we have performed more intensive surveys of the entire Kuparuk drainage from small tributary streams and lakes in the foothills of the Brooks Range to the mainstem Kuparuk near the Arctic Ocean. At this point the river is roughly two orders of magnitude larger in discharge than at the Dalton Highway crossing. Our long term studies of weekly and annual variability at the intensive study sites have been important in our interpretation of these grab samples from a wide diversity of river reaches.

Intensive one year studies of contrasting river reaches have been added recently to the river fertilization and river survey studies. The need for information to develop models of the biogeochemistry and biotic productivity of entire drainages and regions demands that we gain the ability to generalize about the function of arctic streams and rivers of all types and sizes. These intensive study reaches are selected to represent a range of sizes and types of tundra rivers. We perform intensive sampling of the water chemistry, stream food web and hydrology of each reach. Models of the hydrology and of the nitrogen cycle are calibrated with releases of bromide and a stable nitrogen isotope tracer. At the end of the study we have a well calibrated model of the flow of water and of nitrogen for comparison with the well known Kuparuk and Oksrukuyik. One goal is to describe the spiraling of nitrogen and biotically-linked elements such as carbon and phosphorus throughout the stream network of the Kuparuk Drainage.

Research Goals and Hypotheses

Control by resources (bottom up or nutrient control): Our major long-term fertilization experiments on the Kuparuk River (started in 1983) and on Oksrukuyik Creek (started in 1990) have focused on the importance of bottom-up controls of ecosystem processes:

| Hypothesis 1. | The productivity of arctic tundra rivers is strongly limited by the lack of essential nutrients, primarily P and secondarily N. |

This hypothesis was formulated on the basis of pilot nutrient enrichment bioassays (Peterson et al. 1983) coupled with our early observations of extremely low primary productivity in the Kuparuk River (Peterson et al. 1986) in spite of abundant light and solid substrate. The Kuparuk River phosphorus (P) and nitrogen plus phosphorus (P & N) enrichment experiments were designed to test this hypothesis at the ecosystem level. The results of the first few years demonstrated that addition of P or of P & N stimulated algal production on the stream bottom. After a 1-2 year lag, we measured changes in insect population and in year 4 we were able to show marked increases in fish growth. We developed a conceptual model of the impact of nutrients on the entire trophic structure (Fig. 14). This model is now being challenged by the increase in moss cover in the fertilized reach (Bowden et al.).

Top-down controls (grazers and predators): Top-down controls in rivers have not been documented to the same extent as in lakes. However, studies of snails, grazing herbivorous minnows and insects have demonstrated strong control of algae in some streams (Power et al. 1985, 1992). As one of the LTER goals, we tested the importance of top-down controls on river ecosystem processes.

| Hypothesis 2. | The top-down controls of fish predation on insects and of grazing insects on algae would interact with and modify the bottom-up impacts of nutrient enrichment. |

The evidence for top-down control of the structure of the Kuparuk River and Oksrukuyik Creek food webs is not nearly as conclusive as the case for bottom-up control. The first example is a strong interaction rather than a top-down control between Brachycentrus and Prosimulium (Hershey and Hiltner
Figure 14. A summary of the responses of the Kuparuk River biota to phosphorus enrichment. The bottom-up effects of phosphorus as they propagate through the ecosystem are diagrammed flowing from left to right. The top-down or feedback effects are diagrammed across the top from right to left. Solid arrows designate responses determined experimentally and dotted arrows designate hypothesized responses. "POM" and "DOM" stand for particulate and dissolved organic matter, respectively.
Figure 15. A summary graph of the long-term monitoring of the control and fertilized reaches of the Kuparuk River: A. mean summer discharge (~July 1-Aug. 20); B. chlorophyll on rivr bottom rocks in riffles after 3-4 weeks of fertilization; C. mean abundances of *Baetis* in riffle habitat; D. the mean growth of adult grayling from early July to mid-August.
Figure 16. The relationships between mean summer discharge (July 1 - August 20) and growth of adult and young-of-the-year (YOY) grayling in control and fertilized reaches of the Kuparuk River.
When the abundance of *Brachycentrus* becomes very high as it did in the fertilized reach of the Kuparuk, *Prosimum* was apparently displaced. Thus both in the river and in cake experiments, *Prosimum* became less abundant than *Brachycentrus*. Probably this is not predation but disturbance. Later experiments demonstrated that algal biomass also reduced black fly attachment to rocks (Wheeler and Hershey, unpub.).

The strongest set of observations on top-down controls is the control of epilithic algal biomass increased (as measured by chlorophyll) by grazing insects. Chironomids and *Baelea* larvae when abundant appear to control chlorophyll to such an extent that algal biomass and productivity are less than 2-fold greater in the fertilized reach than in the control reach (Gibeau and Miller 1989; Peterson 1992). However, this control is not universally operative. For example, in 1988, algae were not controlled by grazers in the Kuparuk (Deegan and Peterson, in press) and control was absent in the first two years as well.

An experiment designed to examine the effects of varying adult grayling densities demonstrated that grayling growth was decreased at high fish density (Deegan and Peterson, 1992). This indicated that grayling were probably food limited. However, there was no significant effect of grayling on benthic insect abundance or on drift abundances. Experiments with young-of-the-year grayling confined to cages have shown effects on benthic insect abundance and on chlorophyll levels (Golden, unpublished). These experiments can not yet be extrapolated to the whole river because we lack estimates of young-of-the-year grayling density.

**Long-term Monitoring**

Long-term monitoring of river discharge, temperature, nutrients, chlorophyll, primary productivity, insects and fish is being carried out to determine variability, trends and inter-relationships among these attributes of river ecosystems (Fig. 15). Our monitoring program includes both fertilized and control reaches of Oksrukuk and the Kuparuk.

We are beginning to see some relationships that suggest areas of future research. While the export of nutrients of all forms increases with greater discharge, nitrate concentrations have a unique relationship with discharge and season (Julian day). Nitrate concentration declines rapidly with increasing discharge and also increases later in the thaw season for any given level of discharge. This relationship is consistently seen in both the Kuparuk since 1980 and in Oksrukuk in recent years. Mean summer discharge after snowmelt runoff is sustained by summer precipitation and varies by a factor of 10. The abundance of each of the four dominant species of insects is related to the discharge regime. For example, more than 90% of the annual variation in black fly abundance can be related to three factors: fertilization (-), mean spring discharge and annual maximum discharge. Fish growth rates also correlates with mean discharge from year to year (Fig. 16).

Comparison of the magnitude of annual variation in plant, insect and fish production in the unfertilized river with the magnitude of response to nutrient enrichment has shown an interaction (Fig. 15). Experimental nutrient enrichment can boost algae, insect and fish production in either high or low discharge years, but the overall impact of nutrient addition appears to be somewhat less than the observed impact of natural changes in discharge linked to summer precipitation patterns. These observations suggest that tundra rivers will respond both to changes in inputs from the tundra and to changes in seasonal precipitation patterns and amounts as climate change progresses.

**LAKES**

The limnological research on deep, fish-containing lakes in Toolik Region began in 1975 as a complement to the Arctic IBP study of shallow, fish-less ponds. Initial studies at Toolik Lake focused on a variety of process studies at various trophic levels. Much more integrated lake studies began in 1983 with a major limnocorral project to study the top-down or bottom-up control of arctic lake ecosystems (O'Brien et al. 1992). But truly integrated studies awaited the designation of the Toolik Lake Project as an LTER site in 1987 (Hobbie et al. 1995). The LTER drew from the limnocorral experiment and other research to focus our studies on the role of resources or predators in controlling the function and structure of arctic ecosystems and communities. Within this framework the lakes component of the LTER has focused on large-scale lake manipulations, monitoring of these experiments and Toolik Lake as the reference lake.
Global Hypotheses

The Arctic LTER project has two global hypotheses.

1. The structure and function of arctic lakes and ponds is regulated by limited plant resources, i.e., inorganic phosphorus and nitrogen. Early evidence favoring this hypothesis included the very low levels of SRP and DIN in Toolik Lake and the potentially high nutrient sorbing characteristics of the Toolik Lake sediments (Miller et al. 1986) which resulted in an ultra-oligotrophic lake.

2. The structure and function of animal communities in arctic lakes and ponds is regulated by the size and abundance of top predators. Early evidence favoring this hypothesis included the loss of large-bodied zooplankton from Toolik Lake as lake trout abundance declined (Hobbi et al. 1995) as well as experiments showing the importance of sculpin predation in regulating benthic chironomid densities (Hershey and McDonald 1985).

Tests of Global Hypotheses

Hypothesis 1: We have systematically set out to test this hypothesis in a series of whole lake and pond experiments (Table 3). We tested the importance of plant nutrient resources in an experiment where we divided a whole lake (Lake N-2) with a plastic curtain and added inorganic N and P to the downstream side of the lake. During each summer of nutrient addition there was a significant increase in phytoplankton biomass and productivity. However, for the first 4 years of the experiment there was no carryover of nutrients in the water in the following spring (Fig. 17). We are now certain that this was due to the unique nutrient sorbing properties of the sediments of many lakes in the Toolik region (Kitchell 1984). Carry-over effects from one year to the next ultimately occurred and resulted from nutrient fluxes from the sediments due to organic sediments building up to such an extent that nutrients no longer came in significant contact with the unique mineral sediments of the lake. Most years zooplankton also responded to increased phytoplankton biomass; however, a major benthic invertebrate group, chironomids, did not respond. There is evidence that chironomids are regulated by a benthic fish, the slimy sculpin (Hershey 1985).

In a second nutrient addition experiment, we added plant nutrients to a whole lake (N-1). This lake developed much more dense phytoplankton and intense primary productivity than lake N-2, even though the nutrient loading per unit of area of N-1 was one-third that of N-2. Furthermore, zooplankton densities did not increase over pre-nutrient addition levels even with a 10-fold increase in phytoplankton density. Even more surprising, lake trout growth did not increase with increasing plant productivity due in part to low oxygen levels during the winter caused by decomposition of sedimented phytoplankton (Fig. 18).

Hypothesis 2: We have tested this hypothesis in a series of whole lake and pond experiments. In Toolik Lake when the average size and density of lake trout was reduced due to fishing, several species of zooplankton went extinct. We believe this effect in Lake NE-12 by rapidly removing lake trout with gill nets. While we have not observed the extinction of large-bodied zooplankton from the lake we have observed the zooplankton becoming much smaller. In another experiment we added arctic grayling to Lake S-11, a small but deep lake which lacked any fish. This lake had a whole suite of large-bodied zooplankton, including fairy shrimp, amphipods, Chaoborus, and Daphnia middendorffiana. In the first summer of addition, the fish completely eliminated all but the D. middendorffiana from the lake. This further demonstrates the impact of predation in structuring pelagic lake communities.
Table 3. A listing of the manipulated lakes in the LTER project showing the treated lakes and the appropriate reference lake for that treatment.

### Control by Resources

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**Figure 17.** The annual primary production in the plankton of Lake N-2 measured in the control (shaded) and fertilized (solid) sides. Measurements were made each year over the period of 1 July to 15 August (data from M. Miller.)
Figure 18. 1991-1994 under ice oxygen profiles for Lake N1
Summary and Future Directions

Added nutrients always increased phytoplankton production and biomass and sometimes increased zooplankton densities (Limnocorals and N-2 but not in N-1). Increased plant production stimulates snail growth but not chironomid densities. Addition or removal of the top predator, lake trout, can alter the density and habitat distribution of prey fish. Trout removal allows small grayling and lake trout to increase and occupy the pelagia of the lake. With these more planktivorous sizes of fish present, some species of zooplankton are eliminated or only small-bodied individuals remain. With lake trout removed or rare, sculpin occupy more diverse habitats.

Over the duration of the LTER research, much has been learned and new directions taken. Our understanding of the dynamics of lake foodwebs has greatly increased. It is now clear that the Toolik Lake food web is dominated by benthic rather than pelagic organisms. Lake trout and grayling feed on pelagic zooplankton only when small. As adults these dominant fish feed on benthic invertebrates. Thus pelagic production has little impact on higher trophic levels. We need to turn more of our attention to studying benthic production and the population dynamics of benthic invertebrates.

We have also developed some new hypotheses or questions. In terms of bottom-up experiments it is clear that large additions of inorganic nitrogen and phosphorus will stimulate phytoplankton production and ultimately be recycled as the mineral sediments are overwhelmed. However, it is unclear how area lakes will respond to more modest nutrient additions. More study needs to be put into understanding the nutrient sorbing property of area lake sediments and how geographically widespread are such sediments. We have demonstrated that additions of DOM stimulate bacterial growth and production, but we know little about the quality of DOM. We have determined that UV light is rapidly absorbed in area lakes. What is the impact of the absorption of DOM and the photolysis of dissolved humic matter?

In terms of new top-down experiments, we want to determine if arctic char are trophically very similar to lake trout. If so, then we could study redundancy in these simplified arctic systems. Along with this we plan to do much more in the way of modeling food webs and nutrient cycling. We also plan to investigate the regulation of bacteria to determine if nanochromotrophs can really regulate bacterial densities.
REFERENCES


Miller, M. C., unpublished


PROTOCOL FOR ENTERING DATA FILES INTO THE LTER DATABASE

This is a concise explanation of how the data is entered/validated into the LTER database. This process is continually being revised and updated to respond to the growing needs and demands on the database. The final format of the data is in comma delimited ASCII and the documentation is in ASCII. The Documentation is also kept in hardcopy in the ARC LTER office.

(1) Data and documentation files are received at the main office (The Marine Biological Laboratory in Woods Hole, MA) via floppy disk or over the Internet. The documentation and the data are compared to make sure they correspond. Minor changes are made only to the copy on the hard drive (leaving the original unaltered).

(2) If there are any major changes or discrepancies between the data and the documentation, the data manager will either call, e-mail or write to the principal investigator (PI) to reevaluate the data. The process will begin again on the newer version of the file. (Go back to 1)

(3) After all corrections are made, the data files are copied to the LTER database directory on the network server, lupine:/opt/database/lterdata.

(4) After the final versions of the data files are archived in the computer, they are separated according to their availability status. Data files are then copied to the MBL gopher server and documentation files are processed into html pages and copied to the MBL web server.

Availability Status is defined as follows:

Type 1: Published data and 'meta-data' (data about data) are available upon request
Type 2: Collective data of LTER site (usually routine measurements). Available 1 year after data are generated.
Type 3: Data from individual investigators (experimental data). Available 1 year after the termination of the grant or with permission of the investigator.
Type 4: Unusual long-term data collected by individual investigators. Available with permission of the investigator.

Data storage information:

The data are stored on a Unix network server which is backed up on tape twice each week. In addition, the data is backed up to CD read/write disks which are stored in a separate building.

NOTE: The data manager does not validate the accuracy or precision of the data (However, large discrepancies are noted). The PIs are responsible for making sure the data that is submitted into the database is scientifically accurate.

ON-LINE ACCESS INFORMATION

The long term data sets of the Arctic LTER are available through both a gopher server and web page. The address of our web page is: http://www.mbl.edu/html/ECOSYSTEMS/lterhtml/arc.html. The address for the gopher server is: gopher://hoh.mbl.edu:70/00/etc/ecosystems/DATA/.
The data sets include both the monitoring data and data from the whole ecosystem manipulations in the tundra, lakes and streams. The data for the Arctic LTER is in comma delimited ASCII text. Along with the data the web pages contain site descriptions, key documents and a bibliography for the Arctic LTER. Each data file has a documentation file which contains a brief description of the data file, methods, notes, comments, and variable descriptions as well as other information about the data. These documentation files are accessible through the web page and are linked with hypertext directly to their corresponding data file stored on the gopher.
ARCTIC LTER DATABASE DOCUMENTATION FILE

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(2) YEAR: 1986
(3) PI: B.J. Peterson
(4) OTHERS: Berrie Moller, John Hellrich
(6) KEYWORDS: Kuparuk, river, temperature
(7) SITE TYPE: AQUATIC-STREAMS
(8) RESEARCH LOCATION: The Kuparuk River crossing at the Dalton Highway. 66 38.15'N, 149 25.30'W
(9) EXPERIMENTAL METHODS: Temperature readings were taken daily with a 12" blunt stem reotemp dial-head thermometer at a location between the two culverts on the upstream side of the road.
(10) NOTES AND COMMENTS: There are several days for which no temperature data are available. There are also days on which more than one temperature reading was taken.

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(13) FOR MORE INFORMATION, CONTACT: B.J. Peterson
MBL - Ecosystems Center
Woods Hole, Mass. 02543

(14) OTHER DATA FILES TO REFERECE:
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* The order of preference for type of data files that are submitted.
  1) Dbase (.DBF)
  2) spreadsheet - i.e. Lotus (.WK1)
  3) Ascii (.PRN) Please specify format.

(17) NUMBER OF RECORDS: 44 records

(18) STATUS: Type 1

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(19) FOR ARCHIVAL USE:
  DATE RECEIVED: Feb90
  DATA FILE ENTERED BY: Carolyn Bauman and Julie Pallant
  DATA FILE VALIDATION:
  NAME: Julie Pallant
  DATE: 4Oct91

LOG OF CHANGES AND COMMENTS:
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University, Raleigh, NC.


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