

ARCTIC LTER SITE REVIEW JUNE 2007

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THE ARCTIC LTER PROJECT AT TOOLIK LAKE, ALASKA

NSF SITE REVIEW 2007

1. INTRODUCTION

a. History and Description of Site, Project Goals

History of Research

Overview

The Arctic LTER project field site (front cover) is located in the northern foothills of the North Slope, that part of northern Alaska that drains to the Arctic Ocean. The site was chosen in 1975 when the newly opened oil pipeline construction road made a transect accessible. The Dalton Highway is the only road on the North Slope.

The North Slope (the size of New Mexico or 18% of Alaska) has three major physiographic divisions: 1) Coastal plain (70,900 km²), 2) Foothills (100,800 km²), and 3) Mountains (136,200 km²) (back cover). These are, respectively, the size of South Carolina, Tennessee, and Alabama.

Research on the Coastal Plain: NARL and IBP

Expeditions began in the IPY of 1882 with a year-round observatory at Barrow. Various natural history collections were made for the next 60 years. After World War II, a Naval Arctic Research Laboratory (NARL) was established at Barrow (1947-1980). This was a lavishly funded facility with laboratories and dormitories, an air force of five planes, remote camps on an ice flow and on a mountain lake, and some small ships. In 1971-73 the Tundra Biome project of the International Biological Program (IBP, terrestrial and aquatic) was housed at NARL. The overall themes of IBP were 1) to develop a predictive understanding of the Arctic ecosystem, 2) to obtain a database for modeling and comparison, and 3) to use environmental knowledge for problems of degradation, maintenance, and restoration of ecosystems. All of the major ecosystem components such as primary producers, decomposers, herbivores, predators, climate and microclimate, and soils, were studied at an aquatic site and a terrestrial site. Process studies were emphasized, as were system budgets for C, N, and P.

Research in the Foothills: Toolik Lake, R4D, LTER

The oil pipeline haul road opened in fall 1974 and Toolik Lake was chosen as a site for further North Slope limnological research in June 1975 (front cover, Fig. 1). Stream research and terrestrial research began soon after. The R4D project of DOE (1983-91), based at the Toolik Lake camp, worked at nearby Imnavait Creek) to study landscape response to disturbance. In 1987 the Arctic LTER project began. The overall goal of the project is to understand all of the Arctic ecosystems around Toolik Lake, their structure, function, and interactions, to allow prediction of effects of change. **The specific goal of the Arctic LTER Project for 2004-2010 is: To understand changes in the Arctic system at catchment and landscape scales through knowledge of the linkages and interactions among ecosystems.** The LTER research identifies linkages

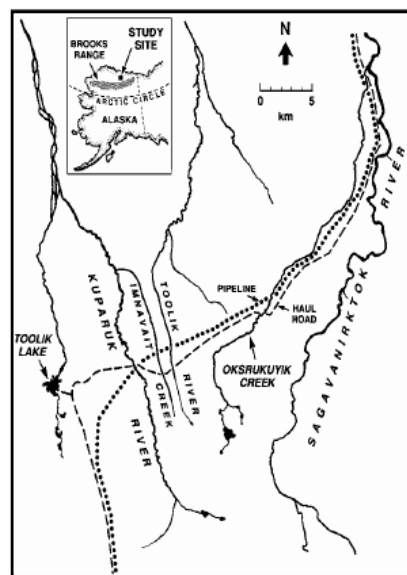


Fig. 1 The LTER study site

within and among the ecosystems of tundra, streams, and lakes, determines controls of linkages and how they will change in future environments, and predicts how the entire landscape will respond to environmental change.

The Natural Setting

The North Slope

This large area (back cover) has remarkable geologic, topographic, and vegetational uniformity from west to east. Thus, the Lisburne Limestone Formation appears at the surface along the front of the Brooks Range from the Beaufort Sea on the west to the Canadian Border on the east. Wet sedge tundra covers the entire coastal plain while tussock tundra covers the foothills. Over the past 500,000 years, mountain glaciers synchronously moved out of the Brooks Range across the North Slope and deposited similar types of glacial till (soil and rocks) across the foothills. One result of this uniformity is a relative ease of scaling; that is, at a coarse level ecological information and predictions developed at Barrow and Toolik apply to the Arctic National Wildlife Reserve (ANWR) as well as to other areas of the North Slope.

The Kuparuk Basin

The basin (Fig. 2) stretches from the northern edge of the Brooks Range to the Arctic Ocean (~9,000 km²). The Arctic LTER site occupies the Upper Kuparuk Basin (southern end of the drainage basin). The Toolik Field Station (TFS) is at 760 m altitude. Summer temperatures (Fig. 2) are coldest near the Arctic Ocean and in the mountains, warmest in the mid-basin area. Wet tundra dominates the coastal plain; much of the watershed is moist acidic tundra (MAT) with *Eriophorum vaginatum* (tussock tundra). Large shrubs (e.g., willow, dwarf birch) are found along the rivers of the foothills and mountains and reach their maximum development in the central part of the watershed. The satellite view (NDVI transformed to leaf area index or LAI) (Fig. 3) shows that the maximum reflectance occurs in the mid-part of the watershed. The NDVI can be converted to leaf area index (LAI), which is the area of leaf per area of land surface. The LAI is highest in the middle parts of the river basin and, reasonably enough, so is the modeled primary productivity (Fig. 3).

The Kuparuk River begins to flow in late May and ceases flow in late September. Shallow ponds are abundant on the coastal plain as are lakes with a maximum depth of 2.5 m.

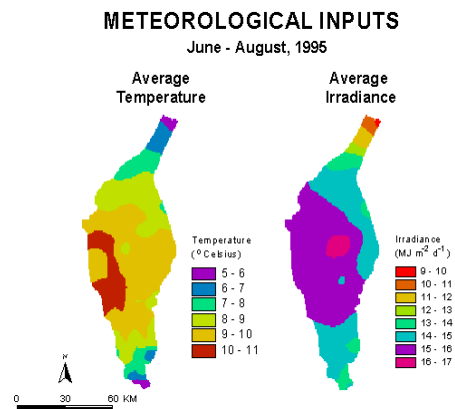


Fig. 2. Kuparuk River Basin average summer temperatures and irradiance.

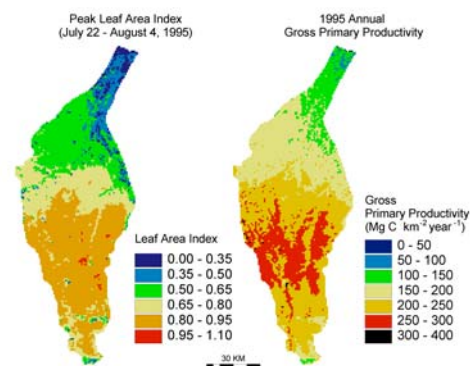


Fig. 3. Leaf area index and gross primary productivity of the Kuparuk River Basin.

The LTER Site

The site (Fig. 1) is located amongst rolling, tundra covered hills. The official LTER site encompasses the upper headwaters of the Kuparuk River, which is the drainage basin of Toolik Lake and the Kuparuk River basin above the confluence of the outlet stream from Toolik Lake. Toolik Lake is at 68° 38'N, 149° 43'W. The main aquatic features are Toolik Lake, a 1.5 km² lake with a maximum depth of ~25 m, and the Kuparuk River. The BLM has designated the entire site as a Research Natural Area (cover Figure) where no camping or other development is allowed.

Natural History of the Toolik area

The climate (Fig. 4) is characterized as low Arctic with an average annual temperature of -8°C. During the summer months of June, July, and August the average temperature may climb above 10°C. Winter temperatures average -20°C in the coldest months. Snow cover, with a maximum depth of ~30 cm, begins in mid-to-late September and lasts until late May. During June, July, and August in a typical year the 3 month rainfall averaged 188 mm; the total annual precipitation ranges from 250 to 350 mm.

The low annual temperature means that permafrost, or permanently frozen ground, is present to a depth of about 200 m throughout the LTER site. Each summer the top layer of soil thaws to a depth of 29-46 cm (1990 to 2000 range) (Fig. 4). Permafrost restricts the rooting zone of plants, seals soils to water penetration and thus creates moist soils, and causes rapid and flashy runoff after a storm. A deep borehole reveals that temperatures at a depth of 20 m are warming over the past decades but are approximately -5°C so the permafrost is in no danger of imminent melt.

The distribution of types of vegetation is dependent upon topography (dry ridge tops, moist hill slopes, areas of water saturated soils) and upon the soil chemistry as determined by the age of the soils, that is, the time since the soils were deposited as till by advances of glaciers moving north from the Brooks Range (Fig. 5). The oldest soils developed on glacial till from the Sagavanirktok glacial advance (>300,000 years ago), the next oldest soils on till from the Itkillik I advance (>56,000 years ago), and the youngest soils developed on till from the Itkillik II advance (25,000-11,500 years ago). As a result of interactions of topography with age of soils, there are four types of terrestrial systems: moist acidic, moist non-acidic, heath, and wet sedge. In the dominant tussock tundra a number of shrubs (willow, dwarf birch) and forbs are always present but the sedge *Eriophorum* dominates. Nitrogen availability limits primary productivity and nitrogen is intensely recycled. The snow and frozen ground delay the start of photosynthesis in the spring until nearly half the annual solar radiation has occurred (Fig. 4). Net ecosystem productivity is around 140 g C m⁻² yr⁻¹. Grazing by large and small herbivores is minimal. Non-acidic vegetation grows on the youngest soils and lacks dwarf birch and tussocks. Caribou herds

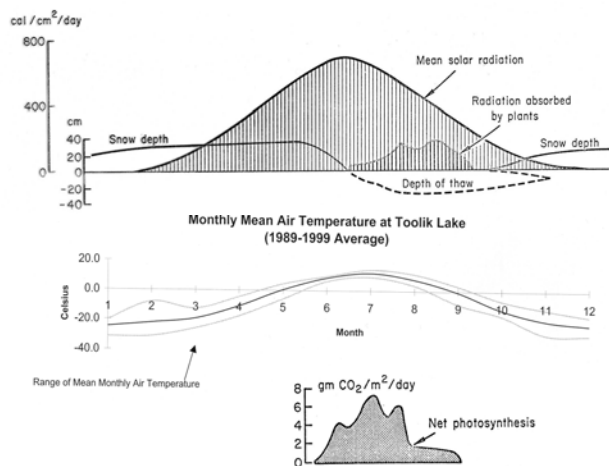


Fig. 4. Generalized environmental regime of northern Alaska (Chapin and Shaver 1985), with air temperature data from Toolik Lake

pass through the site every 5 to 10 years. Grizzly bear and wolves are the chief predators of caribou and arctic ground squirrels.

Streams have rocky bottoms, are small, 1-10 m wide, and shallow. NH_4^+ and PO_4^{3-} are close to the level of detection. Most of the nitrogen and phosphate is bound in organic forms as dissolved organic matter (DOM) but only a little of the nutrients in the DOM are available to microbes and algae. Primary productivity is exceedingly low; most photosynthesis occurs in algae (diatoms) attached either to the rocks of the stream bottom or to tubes of insect larvae. Insect larvae consume the algae and are themselves consumed by other insect larvae or fish. Blackfly larvae filter particles from the water; most of their food is algae dislodged from the rocks. There is only one species of fish, the arctic grayling, living in the streams. Because the streams freeze completely each fall, the fish must migrate some tens of kilometers to deep lakes where they survive the winter beneath the ice cover.

The only large lake in the LTER site is Toolik Lake with a maximum depth of 25 m and an area of 1.5 km². A number of smaller lakes, in the moraines near Toolik Lake, have been used for experiments manipulating nutrients and fish species. All the lakes are ultra oligotrophic with a primary productivity around 10 g C m⁻² y⁻¹. Both N and P are in limiting concentrations.

The planktonic primary productivity in the lake comes mainly from the photosynthesis of very small algae, mostly flagellated forms. Because the algal production and biomass are so low, the zooplankton grazers are also in low numbers and have little control over their prey. Another major source of primary productivity is algae attached to rocks in the shallow regions of the lake. These algae are grazed by snails, which, in turn, are consumed by lake trout, the top of the food web. In fact, the benthic food web feeds the fish in these lakes (eight species). Another source of carbon and energy for bacteria and flagellates is allochthonous DOM.

History of glaciation, vegetation and humans at Toolik

The northern foothills of the Brooks Range have been glaciated repeatedly; in the vicinity of Toolik Lake there were three major glacial advances (Fig. 5). The oldest surface dates to the Sagavanirktok River glaciation >300,000 years BP.

Glaciers reached the Toolik lake area during the Itkillik I (>56,000 years BP) and the Itkillik II (25,000-11,500 years BP) intervals. The prostrate shrub tundra of a colder climate was replaced by a dwarf shrub tundra by about 7,500 years BP. This latter type of tundra has remained unchanged until the present.

The LTER site is close to two of the oldest sites in North America for human habitation. These are sites (11,000-12,000 years BP) where paleoindian hunters would sit and scan the valleys for game (horse, bison, antelope) while reworking flint projectile points and other stone tools. For the past few thousand years, Inuit hunters and fishermen camped on the glacial moraines and other dry locations at the edges of Toolik.

Oil was discovered at Prudhoe Bay in 1968 and in 1970 a construction camp was set up at Toolik Lake. In 1974 the gravel haul road, now the Dalton Highway, was completed from

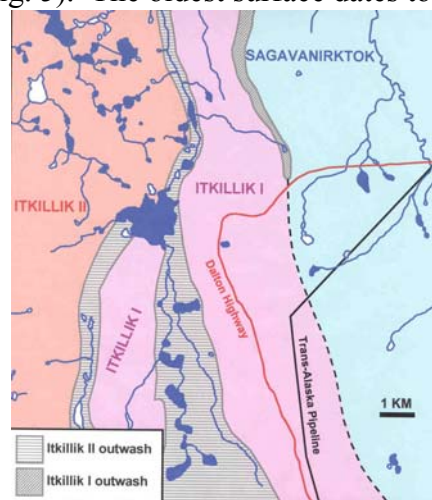


Fig. 5. Glacial advances around Toolik Lake.

Prudhoe Bay to the Yukon River and the construction camp closed soon after the oil pipeline was completed in 1976. The scientific camp was set up in the summer of 1975 and has evolved to become the Toolik Field Station (TFS) of the Institute of Arctic Biology, the University of Alaska Fairbanks (UAF).

Disturbance

Types of Possible Disturbance

The major disturbances of the Toolik landscape are the past glaciers, the present climate warming, and human disturbances during oil development. The minor disturbances of pollution from atmospheric deposition are measurable, including mercury, PCB, and organochlorine pesticides, but no environmental effect can yet be demonstrated. Nitrogen deposition is minimal. Climate-associated disturbances of floods and drought do occur but are short-lived and rare.

Fire does affect some tundra systems and, until three years ago, it was thought that the tundra of this region was too moist. A series of lightning strikes in 2003, however, did start a fire that burned for about one day.

Disturbance by Glaciers

The natural changes that take place in a landscape after disturbance by glaciers include the geomorphic softening of landscape, the leaching and development of soils, the growth of plants, the thickening of soil organic horizons, the erosion of stream channels and formation of water tracks, and the formation of ice wedges. Because the LTER site includes soils of three different ages (Fig. 5) (>300,000, >56,000, <25,000 years), these processes have produced different results across the parts of the landscape. For example, the soils of the <25,000 year old surface have a pH near to 7 while the soils of the 60,000 year old surface are quite acidic because of leaching of carbonates. Sphagnum moss is only found on the low pH surface. Tussocks are not found on the youngest glacial surface.

Climate Disturbance

This region of the Arctic is experiencing warming and has so for the past 150 years. At Barrow, there has been an increase in the annual average air temperature by nearly 2°C in the past 30 years. This climate change is not as well defined in the shorter-period of weather records at Toolik. There are, however, changes in plant communities and water chemistry that are likely caused by climate change. One example is a shift towards shrubbiness in the relative abundance of tundra. Another is the doubling of the average alkalinity of Toolik Lake over a decade. The chemistry change may be the result of increased weathering as soils frozen for 10,000 years begin to thaw. The thawing of permafrost near Toolik may be causing an increase in the slumping of lake shores and stream banks but the changes in rate of this “thermokarsting” are very difficult to document.

Anthropogenic Disturbance

The building of the road and the pipeline was a disturbance to this quite pristine environment. No changes have been noted in the nutrient chemistry of streams and lakes with the exception of the impact of one gravel borrow pit within the Toolik Lake drainage basin. At this pit, the upper several meters of a glacial kame, a small hill of water-sorted material, was removed for road construction. The resulting surface has no organic soil and is very dry. As a result, there is little revegetation; in some cases grasses were seeded and the sites fertilized.

More important, several meters of the underlying permafrost thawed over the years and exposed fresh glacial till and gravels to erosion and weathering. The spring-fed stream near one of these pits supplies 5% of the water entering Toolik Lake but 35% of the phosphate. There has been no measurable effect of the Toolik Field Station on caribou hunting.

A second disturbance from the road is road dust. Since the road opened in 1974, each truck that passes creates a dust plume, especially in the summer. The amount of dust deposited decreases logarithmically with the log of the distance from the road. One effect is an earlier snow melt of days and weeks along the road corridor caused by a lowered albedo of the snow. Another effect is a change in reflectance of the road corridor that is visible in summer satellite pictures. While some environmental changes near the road have occurred, the overall importance of dust deposition is difficult to determine; however, there is no evidence so far of changes caused by the dust in vegetation or water chemistry.

b. Evolution of Research Themes and Research Highlights

Pre-LTER research (1975-1987).

The International Biological Program's U.S. projects (1971-74) included five intensive studies of major biomes: one, the Tundra Biome project at Barrow, Alaska, included a large integrated study of the limnology of tundra ponds. The IBP projects, which were the first large ecosystem studies, emphasized the structure and function of ecological or human systems. At Barrow, the IBP terrestrial and aquatic projects studied the processes and controls of C, N, and P cycling.

After the IBP ended in 1974, limnologists pointed out that little was known about foothills lakes and ponds. NSF Office of Polar Programs agreed to continue the intensive integrated research approach and the Toolik camp was established in 1975 when the pipeline road was completed. The goals of the first projects, which soon included terrestrial ecosystems, were to describe the ecosystem structure and function of tundra, lakes and streams in the foothills.

When the LTER project began, in 1987, the Toolik scientists' earlier accomplishments included:

- Climate data measured, mostly summer only, for the Toolik site except for the gap in 1983 (no funding).
- Descriptions carried out of the ecology of tundra (soil processes, vegetation biomass, productivity, mineral nutrition), streams (production, insect growth, N, P, and C exports and budgets), and lakes (processes, algal productivity, benthic and planktonic animal biomass, and growth rates).
- Long-term experiments (fertilized, light, temperature) set up on four different types of tundra. Soil processes and nutrients were more important for plant growth than light and temperature. We found that a decade or more of experimentation was necessary to understand changes and regulation of processes.
- Experimental manipulations of lake plankton in large limnocorrals (nutrients, top-down by fish) demonstrated the extreme nutrient limitation and food-web truncation.
- Experimental addition of phosphorus to a river began in 1983. Initial algal growth was controlled after several years by an increase of grazing insect larvae.
- Long-term ecological monitoring began (lake and stream chemistry, productivity, and physics, terrestrial biomass and productivity, thaw depth).

LTER I research (1988-1991)

The onset of the LTER produced different expectations and plans for long-term experiments and long-term data sets. Year-round climate measurements began and instrumentation conformed to the LTER standard. Data sets became available on line.

- Bottom up controls of food web structure – studies began in a divided lake fertilized for 5 years.
- Control of growth and flowering of the dominant sedge is linked to climate but growth lags favorable conditions by two years and flowering by three (long-term surveys).
- Top-down control experiments continued in a lake with the removal of the top predator; in terrestrial studies long-term grazer exclusion plots were set up.
- The natural abundance of ^{15}N and ^{13}C revealed a dependence of top lake predators on the benthic food web and partitioning of N sources among major plant types.
- A hierarchical GIS was developed for the Toolik area to foster the linkage of lake characteristics and the underlying geology.

LTER II research (1992-1997)

With support from the Arctic Systems Science program (NSF OPP), we were able to model the terrestrial data from Toolik and extrapolate to the entire Kuparuk Basin.

- Process and control data as well as satellite (NDVI) and climate data was used to model the primary productivity of the entire Kuparuk River basin. Over the next century, carbon sequestration will continue.
- We developed the valuable tool of continuous addition of ^{15}N to a stream and made the first determination (anywhere) of the spiraling distance of ammonium (~ 1 km).
- Long-term fertilization of the Kuparuk River resulted in a species shift to mosses.
- A major study of land-water interactions began. The CO_2 that is supersaturated in streams and lakes originated from respiration in the soil (plant and microbial). Some 20% of C flux back to the atmosphere, as measured traditionally with chambers and flux towers, has been missed because it moves horizontally in the soil water.

LTER III research (1998-2003)

The accumulated data on natural ecosystems and year-to-year variability allowed the determination of ecosystem changes likely caused by climate warming. International comparative study of terrestrial systems began.

- Long-term data reveal that warming induces a shift towards shrubbiness in tundra plant communities and an increase in lake alkalinity.
- Monitoring across the entire LTER site began to make comparisons of soil and water characteristics affected by the glacial age of the soils.
- Molecular analysis indicate strong seasonal succession in the bacterial community of Toolik Lake in response to organic matter from land entering during the spring runoff.
- Year-to-year variability studies show that nutrients and stream discharge control fish growth but not survival.
- Long-term N + P fertilization leads to an overall decrease in C stocks in tundra.
- New in-situ estimates of O_2 change in streams suggest high rates of mineralization of C from the tundra.

- Synthesis of N cycling at sites throughout the U.S., e.g., the LINX projects, developed from ^{15}N tracer studies of the Kuparuk River and the models we have developed.

LTER IV research (2004-2010)

The overall goal remains *to predict the effects of environmental change*. We now are able to expand the goal to include the entire LTER site; this will improve our ability to scale to a larger region and circum-Arctic. It is now clear that there is variability among ecosystems at the site because of differences in glacial age in the soils, in tundra vegetation, in the chemistry of water entering streams and lakes, in stream size, and in size and depth of lakes. It is also clear that the movement of water and materials in the soil and streams links these ecosystems. Accordingly, the next step is to study the linkages among the variety of ecosystems at the catchment and landscape scale.

The goal of the Arctic LTER Project for 2004-2010 is: *To understand changes in the Arctic system at catchment and landscape scales through knowledge of the linkages and interactions among ecosystems.*

The LTER research identifies linkages within and among ecosystems, determines controls of linkages and how they will change in future environments, and predicts how the entire landscape will respond to environmental change.

Terrestrial studies follow water, nutrient, and organic matter movement down a toposequence at nearby Imnavait Creek (Table 1). A ^{15}N -labeling experiment determines more explicitly the rates and forms of downslope N movement. Continuing long-term studies investigate effects of changes in species composition, temperature, light, and nutrients on four types of tundra.

Stream studies investigate inputs of water, nutrients and organic matter from up-slope ecosystems and develop an understanding of how inputs and climate drivers alter stream ecosystem structure, how inputs are in turn altered by stream processes as they travel through stream networks, and in what form they are ultimately exported to lakes. Continuing long-term studies investigate the effects of nutrient loading and variable climate on stream ecosystems.

Lake studies focus on the landscape-to-lake linkages that define how terrestrial patchiness controls patterns of productivity in arctic lakes. They examine how in-lake processes interact with watershed inputs of nutrients, DOM, and major ions to define pelagic and benthic production, food web structure, and benthic and pelagic coupling; and how watershed-stream-lake linkages regulate transformations in water chemistry and patterns of productivity.

Landscape Interactions monitor watersheds for soil water chemistry and primary stream flow and chemistry to connect the production of DOM and nutrients on land to their transformation and transport on the way to streams. The project monitors the chemistry and biology of a series of connected streams and lakes that collectively flow into and affect Toolik Lake.

c. Overview of the following sections of this document

The following sections are summaries of the research and measurements that are occurring at Toolik Lake and the home institutions of the P.I.s of the current ARC LTER project. There are separate sections on terrestrial, stream, lake, and land-water ecosystems. The monitoring and process studies are summarized in Table 2. The large-scale experiments, modeling, and synthesis are summarized in Table 3.

In keeping with the concept that the LTER project and the site should be a magnet for other research projects attracted to the site by the ecological understanding, the ongoing experiments, and the availability of background and current data, the P.I.s and collaborators have obtained funding for other projects that fall under the LTER umbrella of understanding changes

in the Toolik landscape. The current cooperating projects are listed in Table 4, with a complete list in Section 10. We do not identify in this report just which measurements or modeling are under which project.

The following reports cover the 2004-2010 measurements and research only. Some of the measurements are a part of the long-term observations of the natural and experimental systems, one of the tools we employ to understand the ecosystem; most of the other research described here is aimed at studying the linkages and interactions among ecosystems (the goal of our LTER 2004-2010 project).

Location of sampling sites under LTER IV.

Table 1. Sampling sites within the Arctic LTER site. For details of location and description see <http://ecosystems.mbl.edu/ARC/>

Terrestrial	
Toolik Lake area	Multiple sites on Itkillik I and Itkillik II aged surfaces and outwash (<12,500 & >56,000 y old), including moist acidic and nonacidic tundras, wet sedge tundra, riparian tundra, and dry heath
Imnavait Creek	Toposequences on Sagavanirktok-age surface (~300,000 y), ranging from dry heath to wet sedge and riparian shrub communities
Sagavanirktok River Valley	Gunsight Mountain (2-4My) and Anaktuvuk (1M) aged surfaces between Oksrukuyuk Creek and Sagwon; toposequence on Itkillik II surface and outwash in northern foothills
Streams	
Kuparuk River	4 th order, oligotrophic, clear-water tundra stream; 25 km in length from origins to Dalton Hwy. crossing (143 km ² area); draining surfaces 60,000 to 780,000 yr old.
Oksrukuyuk.	3 rd order, oligotrophic, clear-water tundra stream; 12 km in length from origins to Dalton Hwy. crossing (73.5 km ² area); tributary of the Sagavanirktok River. ~300,000 yr old surface
Hershey Creek	2 nd order, beaded tundra stream. Tributary of the Kuparuk River; ~300,000 yr old surface, near crossing of pipeline and Dalton Highway
Upper Kuparuk Watershed surveys	143 km ² watershed encompassing the headwaters of the Kuparuk River; predominantly underlain by older Sagavanirktok aged surfaces (>300,000 yr old), with extreme headwaters draining Itkillik I - aged surface (>56,000 yr old).
Extensive Surveys	Several sites from the Colville, Kuparuk, Sagavanirktok and Sadlerochit drainages, representing Mountain, Glacier, Tundra and Spring streams.
Lakes	
Toolik Lake	25 m deep lake, 1.5 km ² , ultra-oligotrophic
Lakes E-5 and E-6	12 m and 3 m deep lakes on >300,000 yr surface. Low ionic concentration, fertilization experiment ongoing
Fog-2, Fog-4	20 m and 5 m deep lakes serving as reference for fertilization experiment
S-6, 7 NE9b	Small lakes dominated by seepage inflows on <12,500 yr surface near Toolik Lake
I-Series lakes and streams	A series of streams and lakes that form the largest input of water and materials into Toolik Lake, located on the 10,000 yr surface
Landscape Interactions	
Tussock Watershed	1 ha watershed with a primary stream and weir; >56,000 yr old surface
Imnavait Watershed	2.2 km ² watershed with weir on primary stream weir on one of many distinct water tracks; >300,000 yr surface.
Climate and Hydrology	
Toolik Lake and Landscape	Main climate station and several satellite stations, atmospheric deposition monitoring, inlet stream gauge, lake temperature and light
Kuparuk Headwaters	Stream gauge, temperature at Dalton Highway crossing
Imnavait Creek	Climate Station, stream weir, and multiple data loggers along toposequences
Oksrukuyuk Creek	Stream gauge, temperature at Dalton Highway crossing
Sag River Valley	Climate Stations at Sag toposequence and Sagwon

Monitoring and process studies under LTER IV.

Table 2. The monitoring and process studies to be carried out to study linkages within and between various ecosystem components.

Ecosystem and Linkage	Monitoring and Process	Frequency of Sampling
Terrestrial	<i>Protocols and methods at:</i> http://ecosystems.mbl.edu/arc/data_doc/terrest/Terrestmethods.html	
Transport in soil water along toposequences	Imnavait Creek toposequence, weekly monitoring of dissolved N, P, soil temperature, moisture, thaw	Weekly or continuous using data loggers, short-term incubations of resins, occasional early- and late-season, 1-2 spring visits
Transport in soil water, glacial chronosequence	Glacial chronosequence, annual monitoring of dissolved N, P, soil temperature, moisture, thaw; surveys with streams group	Annual surveys in mid-season
Vegetation C and N uptake and allocation	NPP, N uptake, storage in biomass of diverse vegetation types	Major biomass harvests every few years at each site
Streams	<i>Protocols and methods at:</i> http://ecosystems.mbl.edu/ARC/data_doc/streams/streamsdefault.htm	
Transport in river, pelagic/benthic linkages, variations in flow	Kuparuk River, Oksrukuyik Creek, Hershey Creek. Effects of variation in flow on temperature, conductivity, alkalinity, SRP, TDP, PP, NO ₃ , NH ₄ , TDN, PON, DOC, POC, chlorophyll in seston and on rocks, insects, moss cover, fish (young, adult)	3x per summer for nutrients, insects and fish; continuous for flow. Kuparuk-12 sites along 5km reach; Oks. Ck.-3 sites; Hershey Ck.-8 sites
Analysis of BGC and communities in streams feeding 4 th order river	Monitoring in stream network feeding Kuparuk River. Flow, temperature, conductivity, alkalinity, SRP, TDP, PP, NO ₃ , NH ₄ , TDN, PON, DOC, POC, chlorophyll in seston and on rocks, insects, moss cover, fish (young, adult)	1 or 2 times per summer for 50 sites
Regional monitoring in different types of streams	Series of surveys in mountain, glacial, tundra, & spring-fed streams. Flow, temperature, conductivity, alkalinity, SRP, TDP, PP, NO ₃ , NH ₄ , TDN, PON, DOC, POC, chlorophyll in seston and on rocks, insects, moss cover, fish (young, adult)	1 or 2 times per summer for several sites
Lakes	<i>Protocols and methods at:</i> http://ecosystems.mbl.edu/ARC/data_doc/lakes/lakedefault.htm	
Benthic/pelagic linkages	Four study lakes Benthic and pelagic 1 ^o production Zooplankton production and grazing Benthic invertebrate production Sedimentation rates Fish abundance, diet, production Stable isotope analysis of organisms	3 time periods per summer “ “ “ “ 2 X per year (late winter, fall) 1X per year in 8 lakes
Analysis of BGC and communities in lakes	Alkalinity, nutrients, DOM, chlorophyll, zooplankton in seepage and drainage lakes Regional fish survey	1-3X per year in 10 lakes 1X per year in 5 lakes
Linkage between stream inflow and stratified lake	Chemistry, primary and bacterial production, and turbulence measurements at times of wind or rain events	Weekly for chemistry, prim prods. Continuous for temperature at 4 locations in Toolik Lake; Event-based for chemistry and production (hourly-daily)
Landscape Interactions	<i>Protocols and methods at:</i> http://www-personal.umich.edu/~gwk/protocol_v24.pdf	
Soil water chemistry and transfer to primary streams	Soil water and stream nutrients and OM to estimate production in soils and flux out of two small, primary catchments near Toolik Lake and near Imnavait creek.	Weekly for soils at ~30 sites; Weekly plus event-based for stream chemistry.
Inflows into lakes	Chemistry and biological production to determine ecological impacts of storm events (major inflows) on Toolik Lake.	Event-based (hourly to daily) depending on time-scale storms
Series of connected lakes and streams flowing into Toolik	Chemistry, primary & bacterial production to determine interactions of aquatic systems across the landscape	3x/year sampling of 12 lake and 15 stream sites

Experiments under LTER IV.

Table 3. The experiments to be carried out and the modeling and synthesis to study linkages within and between various ecosystem components.

Ecosystem Component And Linkage	Experiments and sampling	Modeling and Synthesis
Terrestrial		
Soil solution chemistry	Long-term fertilizer, warming, shading, and species removal experiments	GEM and MEL models of C-N interactions and budgets
N movement down toposequence	(¹⁵ NH ₄) ₂ SO ₄ addition experiment at 4 locations along Imnavait toposequence	New model of N transport
Belowground C inputs	Root production and C inputs in fertilized sites in wet sedge and tussocks using ¹⁴ C as tracer	Roots model – production of dissolved nutrients and OM
Vegetation C and N uptake and allocation	Long-term fertilizer, warming, shading, and species removal experiments	GEM and MEL
Soil C and N mineralization	Long-term fertilizer, warming, shading, and species removal experiments	GEM and MEL
Streams		
Productivity and community/nutrient supply	Phosphate continual addition to 10 ppb level final concentration	TREM, SISTM, Habitat Template Model
Lakes		
Productivity, zooplankton, benthic community response of lakes on +300k surface	Nutrient addition once per week to increase nutrient loadings by 50%	Compare to ALM output Compare to previous experiments on newer glacial surface
Landscape Interactions		
Effects of water amount on Tussock tundra	Water addition to tundra via pipe from lake	Hydrology model moves water
BGC cycling in tussock and wet sedge tundra		Biogeochemical model
Soil water dissolved materials in Tussock and wet sedge tundra	Root production in fertilized sites in wet sedge and tussocks using ¹⁴ C as tracer	Roots model - OM and nutrient production by roots

Table 4. Projects funded to work at the Toolik Field Station in 2007 and cooperating with LTER.

AGENCY	P.I.'s	Topic
NSF OPP IPY.	Shaver, Hobbie, Rastetter, Bret- Harte, Barnes, Zimov	Arctic Observatory Network. The Toolik site is one of four across the Arctic (with Siberia, Sweden, Greenland) that will make parallel measurements of the flux of carbon, water, and energy.
NSF OPP IPY	Oberbauer.	Plants and carbon cycling in a variety of Arctic sites. Phenology and growth of plants in an international warming experiment
NSF OPP IPY	Romanovsky	Warming of the permafrost in northern Alaska.
NSF OPP IPY	Sturm	The distribution of snow and surface energy exchange.
IPY (Canada)	Deslippe	The distribution and ecophysiology of ectomycorrhizal fungi.
NSF DEB LTER	Hobbie, Shaver, Peterson, Kling, Luecke	The goal of the Arctic LTER Project for 2004-2010 is: <i>To understand changes in the Arctic system at catchment and landscape scales through knowledge of the linkages and interactions among ecosystems.</i>
NSF OPP	Bowden.	Chemistry and biology of the hyporheic zone (flowing water beneath the stream bed)
BioComplexity	Stieglitz, Kling, Hobbie, Griffin, Schimel	Carbon, water, and nutrient flux in a watershed
NSF DEB	Shaver, Rastetter, Giblin.	Landscapes. Carbon and nitrogen interactions and hillslope N budget
NSF OPP	Shaver.	Pan-arctic net ecosystem exchange of CO ₂
NSF OPP	Huryn	Stream communities in spring streams of the North Slope.
NSF OPP	Hobbie and Hobbie	Nitrogen cycling and mycorrhizal fungi
NSF LTREB	Crump and Kling	Microbial community structure in stream-lake systems
NSF RUI	Hershey, O'Brien, Luecke	Studies of benthic productivity in lakes and ponds (GTH)
NSF OPP	Rastetter, Kling, Nadelhoffer, Johnson	Belowground allocation of photosynthetic carbon
NSF DEB	Bret-Harte, Mack	Plant competition
NSF	Hammersmith	Transformations of mercury in arctic lakes.
NSF OPP SNACS	Peterson, McClelland, Holmes	Large river budgets of carbon and nitrogen on the North Slope
NSF DEB	MacIntyre	Internal waves and turbulence affect biological processes in an Arctic lake.
NSF DEB	Gough, Moore,	Herbivory and soil food web
State of Alaska	Kane, Hinzman	Climate and hydrology of the Upper Kuparuk Basin

2. TERRESTRIAL RESEARCH

a. Terrestrial linkages on the landscape:

In several of our long-term fertilizer experiments, where we have been adding N to the tundra for up to 27 years, the total mass of N in fertilized plots is actually *lower* than in unfertilized controls (e.g., Mack et al. 2004, Fig. T-1). Furthermore, the long-term fertilized plots also contain less C than the unfertilized controls despite the fact that the fertilizer has doubled NPP, and thus C inputs, to these plots since the start of the experiment. *Where did all the N go?* The two major possibilities are (1) downslope leaching within the annually-thawed soil active layer (because deep leaching is prevented by the permafrost), and (2) gaseous losses especially by denitrification.

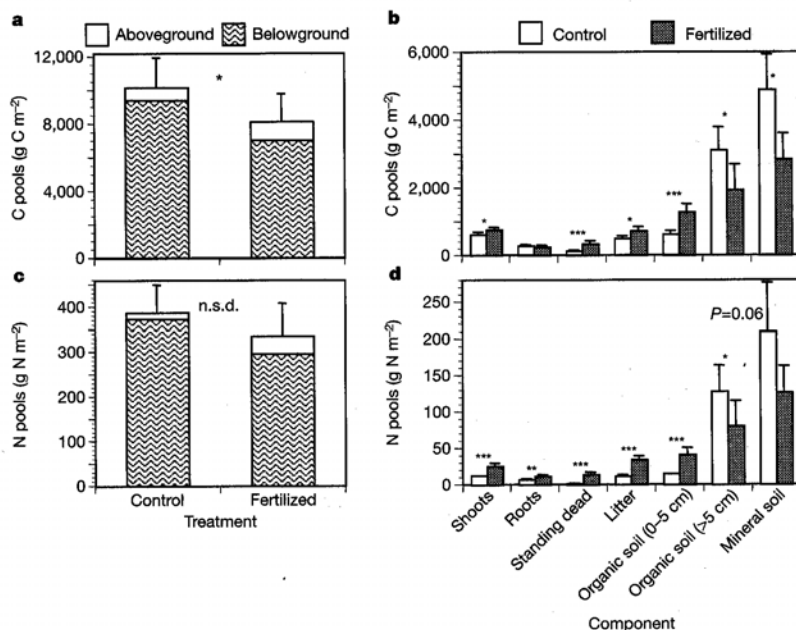


Figure T-1. C and N mass in control and fertilized plots of moist acidic tundra after 20 years of fertilization (Mack et al. 2004). Left panels show totals, above and below ground (C top, N bottom). Right panels show individual components.

(1) Downslope N movement: In 2003 we began a tracer experiment at Imnavait Creek, spraying ¹⁵N ammonium sulfate at non-fertilizer concentrations (58.8 mg N m⁻²) onto the surface vegetation. Labeled plots were located at crest, midslope, footslope, and riparian locations along the Imnavait toposequence (Fig. T-2). The midslope and footslope plots extended into and out of water tracks (areas of greater drainage, with different vegetation; Chapin et al. 1988). Soils and vegetation in these labeled plots have been sampled repeatedly since 2003. Most of the ¹⁵N is still trapped in mosses and vegetation (Fig. T-3). At the crest site only 7% of the added label can be found in soil. Further downslope the amounts are higher, 23%, but still low compared to what is found in vegetation. The field results at Imnavait have confirmed our previous laboratory experiments demonstrating that N is highly retained in these tundra systems. However, we have been able to trace some downslope movement of the tracer. Movement

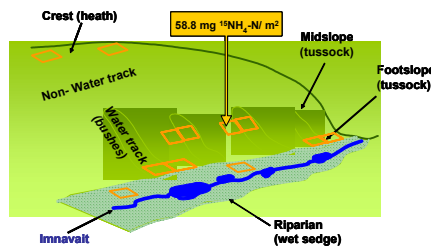


Figure T-2. Summary of locations of ¹⁵N-labeled plots along the hillslope toposequence at Imnavait Creek

of the tracer appears to be confined mainly to the period of snowmelt (Fig T-4).

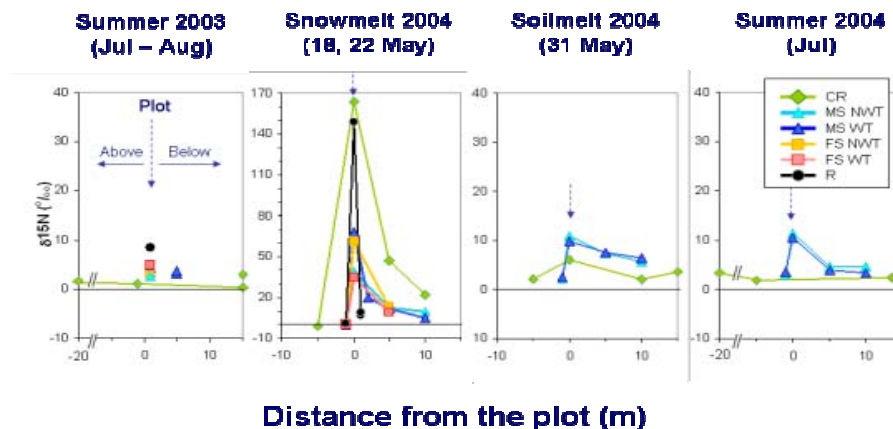


Figure T-3. $\delta^{15}\text{N}$ of total dissolved N in soil solution above, within, and below the labeled plots at Imnavait Creek. CR=crest; MS=midslope; FS=footslope; R= Riparian. WT= water track; NWT=non water track

Although downslope N transport is small, we have also found that the forms of N in soil solutions differ with both landscape position and soil age (time since deglaciation). We analyzed three potentially labile-N fractions, hydrolysable amino acids, hydrolysable amino sugars, and hydrolysable ammonium. At all sites the hydrolysable amino acid fraction was the largest, indicating that proteinacious N may play an important role in N availability. Hydrolyzable amino acids, soluble protein, and water extractable DON all increase with soil age while soil extractable DIN tends to be highest in the youngest soils. Fertilization reverses this pattern and leads to an increase in DIN and a decrease in hydrolysable amino acids.

To examine the effects of downslope N transport on responses to changes in CO_2 and climate, we developed a model that simulates a contiguous 100 m transect of individual 1 m^2 plots of moist tundra (Rastetter et al. 2004). We assumed that water and nutrient move only down slope from one plot to the next (i.e., no convergent or divergent flow) and down-slope plots rely on water and nutrients coming from up slope as well as any inputs from the atmosphere. Based on projected changes in CO_2 and climate, we found that the base of the hill slope should store about 50% more C than the top over the next 100 years (Rastetter et al. 2004; Fig. T-5). However, because down-slope transport of nutrients delays the full response down slope by as much as 1000 years, the difference in C storage between the top and bottom of the slope is likely to be even larger in the long term. This differential response along the hill slope clearly indicates the importance of understanding hill-slope processes before responses of arctic landscapes to changes in CO_2 and climate can be predicted.

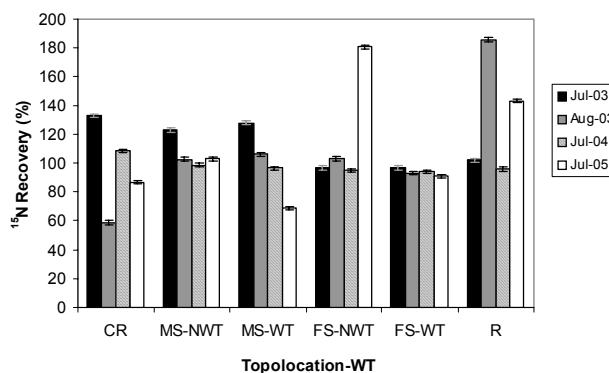


Figure T-4. Figure. Mean ^{15}N recovery in the entire soil column for each sampling date and topolocation.

We used another model to assess the effects of dissolved organic versus inorganic N (DON v. DIN) losses on the response of ecosystems to changes in CO₂ and climate (Rastetter et al. 2005). One way that ecosystems can sequester C is to curtail N losses and thereby sequester incoming N to meet C-N stoichiometric constraints of plants and microbes. If N is lost as DIN, which is readily available to plants and microbes, then elevated CO₂ increases biotic N demand, curtails N losses, and N and C sequestration is large. However, if N is lost as recalcitrant DON unavailable to plants and microbes, then N losses cannot be curtailed by increased biotic demand and C sequestration is only 1/5 to 1/2 of the C sequestration if N is lost as DIN. These results indicate that the form of N movement on hill slopes, as well as the amount, is important for predicting long-term responses to changes in CO₂ and climate.

(2) Gaseous N Inputs and outputs: The focus of our efforts thus far has been on N inputs via fixation and on loss via volatilization and especially denitrification. We completed a two-season survey of nitrogen fixation across the Imnavait toposequence (Hobara et al. 2006). The input of N via N-fixation at Imnavait Creek was estimated to be 46-131 mg N m⁻² y⁻¹. Although this rate is low, it is several times greater than the annual N deposition rate, suggesting that N-fixation is the primary N-input process in this strongly N-limited ecosystem. However, there were no significant differences in the rate along the toposequence. Weiss et al. (2005) carried out a comparison of fixation on young vs. old sites at Toolik Lake and found higher fixation rates on the older surface. Fertilization with N dramatically decreased fixation, largely because the biomass of N fixing lichens precipitously declined with fertilization. A short-term survey of ammonia volatilization was carried out on both control and fertilized plots at Toolik Lake (Koop-Jacobsen and Giblin unpublished data). At these sites soil pH is low enough to prevent any net ammonium volatilization and in most cases the soils were a weak net sink for atmospheric ammonia.

Measurements of denitrification potential (Fig. T-6 TOP) were made using the denitrification enzyme activity (DEA) assay

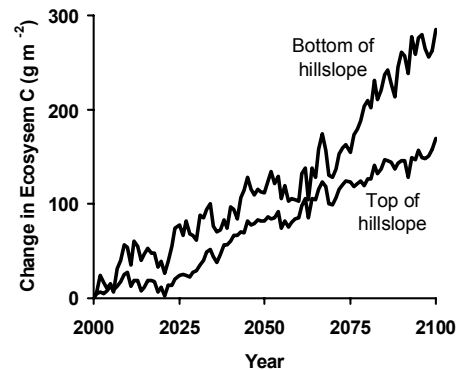


Figure T-5. Predicted change in ecosystem C over the next 100 years for an arctic hillslope (data from Rastetter et al. 2004).

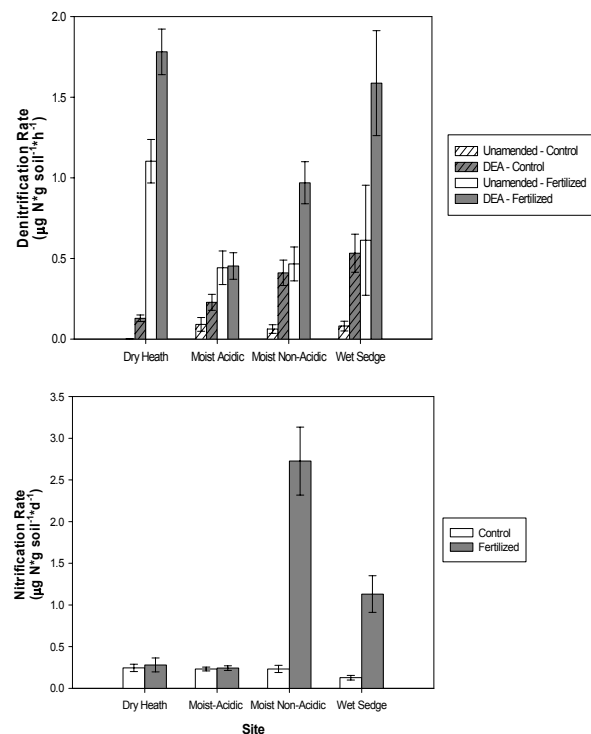


Figure T-6. TOP: Amended ("Potential") and unamended denitrification rates in soils from dry heath, tussock, and wet sedge ecosystems at Toolik Lake BOTTOM: Amended nitrification rate ("Potential Nitrification") in soils from dry heath, tussock, and wet sedge tundras at Toolik Lake.

(Tiedje et. al. 1979). This assay, which is carried out in the presence of added nitrate and glucose under anaerobic conditions, showed that control sites had measurable activity that differed with landscape position and age. On the older surface, potential rates followed the moisture gradient and were lowest in dry heath sites, intermediate in moist tundra, and highest in the wet sedge meadow. Rates on moist acidic tundra were lower than rates on moist nonacidic tundra (a younger landscape). At all sites, fertilized plots had a markedly higher capacity for denitrification.

We also measured denitrification activity of these soils using a modification of the acetylene block technique (i.e., DEA without added glucose or nitrate: shown as “non-amended” Fig. T-6 TOP). At control sites we found very low rates, ranging from non-detectable in the dry heath to about $0.05 \mu\text{g N (g soil)}^{-1} \text{ hr}^{-1}$ in wet sedge. In contrast, rates in fertilized sites were much higher and exceeded $0.5 \mu\text{g N (g soil)}^{-1} \text{ hr}^{-1}$ at all sites. This suggests that denitrification is a substantial sink for nitrogen in the fertilized plots but that denitrification removes less N than enters from fixation on unfertilized control sites. Further insights into potential controls of denitrification came from experiments where we examine potential nitrification (Fig T-6 BOTTOM). Potential nitrification was low at all control sites and showed no patterns with landscape position or age. There was no stimulation of potential nitrification with fertilization on any of the sites on the older surface except wet sedge meadow. On the younger surface, fertilization increased potential nitrification rates by an order of magnitude.

On the whole, we conclude from this denitrification survey that soils of all sites examined have a surprisingly high potential for N losses by denitrification. On an annual basis, potential denitrification rates even in unfertilized plots may be as high as $1 \text{ g N m}^{-2} \text{ y}^{-1}$, about the same magnitude as the annual plant uptake requirement, although this rate is likely reached only in fertilized plots where the potential losses due to denitrification may be $>5 \text{ g N m}^{-2} \text{ y}^{-1}$. Thus, denitrification may account for much or most of the observed N loss in long-term fertilized plots (Mack et al. 2004).

b. Scaling up from small plots to the PanArctic region:

Over the past 15 years, one of our most striking and consistent results is the demonstration that vegetation leaf area and canopy N content are tightly correlated with each other at a wide range of tundra sites in Alaska and Scandinavia (Williams and Rastetter 1999, van Wijk et al. 2005). This tight correlation (Fig. T-7) suggests a strong convergence in regulation of canopy CO_2 exchange despite major differences in vegetation composition. For the past 5 years we have pursued the implications of this consistent canopy structure by measuring the light responses of whole-canopy CO_2 fluxes in diverse arctic plant canopies in

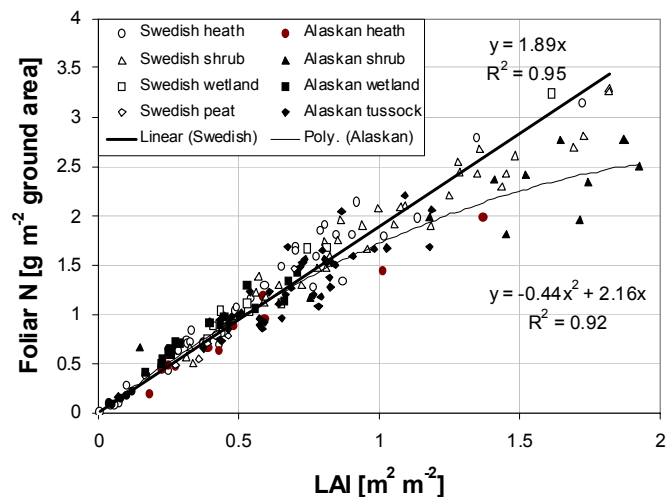


Figure 2. Across a wide range of tundra vegetation in both Alaska and Sweden, leaf area and N content are closely correlated, suggesting tight control over canopy architecture and N use in arctic vegetation (van Wijk et al. 2005). LAI=Leaf area index ($\text{m}^2 \text{ leaf per m}^2 \text{ ground surface}$).

Figure T-7. van Wijk et al. 2005

Alaska, northern Sweden Svalbard, and Greenland. In this work we showed that canopy leaf area *alone* is an excellent predictor of whole-canopy photosynthesis, explaining about 80% of the variance in Gross Primary Production (GPP) at constant irradiance (PPFD=600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) across a wide range of plant canopies (Fig. T-8; Street et al. 2006). Furthermore, for unfertilized plots the relationship between GPP and leaf area is the same at both Toolik Lake, Alaska, and at Abisko, Sweden. This is a key finding suggesting that a single model parameterization can be used to predict CO_2 flux for whole canopies of diverse species composition, at least throughout the Low Arctic region.

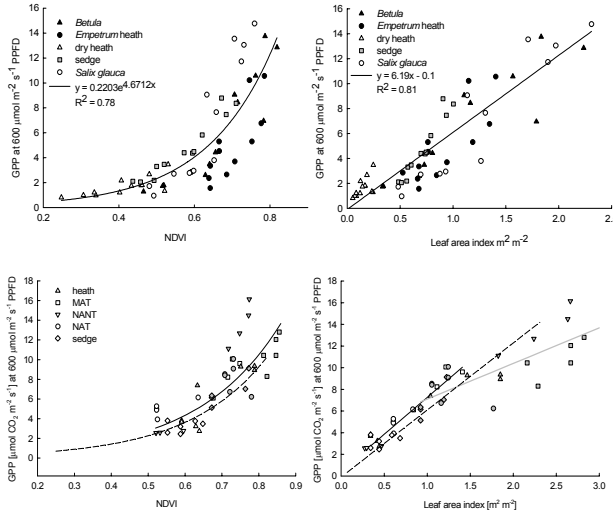


Figure T-8. (from Street et al. in press). Upper panels show the relationship between GPP600 and (A) NDVI and (B) predicted LAI for 5 vegetation types at Abisko, Sweden. Lower panels show the relationship between GPP600 and (C) NDVI or (D) leaf area for control and fertilized plots in 5 vegetation types at Toolik Lake, Alaska. Filled symbols in (C) and (D) are fertilized plots. Gray line in (D) is the best-fit linear regression for fertilized plots only ($R^2 = 0.63$), solid line in (D) is for Toolik 2004 control plots only ($R^2 = 0.89$). Dashed lines in (C) and (D) are regression lines derived using Abisko data in upper panels.

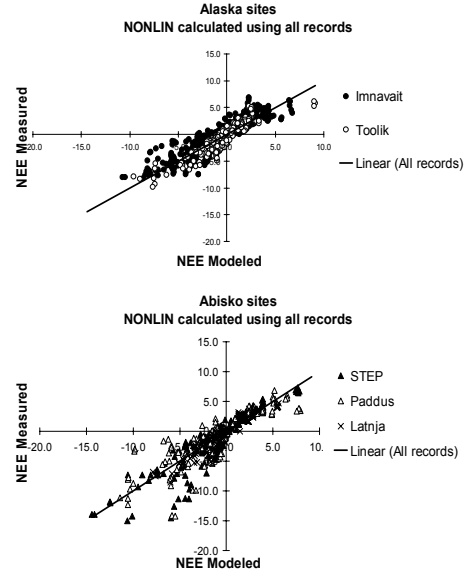


Figure T-9. Measured versus modeled NEE, using all available data from 32 site/vegetation type combinations. Predicted and measured values from Alaska and Sweden are on separate panels to facilitate viewing only. Also to facilitate comparison, the same overall regression line is plotted in both panels. Overall r^2 for this parameterization is 0.799, the slope is 1.000, the intercept is 0.000, and the root mean square error (RMSE) is 1.529 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Using this data set, we developed a new model of Net Ecosystem CO_2 Exchange (NEE), where:

$$\text{NEE} = ((R_0 * e^{\beta T} * \text{LAI}) + R_x) - \left(\frac{P_{\text{maxL}} * \ln \left(\frac{P_{\text{maxL}} + E_0 * I}{P_{\text{maxL}} + E_0 * I * e^{-k * \text{LAI}}} \right) \right) \quad (\text{Equation 1})$$

In this model, the first term describes ecosystem respiration (R_E) as the sum of a constant, basal respiration rate (R_x) and a respiration component (R_0) that increases with both temperature and leaf area. The second term of the model is adapted from Rastetter et al. (1992) and describes canopy photosynthesis (GPP) as a function of a maximum photosynthetic rate per unit leaf area (P_{maxL}), a light extinction coefficient (k), a quantum efficiency (E_0), leaf area (LAI), and photosynthetically active photon flux (I).

To apply the model, we use nonlinear regression to estimate the six parameters (R_x , R_0 , β , P_{maxL} , k , and E_0) of Equation 1 (Shaver et al. in press). We then use the measured values of LAI, air temperature (T), and photon flux (I) to predict NEE, substituting using the six estimated parameters into Equation 1. When we use the entire data set to do this, we have a measure of the

ability of the model to encapsulate the variability in NEE within a single equation. In Fig. T-9, we used 1410 individual measurements of NEE in 79 plots of 32 different site/vegetation type combinations in Alaska and Sweden to estimate the model parameters and predict NEE. The model explains 80% of the measured variance in NEE with zero bias (slope =1.000, intercept =0.000) across the full range of measured and modeled values.

To evaluate our ability to use data from one site, vegetation type, or region to predict NEE, GPP, or R_E in other places we use different subsets of the data for parameter generation vs. tests of model predictions. For example, we can use the data from all Alaskan sites to develop model parameters (by nonlinear regression on Equation 1), and then use those parameters to predict NEE at all Swedish sites and to compare predicted with measured NEE. In general the model does extremely well at predicting NEE in one place with parameters developed from measurements in another place. The r^2 of predicted vs measured NEE is almost always >0.75; the slope and intercept are very close to 1.00 and zero, respectively; and the RMSE varies from 1.0 to 2.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The predictions are most accurate and precise when we use a survey of CO_2 flux in diverse vegetation types within a local region to parameterize the model, as opposed to using measurements from just a single vegetation type to develop parameters that are then used to predict NEE in very different kinds of vegetation.

Overall, the *primary conclusion* of the past five years of work on this project is that all of the Low Arctic tundras that we have examined seem to be following the same rules with respect to regulation of their canopy-level CO_2 exchange. Because leaf area, and its N content, are tightly constrained across diverse kinds of plant canopies, we can parameterize the model described in Equation 1 using a survey of CO_2 fluxes in one part of the Arctic, and we can use that parameterization to predict NEE with acceptable accuracy and precision in other parts of the Arctic. To do this we need to know only (1) total canopy leaf area, (2) photosynthetically active photon flux, and (3) air temperature, all of which can be sensed remotely (by satellite, airplane, or hand-held instrument) at the site where NEE is to be predicted. This is a major step forward in development of a PanArctic CO_2 flux model, as well as a major step toward confirmation of our overall hypothesis that natural selection places very tight constraints on how plant canopies can develop in arctic vegetation.

c. Long Term Experiments:

The ARC terrestrial group currently maintains 12 long-term, whole-system manipulation experiments, the earliest of which began in 1981 (Table T-1). Each summer we complete a major harvest of one or more of these experiments. The general aim is to harvest each experiment at least once every 3-6 years, but the schedule is kept flexible to allow coordination of our harvests with collaborating, independently-funded projects. The LTER experiments were designed to accommodate this coordinated sampling, mainly by establishing much larger plots than would otherwise be needed, and by incorporating extra plots within each block of treatments for additional sampling or future treatments. We also restrict the area within each plot that is available for “destructive” sampling, so that at least part of every plot is kept undisturbed for long-term observation.

Because these ecosystems continue to respond to our treatments, we gain new insights about ecosystem regulation with each harvest. In the last 3-5 years, we have shifted emphasis to two of the newer long-term experiments, one focused on long-term effects of herbivory and the second on effects of individual species and plant functional types on element cycling. Both of

these experiments include analysis of factorial interactions with fertilizer addition, the most important treatment variable in our earlier experiments (Table T-1).

Table T-1. Experimental Designs for Terrestrial Research of the Arctic LTER Project.

Location	Year Started	Ecosystem Type	Treatments	Major Harvests
Toolik Lake (Historic site)	1980	Acidic Tussock	Control, N+P Fert	1982, 1983, 1984, 1989, 1995, 2000
Toolik Lake (main LTER site)	1988	Acidic Tussock Wet Sedge Dry Heath Riparian Shrub	Control N, P, N+P Greenhouse Shade Greenhouse+N+P Shade +N+P	Tussock 2001, 2002 Sedge 1994, 2001 Heath 1996
	1994	Acidic tussock Dry heath	Snowfence	Annual point-frame monitoring, 1994-2003
	1996	Acidic Tussock Dry Heath	Control N+P Herbivore Exclosure Exclosure+N+P	Tussock 1999-2002
	1997	Nonacidic Tussock Nonacidic Nontussock	Control N, P, N+P Greenhouse Greenhouse+N+P	Tussock 1999-2001
	1997	Acidic tussock	Species removal N+P Removal+N+P	1999, 2003
	1998	Acidic tussock Nonacidic Tussock Nonacidic Nontussock	Sulfur Lime	
	2001, 2002	Wet sedge (2001) Acidic Tussock (2002)	¹⁴ C addition, control and N+P fert	2001, 2002, 2003, 2004, 2005
	2006	Acidic tussock	Low-level NxP	
	2006	Acidic tussock, Riparian Shrub	Snow fence	
	2007	Dry Heath	Rainfall exclusion	
Sag River Toposequence	1984	Moist Tussock Dry Heath Snowbed Equisetum/Forb Wet Sedge Riparian Shrub	Control N P N+P C enrichment (starch, sawdust) Lime	All sites 1988; Wet sedge 1994, 2001

(1) Herbivore exclosures: The central hypothesis of this experiment is that herbivores play an important role in controlling tundra plant species composition, but are less important as direct controls on productivity or nutrient turnover at 1-10 year scales. We also hypothesized that herbivores induce changes in species composition more rapidly under fertilization, but that fertilized plots with or without herbivores will converge to similar species composition after about 10 years. The herbivory manipulation consists of a nested exclosure treatment with an outer, large-mesh fence (LF) excluding caribou and an inner, small-mesh fence (SF) excluding lemmings, voles, and ground squirrels. We set up this experiment in July 1996, with harvests in 1999, 2003, and 2006.

After ten years of treatment the Moist Acidic Tundra (MAT) shows little if any impact of herbivore exclusion on above or belowground plant biomass (Fig. T-10A: earlier results in Gough et al. in press). The fertilizer only treatment did reproduce our previous results (Chapin et al. 1995, Shaver et al. 2001, Mack et al. 2004), with a shift in species composition toward dominance by deciduous shrubs and major reductions or complete loss of lichens, mosses, and evergreens. In the Dry Heath tundra, however, herbivore exclusion resulted in greater aboveground biomass both with and without fertilizer addition (Fig. T-10B). As in the MAT, in Dry Heath the fertilizer greatly reduced aboveground lichen, moss, and evergreen biomass but the reductions were smaller in fertilized exclosures. A final trend is that the increase in graminoids in fertilized plots at both sites appears to be reduced in the exclosures; this may be the result of herbivory favoring graminoids in fertilized plots or a lack of herbivory favoring deciduous shrubs, or both.

The herbivory study also developed a key data set on soil food webs in fertilized and control plots, used in a theoretical analysis of the stability and symmetry of food webs. In this analysis, Rooney et al. (2006) showed that coupling between fast and slow energy channels of food webs was a major control over food web stability. Disturbances, including fertilizer addition, led to an erosion of this coupling, and thus a decrease in food web stability.

(2) Species removal experiment: The aim of this experiment is to evaluate the relative impacts of individual plant species and functional types on productivity and element cycling of MAT. This is done by removing selected species from the vegetation by hand-weeding, both with and without annual fertilizer addition. This experiment was begun in 1997 and is now among the oldest of its kind in the world. Results from the most recent (2003) harvest show that total primary production and the total N content of primary production are remarkably consistent across removal treatments (Fig. T-11), suggesting that the species composition is relatively unimportant. Furthermore, fertilizer addition increased both production and its N content by about the same amount in all removal treatments (the moss removal treatment was a possible exception), suggesting that production of the whole community is much more closely regulated by its N supply than by its species composition. Differences in biomass and its N content were more variable among treatments, reflecting differences in C and N allocation among tissues in the different plant functional types.

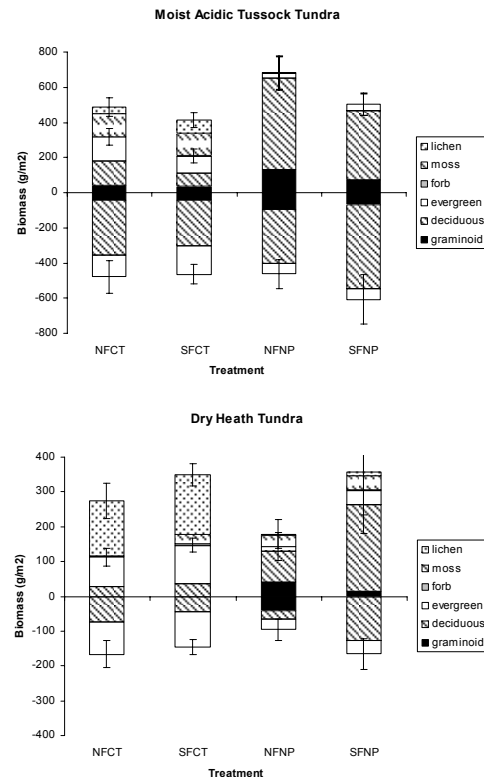


Figure T-10. Above and belowground biomass (rhizomes only; no roots) in the 2006 harvest of the herbivore exclusion experiment. (Gough et al. unpublished data) NF=no fence; SF=small-mesh fence; CT=unfertilized control; NP = N+P fertilizer. 2006 was the 10th year of treatment.

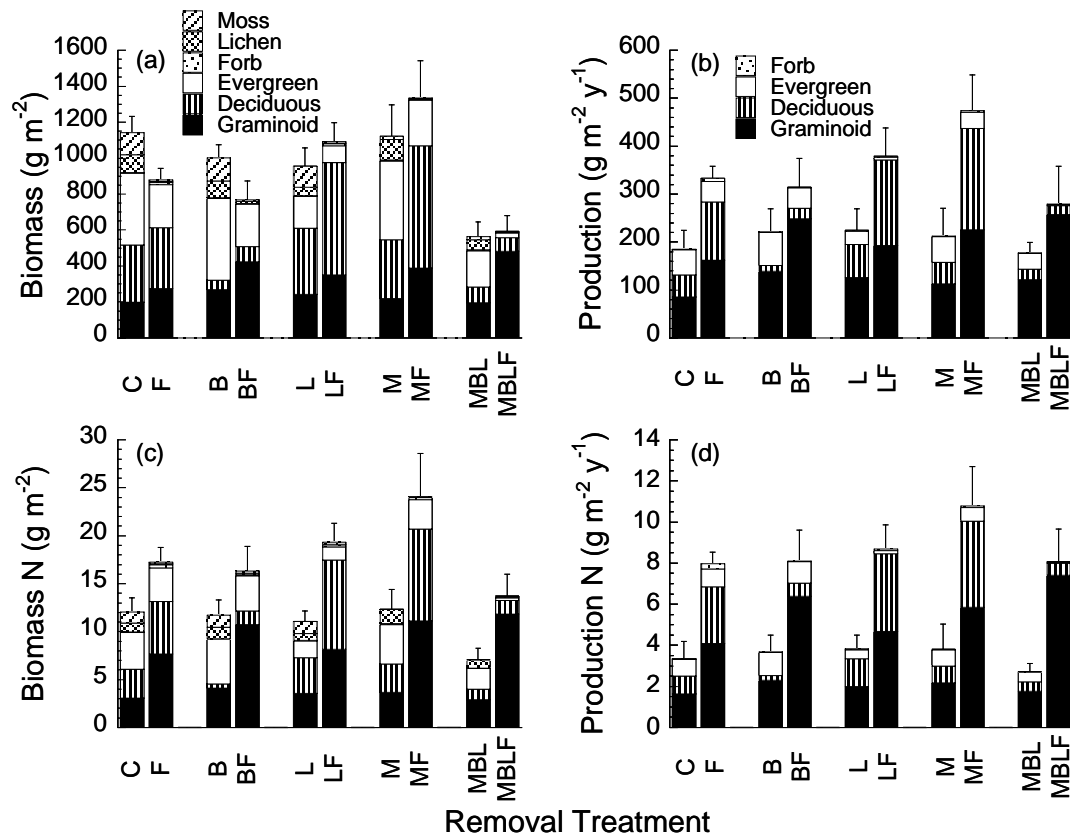


Figure T-11. Aboveground biomass and above ground production in the 2003 harvest of the species removal experiment (7th year of treatment). C=Control; F=Fertilized; B= *Betula nana* removal; L=*Ledum palustre* removal; M=Moss removal; MBL=Moss, *Betula*, and *Ledum* removal (Bret-Harte et al. unpublished data).

d. Ecosystem regulation and processes:

Over time, the ARC terrestrial group is gradually building a comprehensive understanding of individual ecosystem processes and their controls. The focus of these process studies evolves continually and typically depends on collaborations with independently-funded projects that work in the ARC experimental plots or use LTER data and models. Since 2004 this work has focused on soil processes including: (1) studies of belowground C allocation and turnover, and (2) evaluation of the potential importance of mycorrhizae in the uptake of N by tundra vegetation.

(1) Belowground C allocation: Because >90% of the C in tundra ecosystems is below ground and the total amounts are globally significant, it is important to understand how this soil C gets there and how it is regulated. In one recent study, Shaver et al. (2004) showed that all of the major chemical fractions in tundra soils are actively turning over, including fractions typically considered relatively non-labile. In another study, Nadelhoffer, Kling, Sommerkorn, Rastetter, and colleagues (in preparation) used ^{14}C labeling to show that photosynthetically-fixed CO_2 is translocated through the roots and into the soil within half an hour of fixation in the leaves. The total proportion of newly-fixed CO_2 that is transported by this pathway exceeds 15% of gross primary production in both wet sedge tundra and moist acidic tundra at Toolik Lake.

(2) Mycorrhizae: Productivity of tundra vegetation is almost always strongly N-limited, and tundra plant species have been shown to use a wide range of uptake mechanisms to acquire this essential element (e.g., McKane et al. 2002). Recent research of the terrestrial LTER group has focused on mycorrhizal N uptake and its costs to the plants that use this pathway. Using a mixing model based on the natural abundance of ^{15}N in bulk soil, plant foliage, and mycorrhizal fungi, Hobbie and Hobbie (2006) recently showed that for ectomycorrhizal plants such as the dwarf birch, Betula nana, as much as 61-87% of their N uptake may come via mycorrhizae, at a cost of 8-17% of the net C fixation by the plant. Moreover, mycorrhizal fungi are not just a conduit for N scavenged in the soil; they also actively break down soil organic matter and thus make N available to plants (Hobbie and Hobbie in prep.). The importance of mycorrhizae in providing N to plants is likely to increase with climate change, due mainly to an expected increase in abundance of mycorrhizal species such as birch, as shown in the LTER fertilized plots (Clemmensen et al. 2006).

3. STREAM RESEARCH

a. Long-term monitoring and fertilization.

We have carried out three stream fertilization and monitoring studies as part of the Arctic LTER research. The first and longest is the Kuparuk River fertilization experiment, which remains the flagship experiment of the streams research (Peterson et al. 1985, Slavik et al. 2004). A six-year fertilization of Oksrukuyik Creek was carried out for comparison of responses in a second meandering tundra stream (Harvey et al. 1998). A one-year fertilization was performed in a beaded tundra stream for comparison with the meandering stream responses (Benstead et al. 2005). Finally recovery from fertilization was studied for several years at the Oksrukuyik and Kuparuk sites (Benstead et al. 2007).

The Kuparuk River has been studied intensively from 1978 until the present. Starting in summer 1983, whole-stream fertilization of the river with constant drip to give a stream concentration of 10 $\mu\text{g P/l}$ stimulated algal production by about 1.5 to 2 fold on average (Peterson et al. 1993, Slavik et al. 2004). The fertilization also increased bacterial activity and rates of decomposition of recalcitrant substrates such as lignin and lignocellulose (Peterson et al. 1985). The bottom-up impacts of P addition increased the abundance of insects such as *Brachycentrus* and *Baetis* and the increased insect abundance stimulated the growth of both adult and young-of-the-year (YOY) grayling in the fertilized reach relative to the reference reach (Deegan and Peterson 1992).

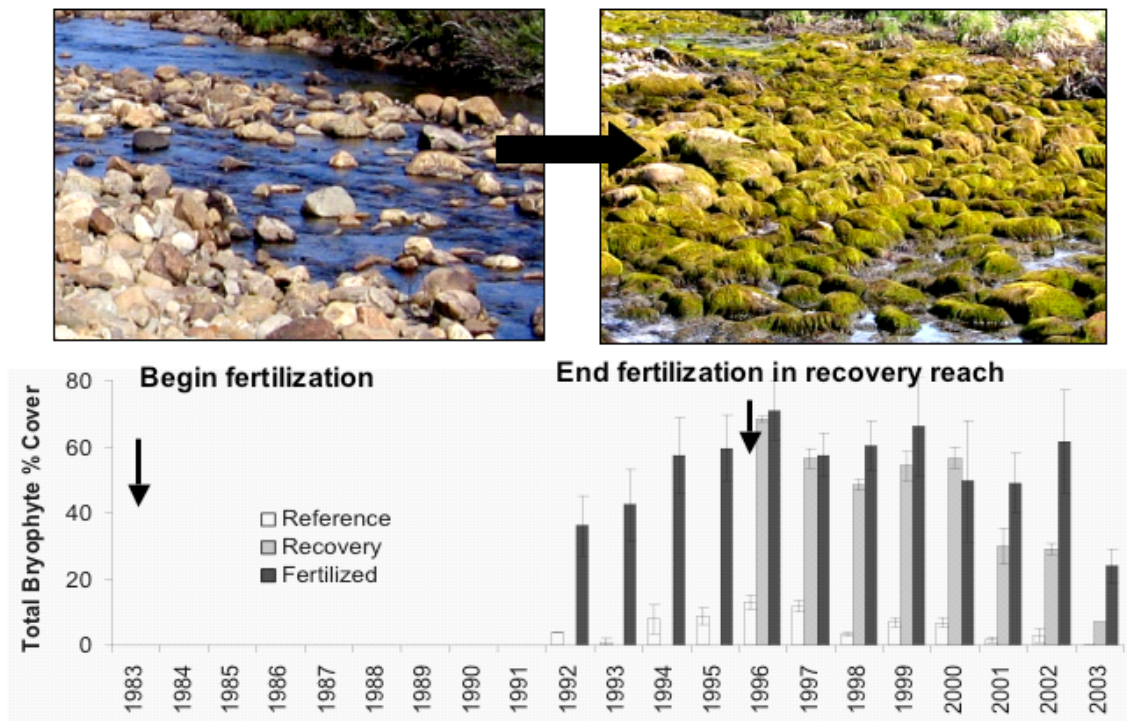


Fig. S1. The photographs illustrate the difference in bottom coverage between the diatom state (reference; left) and the fertilized, moss state (right). These photos were taken during a drought when the riffles were exposed but normally these sites are submerged. The graph shows the cover of moss in the reference, recovery and fertilized reaches of the Kuparuk River.

In spite of consistent responses to fertilization, the populations of algae and insects and the rates of fish growth proved to be highly variable (~10X) from year to year in both reference and fertilized reaches (Hershey et al. 1997, Deegan and Peterson 1992, Slavik et al. 2004). Much of this variability was correlated with year-to-year variations in precipitation and discharge. Under high discharge conditions, algal biomass was only half as great as under low discharge conditions. Black fly abundance was also affected by flow (Hershey et al. 1997). Adult fish thrived when discharge was high but the young of the year (YOY) grayling grew poorly under high flow conditions that are also associated with low temperatures (Deegan et al. 1999).

After nearly a decade of continuous summer fertilization the riffle habitat became covered with a carpet of the moss *Hygrohypnum* (Fig. S1, Bowden et al. 1994, Slavik et al. 2004). This was a surprise because this species was not observed in these reaches of the Kuparuk prior to fertilization. *Hygrohypnum* provides a large amount of surface area for algal epiphytes and the moss community (moss plus epiphytic algae) is several-fold more productive than the epilithic biofilm in the reference reach (Arscott et al. 1998). The moss fronds create a matrix that traps and store a large amount of fine particulate matter. The moss habitat is host to an insect community quite different than found in the rocky-bottom reference reach (Lee and Hershey 2000, Slavik et al. 2004). Chironomids, *Brachycentrus* and a large mayfly (*Ephemerella*) are more abundant by an order of magnitude in the mossy fertilized reach whereas other common insects including *Baetis*, black flies and *Orthocladus* are less abundant. In spite of higher insect biomass in the fertilized reach, the growth of adult drift-feeding grayling is no longer significantly greater than in the reference reach. Some aspect of the link between insect production and fish growth has been changed by the P-induced moss invasion but further work is required to understand this paradox.

The Kuparuk fertilization results have led to submitted proposals to address the hypothesis that landscape disturbance associated with rapid warming and permafrost thaw may lead to widespread enrichment of tundra streams and a consequent increase in moss distribution and abundance.

b. Hyporheic processes

Substantial evidence from temperate streams (Duff and Triska 1990, Triska et al. 1990, Wondzell and Swanson 1996a, Mulholland et al. 1997, Dahm et al. 1998, Hill et al. 1998, Baker et al. 1999, Chapra and Runkel 1999, Bencala 2000) suggests that the hyporheic zone can be an important – perhaps critical – source of organic matter turnover and nutrient regeneration. Results from field studies on streams and rivers around Toolik reported by Edwardson (1997) and Edwardson et al. (2003) are consistent with results from these previous studies. In particular, we found that geomorphic profiles of stream channels (longitudinal more so than lateral) provide the necessary hydraulic gradients to drive hyporheic exchange through the streambed, as shown by Harvey and Bencala (1993) and Kasahara and Wondzell (2003). We also showed that biogeochemical processing could potentially supply from 14 to 162% of the benthic N uptake requirements in the Kuparuk River. Johnston et al. (in preparation) used hyporheic microcosms to demonstrate that there is a stoichiometric relationship between oxygen consumption and respiration in hyporheic sediments and to explore how key environmental driving variables (N concentration, C source, temperature, oxygen level) affect N and P dynamics in hyporheic sediments.

Our subsequent research on headwater streams near Toolik has shown that ground penetrating radar (GPR) can be used to image changes in the thawed zone under fast-flowing,

cobble-bottomed streams as well as slow-flowing, peat bottomed streams in headwater areas (Bradford et al. 2005). We have used this approach to follow the progression of thaw depth over the summer season (Fig. S2, Brosten et al. 2006) by obtaining a series of GPR profiles at five sites from May - September 2004 in fast-flowing, cobble-bottomed (alluvial) streams as well as slow-flowing, peat bottomed streams. We found that thaw bulb development within the two stream environments was distinctly different. Thaw depths within cobble-bottom streams were observed to increase in thickness up to 1 m within the first four weeks but only 32 cm in the peat-bottomed streams (Fig. S2). Rapid heat absorption and loss occurs in the cobble-bottom stream sites while peat insulates the permafrost and introduces a lag in the seasonal thermal profile.

Using conservative tracer additions, we found that transient storage indicators such as mean storage residence time, storage zone area, hydraulic retention, and storage exchange rates were sensitive to discharge and strongly correlated with total stream power (Fig. S3 and Zarnetske et al. in press). Transient storage indicators increased with increasing thaw depths under base- and low-flow conditions but these relationships diminished at high flow. Our current work suggests that stream power is a good predictor of transient storage characteristics because it normalizes simple characteristics of hydraulics and morphology, thereby allowing better comparisons across streams that differ widely in these characteristics (Fig. S3). Our results in arctic streams are comparable to those in temperate streams (Legrand-Marcq and Laudelout 1985, D'Angelo et al. 1993, Harvey et al. 2003) indicating that our findings are likely transferable to non-arctic streams.

We also examined biogeochemical dynamics in the hyporheic zones of the streams we used for our GPR and conservative tracer addition experiments. In the cobble-bottom stream – which had a greater depth of thaw – stream water penetrated the hyporheic zone to a depth of up to 54 cm. In the peat-bottom stream, which had a much shallower depth of thaw, the actively functioning hyporheic zone was limited to a depth of 10 cm or

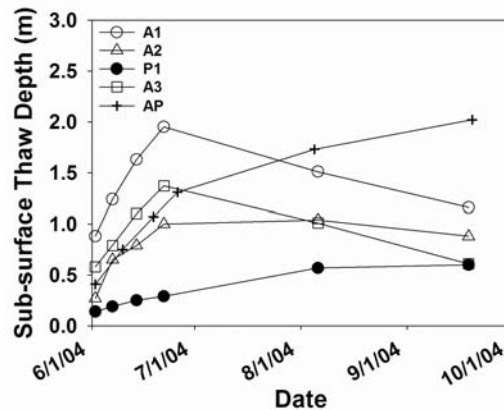


Figure S2. Maximum thaw depth development at five study sites where interpretations were made from repeated GPR transects collected throughout the summer season at each site. The “A” reaches are alluvial, high-gradient, cobble-bottom reaches; the “P” reaches are low-gradient, peat-bottomed reaches. The “AP” site is a mixed alluvial-peat site.

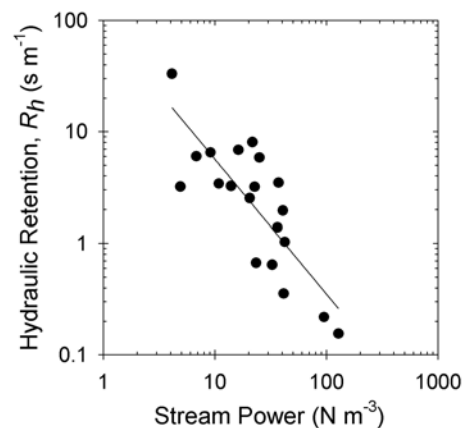


Figure S3. Relationship between hydraulic retention, representing the time spent in storage per m length of stream and stream power, as determined by numerous conservative solute tracer experiments in arctic streams

less. In both streams we found that the maximum extent of hyporheic penetration was much less than the maximum extent of thaw. This is an important finding because it suggests that while climate warming in the Arctic may increase the depths of the active layer under the tundra and the thaw layer under streams, it is unlikely to increase the depth of hyporheic exchange. Thus, the primary effect of climate change will be to extend the length of the season for active hyporheic exchange.

c. Thermokarst

i. Toolik Region: In the past several years we have observed that a number of new thermokarst features have formed in the Toolik Lake area. Thermokarst is the thawing of ice in soils that causes the formation of a pit or depression. In 2006 we conducted a low-altitude aerial survey and identified at least 34 active thermokarst features in an area approximately 25 km x 25 km between Toolik Lake and areas east of Happy Valley to the north (Bowden et al. in review). We suspected that this represented a greater rate of thermokarst formation than we have experienced in the last 30 years and began to wonder how thermokarst features may impact headwater streams in Arctic tundra foothills.

One of the thermokarst features we observed formed quite suddenly in late July 2003 in the headwaters of the Toolik River after a period of heavy rainfall (Fig. S4). During the 2004 field season an NSF-supported REU student (A. Duling, University of Vermont) measured total suspended sediment concentrations (TSS) above and below the TRTK on two different dates. Results from these analyses show that the TSS levels below the thermokarst were 2 to 3 orders of magnitude higher than just above the thermokarst. Similar results were obtained from two other recent thermokarst sites we visited in the area (Fig. S5A). We also measured ammonium and phosphate concentrations above and below the thermokarst (Fig. S5B and S5C). Concentrations of ammonium and soluble reactive phosphate above the thermokarst were very low and consistent with our long-term observations from other pristine streams and rivers in the area. However, ammonium and phosphate concentrations downstream of the thermokarst were unusually high. Ammonium concentrations were among the highest we have measured anywhere in the region and phosphate concentrations were similar to the target levels we have used for our long-term experimental fertilization of the Kuparuk River (Peterson et al. 1993, Slavik et al. 2004). That research has documented numerous significant changes to the structure and function of streams exposed to these relatively high levels of phosphorus.

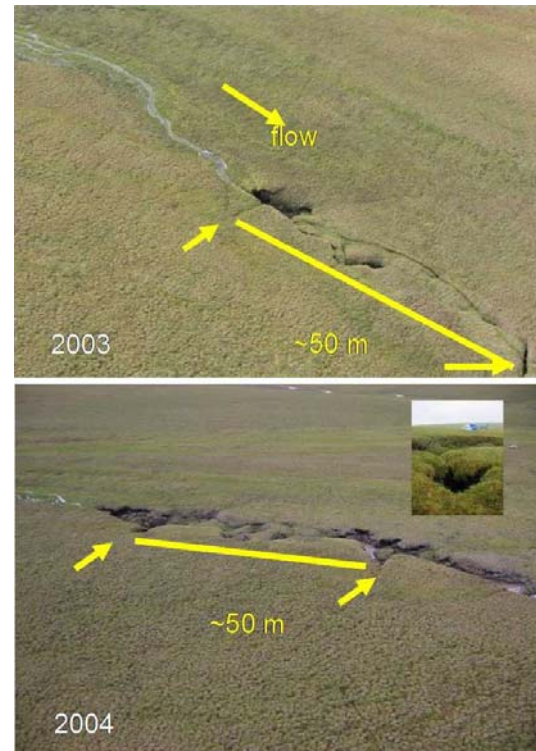


Figure S4. The TRTK site in 2003 shortly after it formed and in 2004, showing expansion. Inset in 2004 shows a helicopter for scale. (photo credits: Bowden)

It is instructive to consider the impact of this single thermokarst feature in the context of the background levels of sediment generation and transport in the Kuparuk River. Kriet et al.

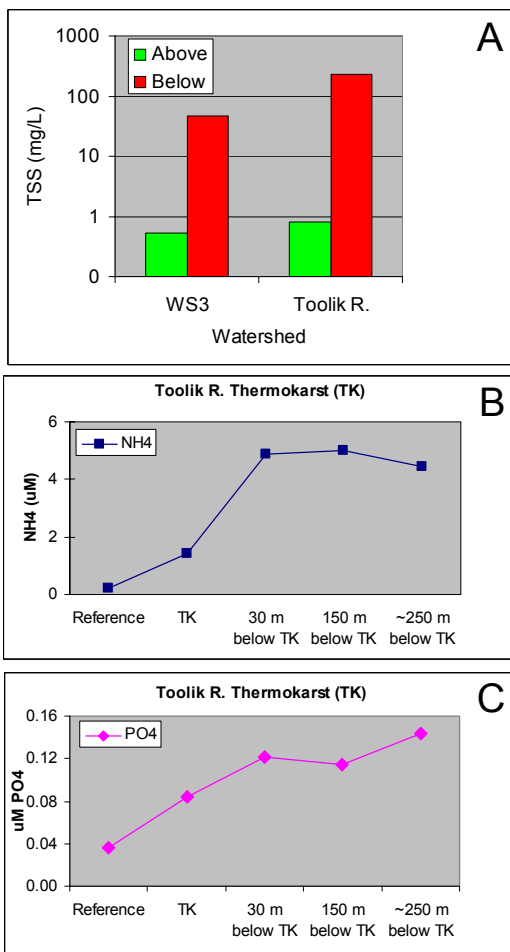


Figure S5. Sediment (A), ammonium (B), and soluble reactive phosphate (C) concentrations above and below thermokarsts in the Toolik area. (A – A..Duling, B and C, A. Green).

(1992) measured an average annual sediment yield of 1.7 t km^{-2} or 224 t for the entire 132 km^2 upper Kuparuk River basin. For comparison, we estimate that at least 2000 m^3 of soil was displaced at the thermokarst feature on the Toolik River in the first 2-3 years that it existed. If this material had a density of 2 t m^{-3} (not unusual for a silty soil) it would have yielded 4000 t of sediments (less minor volumes of organic matter and boulders). Thus, over a period of three years this single thermokarst feature in a small (0.9 km^2) sub-watershed on the Toolik River delivered 6x more sediment than would normally be delivered by the entire 132 km^2 upper Kuparuk River over the same time period.

These calculations illustrate that an apparently minor disruption on the landscape can deliver very large quantities of sediment to otherwise relatively stable streams. Despite the fact that the thermokarst features we observed in the Toolik region were relatively small and dispersed, sediment loading from these disturbance features in hilly terrain could have important impacts on stream ecosystems in the foothills region.

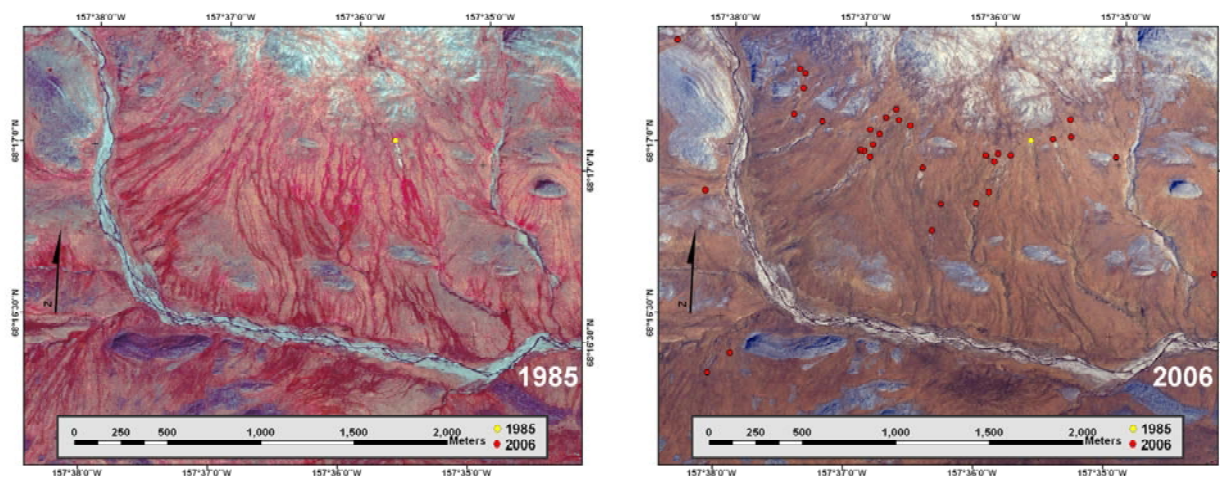
ii. Noatak Region Thermokarsts:

In summer 2006, we expanded our survey to include the Feniak Lake area within the Noatak National Preserve in mountains

immediately south of the crest of the Brooks Range (Figure S6). Helicopter-based field measurements were augmented by acquisition of five separate flight lines of air photos to develop distribution and characteristics for these features. Thermokarsts on hillslopes in the Feniak Lake area sometimes occurred in densities exceeding 20 km^{-2} . Perhaps more remarkable is the rate of increase since the early 1980s. With air photo analysis, over 70 have been found so far, compared with six for the same area in 1980 (from Alaska High Altitude Photography – AHAP - photos)(Fig. S6 Balser et al. in preparation).

These regional results show that thermokarst features in the foothills of the Brooks Range can significantly alter the loadings of sediments and nutrients to headwater stream ecosystems. Our work in the Feniak Lake region suggests that numerous new thermokarst features have developed here in the last 25-30 years. We currently need to determine whether the regional rate of thermokarst formation is actually increasing and whether the increased loadings we have

observed cause important changes to the structure and function of these headwater streams. We currently have proposals in review to pursue these questions.



“Figure S6. Thermokarst Distribution near Feniak Lake over the past 21 years. A) 1985 color-infrared airphoto showing one active Tundra Chute present (yellow dot). B) 2006 real-color airphoto showing 33 active features in the same area (red dots), with the 1985 feature retained for reference.

d. Winter Studies of Arctic Springs.

Spring-fed streams with perennial flow and near-constant water temperatures (3-7°C) are relatively common on the eastern North Slope of Alaska, where most other streams freeze solid for >6 months of the year. These streams, which represent only 1% of the region’s flowing water habitat, play two major roles in this Arctic landscape: 1) they are “hot spots” of biological productivity and taxonomic richness, and 2) they provide vital over-wintering habitat for many freeze-intolerant stream taxa and are essential to maintaining regional biodiversity. Spring streams are critical as spawning and over-wintering habitat for northern Dolly Varden char (*Salvelinus malma*), the migratory movements of which connect aquatic ecosystems across the whole North Slope landscape, from the Brooks Range to the coastal Beaufort Sea. In turn, the annual influx of over-wintering fish may be a key driver of ecological processes in the spring streams themselves. The relatively constant and moderate temperatures of spring streams result in significant year-round biological activity, despite annual fluctuations in air temperature of almost 70°C. The combination of a shallow, headwater stream habitat with relatively constant physical conditions, embedded in the intensely seasonal Arctic environment, provides a unique context for ecological research. Alex Huryn and Jonathan Benstead have just started a winter research project that will provide the basis for a predictive understanding of the ecological role of Arctic spring ecosystems by testing the following hypotheses. Heterotrophic biological activity (e.g., secondary production, ecosystem respiration) will not differ between the summer and winter. Rates of primary production, however, will be limited by light and so will differ dramatically between seasons due to annual cycles in day length, potentially forcing cycles in related ecological processes (e.g., herbivory). Finally, the movement of migrating char in and out of spring streams presumably affects nutrient supply, a process that should further accentuate seasonal patterns of ecosystem metabolism. These hypotheses are based largely on extrapolation

of summer structure and processes to assumed winter conditions, without the benefit of winter observations. They will now be tested with winter measurements and experiments.

e. Landscape Linkages.

The Arctic region supports a remarkable diversity of stream types (i.e., mountain, spring and glacier streams), which are known to differ greatly in community structure and controls on productivity (Craig and McCart 1975, Huryn et al. 2005). We are using habitat-template theory to gain predictive understanding of how spatial patterns of the diversity of stream communities affects regional patterns of biodiversity. Habitat-template theory is based on the realization that habitat provides a template upon which evolutionary processes shape the suites of life-history strategies that characterize different biotic communities (Southwood 1988). Specific environmental factors can thus be used to develop a predictive knowledge of the life-history traits required for populations able to persist in a given habitat (Scarsbrook and Townsend 1993). We are using the habitat-template approach to examine the distribution of Arctic stream invertebrates at both the landscape (Huryn et al. 2005, Stephanie M. Parker, dissertation research in progress, Heidi M. Rantala, dissertation research in progress) and catchment scales (Parker 2004, Parker and Huryn in press).

i. **Landscape Scale.** For this project, the habitat-template approach was used to explain variability among ecosystem attributes of headwater streams as a step in scaling-up current understanding of the ecology of North Slope drainages. We predicted *a priori* that substratum freezing and instability would be major determinants of the variability of stream community structure of Arctic streams. The effects of these factors were conceptualized as a 2-D habitat-template that was assessed at the landscape scale using a natural experiment based on five stream types [mountain-spring (MTNSPR), tundra-spring (TNDSPR), tundra (TND), mountain (MTN), glacier (GLC)]. Ordination procedures indicated functionally and taxonomically distinct communities for each stream type (Fig. S7). Community position within ordination biplots were

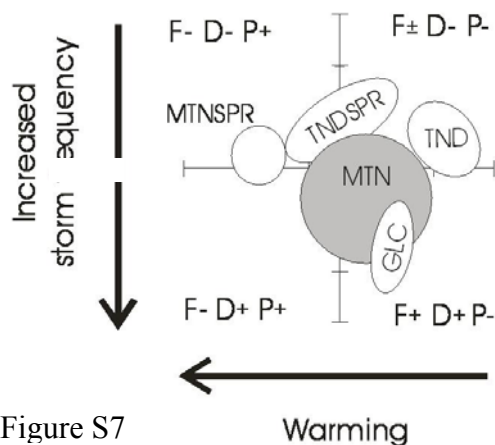


Figure S7

Figure 4. Changes in macroinvertebrate community attributes predicted in response to expected pattern of climate change during next century. D = low (-) and high (+) levels of substratum disturbance, F = low (-), high (+), and uncertain (±) probabilities of substratum freezing, P = low (-) and (+) high SRP supply. Increased precipitation and storm frequency is expected to result in increased intensities of substratum disturbance. Warming is expected to reduce the probability of substratum freezing and increase SRP supply due to melting of permafrost and exposure of previously frozen sediments to weathering. Changes in the position of macroinvertebrate assemblages within the biplot are predicted to follow the direction of the arrows. Acronyms designating stream types are explained in the text.

used to assess factors controlling its structure. Springs separated from other stream types along a gradient of nutrient concentration and freezing probability. Glacier and mountain streams separated substratum instability and freezing probability. Due to differences in sources of discharge to streams, the effects of nutrients and substratum stability could not be separated from freezing. Although many factors likely contribute to the variability of Arctic stream communities, the major determinants may be accurately conceptualized as a template structured by gradients in nutrient supply + substratum freezing and substratum instability + substratum freezing.

This template provides a basis for predicting the response of Arctic stream communities to climate change (Figure S7). Stephanie Parker and Heidi Rantala (PhD students) are currently further developing and refining the template as the basis for a conceptual model that predicts changes in Arctic stream food webs that may occur in response to

climate change. In particular, perennial springs — which are widespread on the eastern North Slope — are viewed as one possible “end point” toward which the communities of Arctic streams may converge as climate warming proceeds (i.e., longer open water seasons, more under ice flows, more weathering-derived minerals and nutrients, etc). The study of springs provides an excellent opportunity to understand how climate warming may affect Arctic headwater streams.

ii. Catchment scale research (Parker 2004; Parker and Huryn 2006). Stephanie Parker (MSc student with Alex Huryn) focused on the effects of substratum movement and water-column freezing on the communities of adjacent mountain and spring tributaries of the Ivishak River (i.e., “Ivishak Hot Spring” 69° 01’ N, 147° 43’ W). She predicted that the mountain stream would freeze during winter and have significant bed movement during summer while the spring stream would have perennial flow and negligible bed movement. She further predicted that the mountain stream would be inhabited only by taxa able to cope with both freezing and frequent bed movement. As a consequence of these constraints, it was anticipated that the mountain stream would have a food web with lower trophic height and connectance than the spring stream.

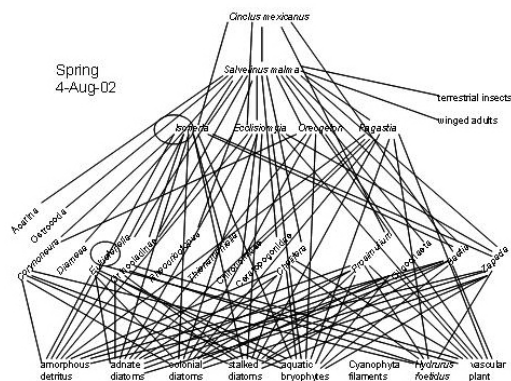


Figure S8 Connectance food web for Ivishak Spring stream. Algal taxa are summarized as functional groups to simplify the food web diagrams.

difference between streams, however, were the contrasts in consumer biomass and the proportion of biomass contributing to different trophic groups (Figure S9). These contrasts indicate fundamental differences in food-web function between perennial spring communities and other Arctic stream types, particularly in the relative roles of predation in shaping energy and nutrient dynamics.

The results of these studies are particularly significant advances to understanding of Arctic ecosystems for two reasons: 1) they show that perennial spring streams of the North Slope almost certainly have unusually high levels of secondary production, even when compared to temperate or tropical streams, and 2) they show unusually high ratios of predator to prey biomass, compared with other types of Arctic streams. These

The results of Parker’s study showed that the mean food-chain length was longer in the spring stream (~3) compared with the mountain stream (~2). This result was due primarily to the presence of a population of American dippers (*Cinclus mexicanus*), a predacious semi-aquatic passerine bird, in the spring stream (Figure S8). Perhaps the most striking

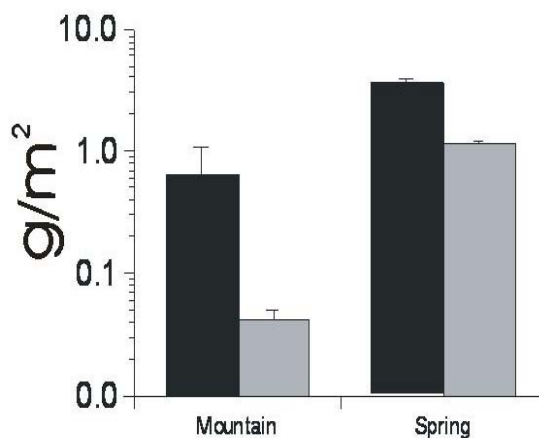


Figure S9 Macroinvertebrate biomass measured in Ivishak mountain and spring streams. Primary consumer biomass is indicated by black bars. Predator biomass is indicated by gray bars. Biomass is reported as dry mass. Error bars = +1 standard error.

findings indicate that processes controlling and shaping food web function in Arctic spring streams are fundamentally different from those of most other stream types, whether in the Arctic or elsewhere.

f. Stream-Lake Interactions.

Does stream fish migration provide a key trophic subsidy to top predators in overwintering lakes? Stream dwelling fishes in the Arctic face an important environmental challenge because rivers are frozen solid during the long winter. Thus, fish must move from streams and rivers into lakes or springs where some water remains unfrozen. However, the number of over-wintering areas is restricted by geology and large numbers of stream dwelling fish concentrate in those few areas, often traveling long distances. Lakes that have enough under-ice water to support a migratory population of fish usually support resident populations of piscivorous fishes. Thus while migrating from rivers to lakes is necessary for survival over the winter, fish may experience high predation in the overwintering habitat.

We have studied the migration of grayling from the Upper Kuparuk River into Green Cabin Lake for many years in order to address two questions. 1. What is the subsidy to lakes from streams provided by Arctic grayling migration? 2. What is the impact of the migration of arctic grayling on lake char, lake food webs and lake physical conditions?

In the Kuparuk River, we estimate that approximately 6,000 to 10,000 adult grayling (>29 cm TL) spend the winter in the headwater lake (Fig. S10). The number of smaller fish that overwinter is not as well known, but in one day over a thousand migrating small fish (< 20 cm) entered the lake (Deegan, pers. obs.). Although we have documented the large number of fish that migrate to spend the winter in the headwater lake of the Kuparuk River, we do not know

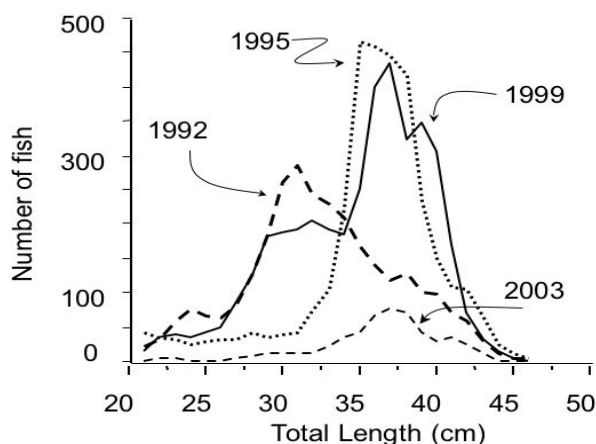


Figure S10. The number and size of grayling migrating into the headwater lake (Green Cabin Lake) varies among years as cohorts from strong year-classes mature.

their impact on lake environmental conditions and productivity. However, calculations based on the number of migrants and literature values of grayling respiration indicate that grayling metabolism alone may be sufficient to consume a significant fraction of the available oxygen under ice during the winter. If this turns out to be accurate, the fish will be important as suppliers of limiting nutrients to the lake as well. Lake char readily feed on grayling but further research is needed to determine to what extent these fish contribute to the support of the large population of lake char in this headwater lake? A proposal has been submitted to OPP to pursue the next steps in this research.

g. Land-Ocean Linkages.

The climate of the arctic is changing and every week Arctic climate warming, melting ice, and polar bears are in the popular news. The Arctic LTER site has shared in this remarkable warming that has encompassed most of the Arctic and Subarctic since the 1970s (Serreze 2000).

The wide-spread warming has been accompanied by a remarkable series of positive values of the NAO (North Atlantic Oscillation) and these two factors have impacted the pan-arctic freshwater cycle through increases in precipitation and river runoff, glacier and ice sheet melt and sea ice attrition (Peterson et al. 2006). The loss of snow and sea ice cover itself amplifies the high-latitude warming and accelerates the atmospheric moisture flow from ocean to land. The observations of progressive changes in arctic climate and the hydrologic cycle lead us to ask if the biogeochemical links between the arctic watershed and the Arctic Ocean are also changing.

The Arctic Ocean is the most landlocked ocean on Earth and runoff from the pan-arctic watershed exerts strong control over ocean circulation and biogeochemistry. Our SNACS (Study of the Northern Alaska Coastal System) project led by Marc Stieglitz investigates the linkage between hydrologic variables and the fluxes of nutrients and organic matter (constituents) from the North Slope of Alaska to the Beaufort Sea. This work is part of an integrated Arctic Systems Science (ARCSS) program focusing on land-shelf linkages that includes coastal erosion, shelf oceanography and Bowhead whale ecology as well. The primary question for our project is: What are the relationships between discharge and constituent concentrations in the three largest North Slope basins (Kuparuk, Colville, and Sagavanirktok) and have these relationships changed over the past 25 years of rapid warming in the Arctic? Unfortunately long time-series of chemical concentration data are very rare for arctic rivers. However by synthesizing the long-term LTER data (1978 to present) from the upper Kuparuk River, McClelland et al. (2007) showed that the export of NO_3 increased several fold in the past 15 years (Fig. S11). Sampling these rivers at the coast during 2006 has shown that the spring runoff peak delivers to the coastal ocean large quantities of dissolved organic carbon that is much more labile than carbon exported during the rest of the season.

The PARTNERS project of the ARCSS Freshwater Initiative is examining the land-ocean linkages via river biogeochemical fluxes at the larger pan-arctic scale. Here the primary mission is to measure biogeochemical tracers of freshwater that can be employed in catchment and Arctic Ocean modeling of the freshwater cycle. The six largest rivers have distinctive chemical fingerprints that allow us to identify the sources of freshwater even after great dilution over several years in the Arctic Ocean-North Atlantic circulation. We also measure the large fluxes of terrestrial organic matter that have a significant impact of the carbon budget and metabolism of the Arctic Ocean (Cooper et al. 2005, Raymond et al. 2007). In synthesis research on the carbon cycle we are using the arctic river carbon flux data to test continental-scale models of carbon balances and provide substrate for microbial metabolism in the MIT ocean carbon cycle model.

Overall, it has been remarkable that the approaches to small ecosystem analysis (mass balance, hydrologic fluxes, biogeochemical processes, tracers and modeling) we have developed over decades at the Arctic LTER site have proven so useful recently in understanding the Arctic as a linked atmosphere-land-ocean System.

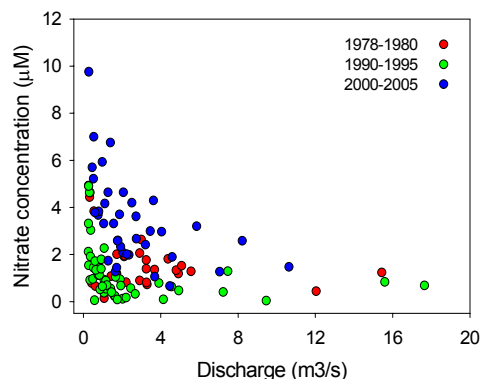


Figure S11. Changes in the nitrate-discharge relationship for the Kuparuk River from 1978-2005.

4. LAKES RESEARCH

The arctic lakes research program involves monitoring of a suite of lakes to detect environmental change over time, intensive studies of specific lakes to understand ecosystem processes, and long-term whole-lake experiments to assess the response to changing environmental conditions. We employ landscape methodologies and simulation modeling to expand the inference of small-scale analyses to ecosystems and watersheds.

a. Monitoring of arctic lakes

Toolik Lake serves as our primary long term monitoring site for lake systems. Thermal structure, nutrient, and major ion measurements have been made in the water column for the past 30 years. The average July temperature of Toolik Lake at 2 m depth varies greatly among years, but shows no overall significant warming trend during the 1975-2005 sampling period (Fig. L1).

During most of our study period, the Arctic Oscillation and related Pacific Decadal Oscillation (Mantua et al. 1997) have been in their high phase with occasional shifts to a low phase. These atmospheric pressure oscillations exert a small but measurable influence on inter-annual thermal conditions of the lakes in the Toolik region.

Observations indicate that mid-summer lake temperatures are influenced by local and regional climatic events as opposed to long-term warming trends or decadal oscillations. These differences between years are important for vertical exchanges and the fate of incoming stream waters which introduce phytoplankton, bacteria, and nutrients from higher in the watershed (MacIntyre et al. 2006).

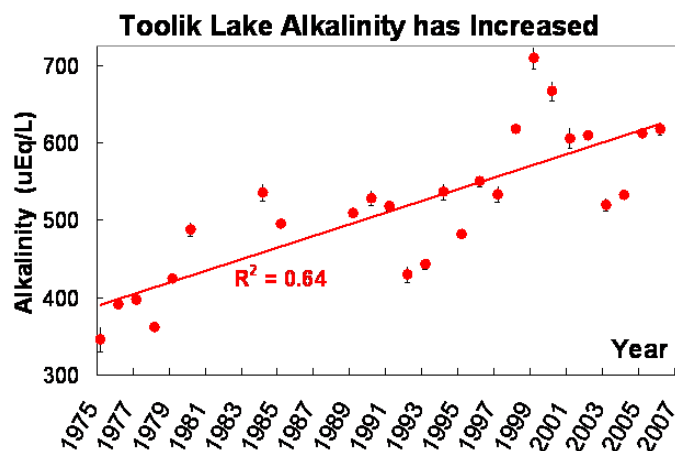


Fig. L2. Total alkalinity in Toolik Lake at a depth of 3 m, 1990-2003. Linear regression indicated a significant increase in alkalinity during this time period. Date explained 36% of the variation in alkalinity.

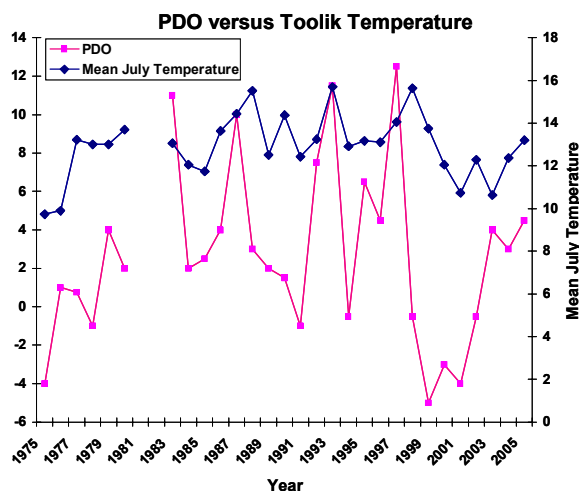


Fig. L1. Index of the North Pacific Decadal Oscillation (PDO) and mean temperature ($^{\circ}\text{C}$) of Toolik Lake at a depth of 3 m during July from 1975-2005. No significant increase in summer temperature of the lake was apparent. Higher values of PDO do correlate with warmer coastal ocean temperatures off the western coast of Alaska and correspond to higher temperatures in Toolik Lake. Linear regression of PDO versus mean lake temperatures was significant with PDO values explaining 18.6% of the variation in temperature of Toolik Lake.

Although mid-summer surface temperatures in Toolik have not increased in recent years, the alkalinity of lake water has increased substantially (Fig. L2). The increase in lake alkalinity is concurrent with changes in stream chemistry, indicating a deepening of the summer thaw depths in soils of the Toolik catchment (see Land-water section for detail, Fig. LW-11 and LW-12).

Long term records of nutrient, other solutes, chlorophyll and zooplankton in Toolik and 14 other monitoring lakes show little overall

trend in changes in the limnology in the LTER region from 1975 to the present. Lake morphometry explains much of the variation among lakes (Table L1) with small, shallow lakes containing high concentrations of solutes and chlorophyll compared with deeper lakes with less sediment-water contact. The shallow lakes are polymictic during summer and generally fishless due to freezing and low oxygen concentration during winter. The fishless lakes support high biomass of zooplankton and benthic invertebrates (O'Brien et al. 2004, Burkart 2007). The deeper lakes in the region are extremely oligotrophic with water column nutrient concentrations at near detection and correspondingly low biomasses of phytoplankton, zooplankton, and fish.

Our current research focuses on understanding spatial and temporal variability in lake characteristics and in examining how environmental disturbance influences lake condition. We examine these issues through process studies at particular sites and through long-term, large-scale experiments designed to assess how environmental change will influence lake ecosystems.

b. Process Studies

Local meteorological effects determine thermal stratification patterns and the degree to which physical mixing processes transport nutrients within a lake. Process studies have been undertaken in recent years to decipher the effects of winds and stream inflows on the primary productivity of Toolik and Lake E-5 (MacIntyre et al. 2006; Evans 2007). During the last seven years, we have been fortunate to capture some extremes in summer stratification. In Toolik Lake thermal structure varied considerably between 2003 and 2004 (Fig. L3). Maximal water temperatures were near 16°C in Toolik Lake in the cooler year 2003, and metalimnetic thickness ranged from 1 to 4 m. In contrast, in 2004, temperatures were over 18°C for extended periods and the metalimnion was 4 to 8 m thick. These two years demonstrate contrasting stratification dynamics. Wind and rain events after 20 July in 2003 were sufficient to cause rapid deepening of the mixed layer and further thinning of the thermocline in Toolik and loss of stratification in Lake E-5 (E-5 data not shown). While cooling occurred after 20 July in 2004, the thickness of the metalimnion did not diminish and thermal stratification in Lake E-5 persisted past mid-August.

The differences in thermal stratification and mixing in warm versus cold years affected vertical transport of nutrients (MacIntyre et al. 2006). Primary productivity increased after wind mixing (Evans 2007) due to nutrients being mixed from depth up to the surface. Nutrient and particulate delivery is time-dependent in arctic lakes because the incoming stream waters decrease in temperature during storms due to cooler air temperatures and their interaction with cold soils. The temperature of the inflows determines density and directs the water into different layers in the lakes. This inflow water has different concentrations of solutes and particulates. Therefore, when injected at different depths in the lake the inflows can lead to the development of different rates of biological processes (MacIntyre et al. 2006, Rueda et al. in prep). In addition to particular storm events, inter-annual differences in thermal stratification also affect many biological processes. For example, during the warm summer of 2004, grazing rates of crustacean zooplankton increased by 30% compared to 2003 values (Burkart 2007). Higher epilimnetic temperatures also shorten cladoceran egg development time, resulting in increased population growth rates of these zooplankton taxa.

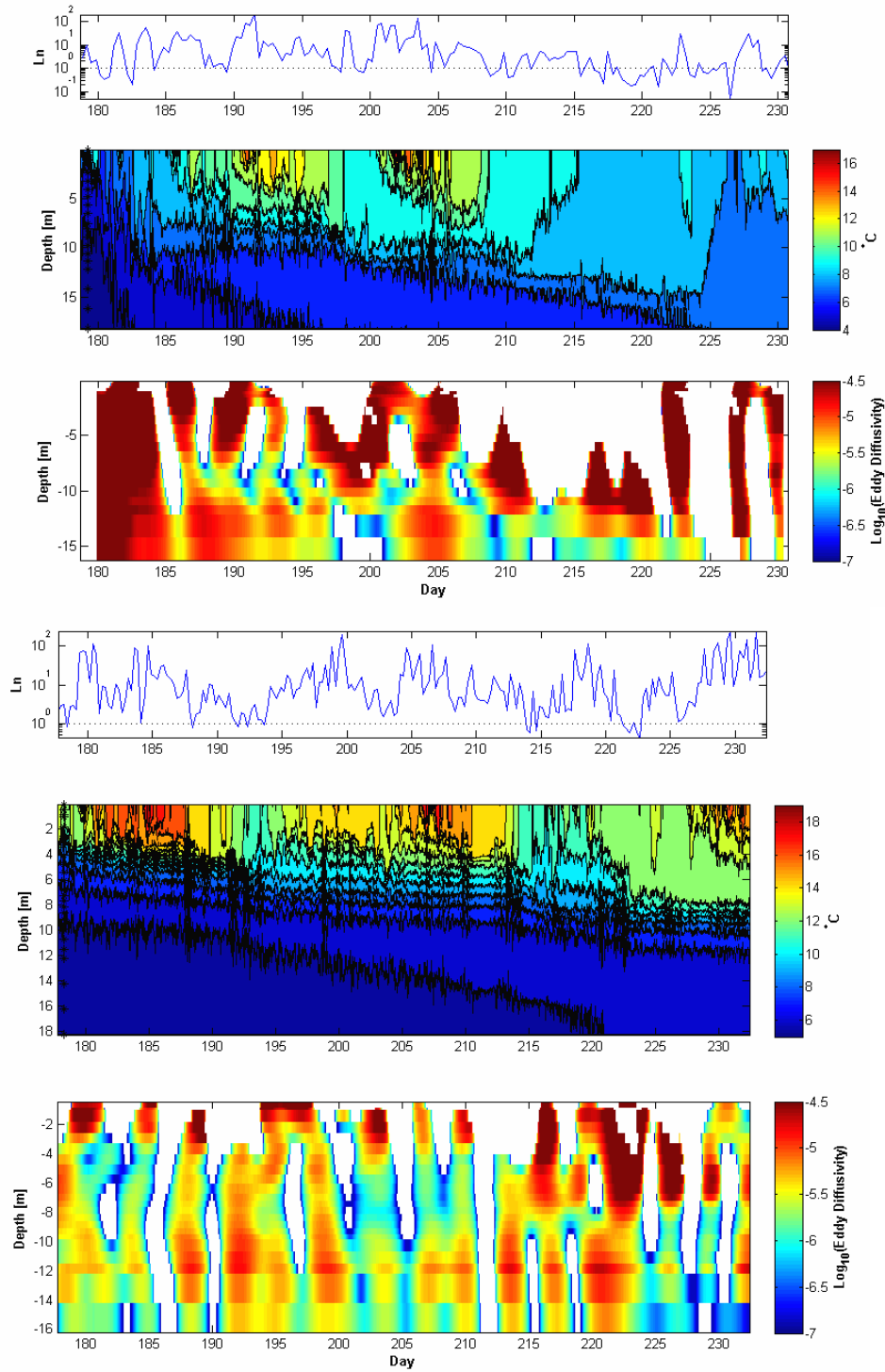


Figure L3. Time series of Lake number (LN) which indicates the degree of non-linearity of the internal wave field, isotherms, and coefficient of eddy diffusivity computed beginning shortly after ice off through mid-August (2003, top 3 panels; 2004, bottom 3 panels). Lake numbers are filtered over 4 hours, 1°C contours for isotherms, Kz are based on filtering over a 3 day time scale to avoid contamination by internal waves and are on a logarithmic scale. White gaps below the metalimnion indicate no change in heat content and diffusion at molecular rates. White areas above the metalimnion indicate cooling periods in which Kz increases to $\sim 0.01 \text{ m}^2 \text{ s}^{-1}$ based on model results (F. Rueda, personal communication) and our calculations from surface energy budgets (e.g., Banerjee and MacIntyre 2004). (S. MacIntyre, unpublished data).

c. Long Term Experimentation in Lakes

Previous results of long-term high-level nutrient addition experiments demonstrated the severe nutrient limitation typical of arctic lakes (O'Brien et al. 1997). These experiments, which demonstrated large changes in phytoplankton production, lake oxygen concentrations, and organisms occupying higher trophic levels, involved nutrient additions more typically associated with local human activity (Carpenter et al. 1998). Recent increases in thermokarst activity and the potential mineralization of tundra soils with increasing nutrients such as P released to surface waters (Hobbie et al. 1999, Brown et al. 2002, Keller et al. 2007) focused our research on impacts of low levels of nutrient additions to lakes. That is, at levels of nutrient loading that will likely occur with these changes to the arctic landscape. In 2001 we began a long-term experiment designed to assess the impacts of low-level increases in nutrient loading likely resulting from landscape disturbances to Lakes E-5 and E-6 near the Toolik Field Station. These lake fertilizations increase ambient nutrient loadings by approximately 50% and include a lake deep enough to stratify in summer (Lake E-5) and a shallow polymictic lake with greater potential for frequent biogeochemical interactions between pelagic and benthic regions (Lake E-6).

Photosynthesis increased dramatically in the fertilized lakes during July and August (Fig. L4a). Primary production was twice as high in both E-5 and E-6 by 2002 than prior to fertilization and at least three times as high beginning in 2004. Toolik Lake had a slightly negative slope for the time vs. photosynthesis regression in both July and August (the unmanipulated "control") whereas E-5 and E-6 both had positive slopes in these months (Fig. L4b and L4c). These differences reflect the importance of increased nutrient supply for maintenance of productivity in arctic lakes. The E-5 increases in production (slope of production over time) were greater ($38.5 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ y}^{-1}$ and $22.8 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ y}^{-1}$ for July and August, respectively) than those for E-6 ($18.9 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ y}^{-1}$ and $12.7 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ y}^{-1}$ for July and August, respectively). This result supports our initial hypothesis that the stratified lake would respond more strongly to fertilization as nutrients would not be lost to the sediments. As fertilization began in

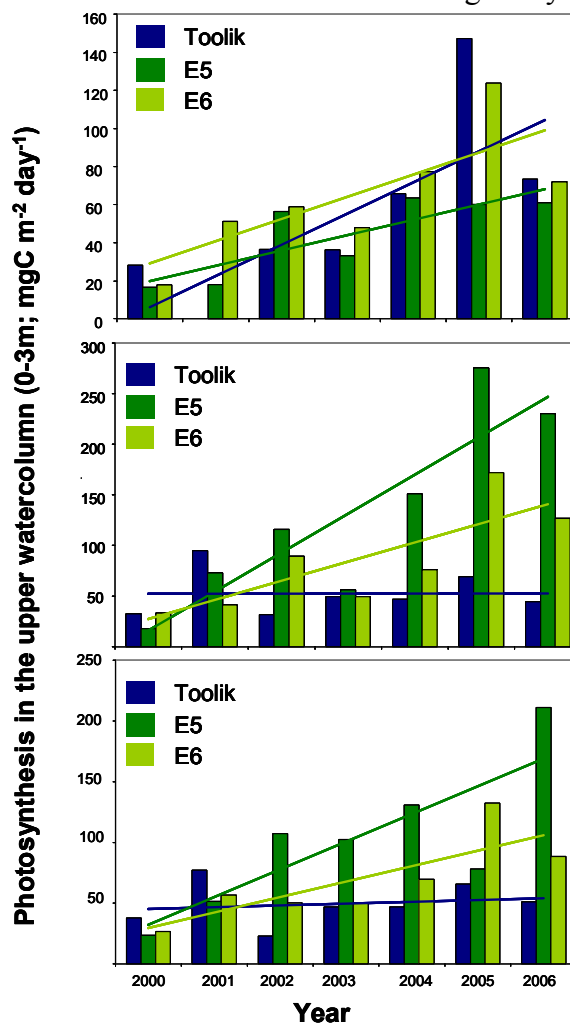


Figure 4: Average monthly photosynthesis in the epilimnion ($Z < 3 \text{ m}$) of Toolik Lake and lakes E5 and E6 for years 2000-2006. Top panel is June, middle July, and bottom panel August of each year. Nutrient (N and P) were continually added to lakes E6 and E6 during July and August of years 2001-2006.

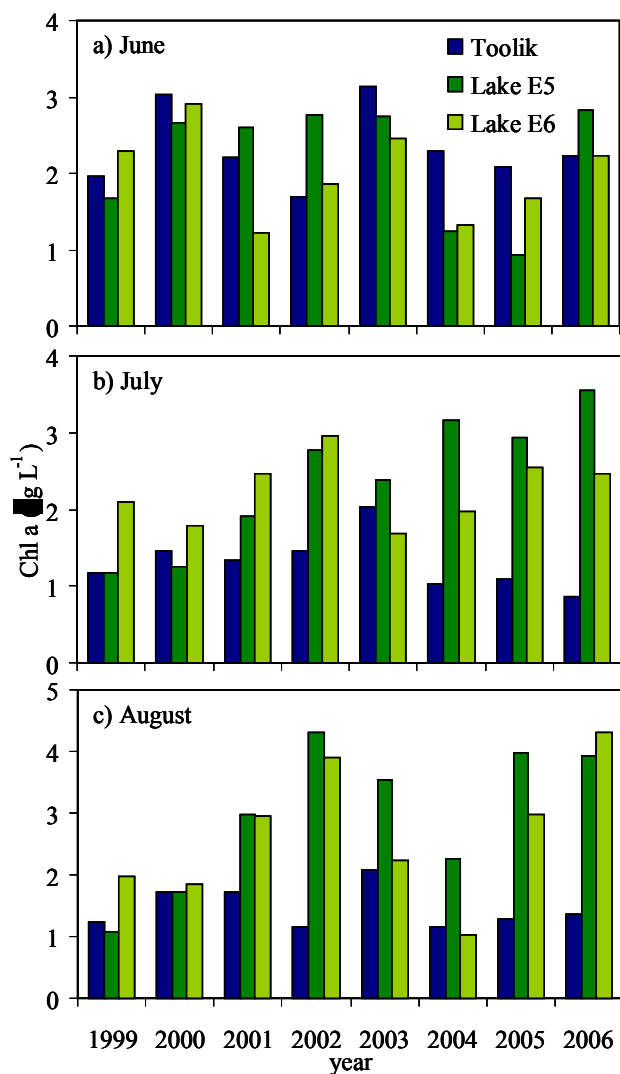


Fig. L5: Average monthly chlorophyll *a* concentration in the epilimnion ($Z < 3$ m) of Toolik Lake and lakes E-5 and E-6 for years 1999-2006. Nutrients (N and P) were continually added to lakes E-5 and E-6 during July and August of years 2001-2006.

the beginning of July, the June data are indicative of any carryover of nutrients from fertilization in all years.

In addition, the inter-seasonal variability of photosynthesis was elevated in the fertilized lakes relative to Toolik Lake. The coefficient of variation of average July photosynthesis (years 2001 - 2006) was 58% for E-5 and 56% for E-6, compared to 40% for Toolik. Differences in thermal stratification and the resulting timing of fluxes between the upper and lower water column within and across years help explain the variability. For instance, primary productivity in E-5 in July 2003 was lower than in July 2004 as were chlorophyll concentrations. In 2003, rates of mixing in July were high leading to flux of nutrients and biomass to the lower water column. After the cooling in late July 2003, both nutrients and chlorophyll concentrations increased in the upper water column and primary productivity increased. Average epilimnetic chlorophyll *a* concentration responded less strongly to lake fertilization than did photosynthesis, but followed a similar pattern of response (Fig. L5).

Response of benthic algae to fertilization differed between the lakes (Fig. L6). In the deeper lake E-5, benthic chlorophyll concentrations only increased in 2003 and may have been a response to the increased nutrient fluxes to the lower water column in that year. There was no sustained increase in benthic primary production. At

the deeper site in E-5 (5-7 m) GPP (gross primary production), which had been low before fertilization, went to zero (data not shown). Benthic primary production doubled and benthic chlorophyll tripled in the shallow lake E-6 after fertilization. We believe that differences in the response of the two lakes were due to changes in light and nutrient availability. In E-6 benthic producers had access to both high light and increased nutrients with fertilization, whereas in the deeper E5 there was less light penetration to benthic communities.

In addition to increases in benthic primary production, addition of nutrients to lakes E-5 and E-6 greatly reduced rates of benthic nitrogen fixation in benthic regions of the lake (Gettel 2007). The increased availability of nitrate and ammonia in the fertilized lakes reduced rates of nitrogen fixation by about 70% within two years of fertilizer addition (Gettel 2007).

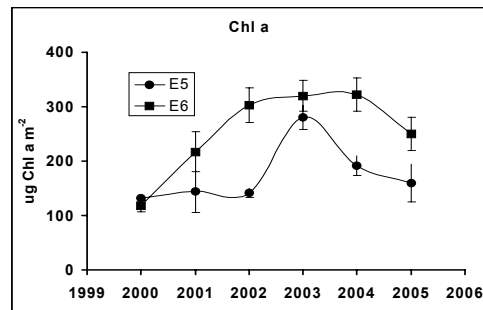
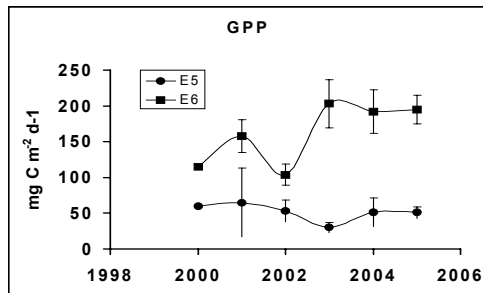


Fig. L6. (Top) Rates of carbon fixation (gross primary production in $\text{mg C m}^{-2} \text{d}^{-1}$) measured in benthic chambers placed at 3 m in lakes E-5 and E-6 during July of 2000-2005. (Bottom) Measurement of chlorophyll a ($\mu\text{g m}^{-2}$) in benthic cores collected from lakes E-5 and E-6 at 3 m during July of 2000-2005. Data from Gettel (2007); and Giblin unpublished.

population in our reference lake has significantly increased during the time period of our experiment (a substantial new cohort), indicating that our sampling protocols are sufficient to detect change in these fish populations. Analysis of annual growth rates from marked char in these populations indicated that char density has a strong effect on individual growth. This effect of competition suggests that food availability may limit the production of Arctic char in these lakes, and provides the potential for response of char to nutrient additions to lakes. In addition, it is clear that fertilization experiments must be long term to capture fish dynamics, especially the impact of strong cohorts of fish which may have lasting impacts on lake food webs.

Our data indicate that solutes and particulates were transported from the pelagic zone to the benthic boundary layer. To better understand the conditions that affect benthic-pelagic linkages and to assess their importance to lake productivity, we added small

The response of organisms occupying higher trophic levels to increased levels of primary productivity in the lakes has been mixed. Increased biomass of zooplankton was observed in E-5 during warm summers (2002, 2004 and 2005, 2006), but not in cool summers (2001, 2003) (Fig. L7). The difference between zooplankton biomass in fertilized and reference lakes was dependent on thermal conditions, with the greatest response of zooplankton biomass to fertilization occurring in the warmest summers. Arctic char are present in Lake E-5 but to date no increases in either individual growth rate or abundance have been observed. A similar char

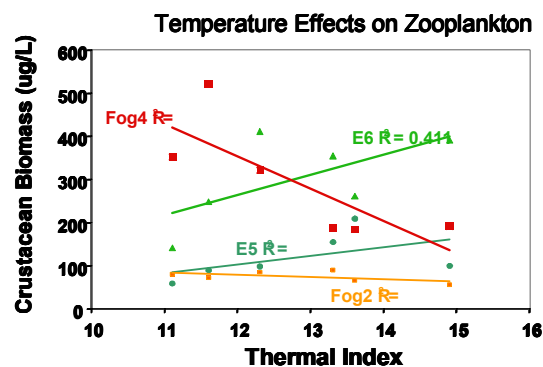
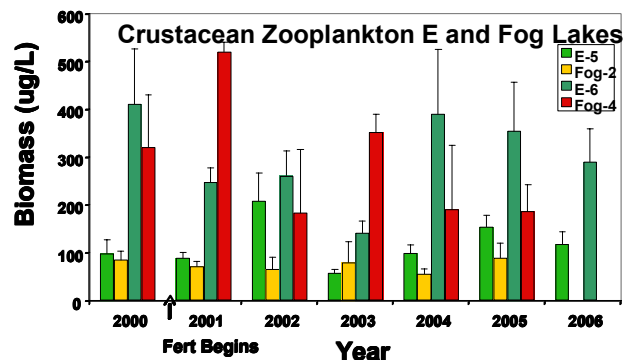


Figure L7. Top – Biomass of crustacean zooplankton in E and Fog Lakes during summers of 2000-2006. Mean (+SE) of samples collected from 0-3 m depth strata are shown. Fertilization of Lakes E5 and E6 began in early from 2001-2006. Fog2 and Fog4 served as reference systems. Bottom – Mean crustacean biomass of epilimnetic zooplankton plotted as a function of the thermal index (mean epilimnetic temperature in July) of all four lakes after fertilization was initiated in 2001.

quantities of ^{15}N to our nutrient additions to serve as a tracer for trophic transfers among food web components. Time course uptake kinetics for ^{15}N indicated that phytoplankton and pelagic consumers benefited from the nutrient additions very quickly each year. The delay in increases in ^{15}N in benthic consumers and fish suggest that sedimentation of phytoplankton from the pelagic zone fuels benthic productivity (Fig. L8). This new result augments our understanding of the dynamics and complexity of lake food webs. Previous research indicated that almost all of the fish production in arctic lakes derived from benthic invertebrates. Results from our experiment indicated that the benthic invertebrates are fueled by pelagic primary production to a much greater extent than was previously realized (Burkart 2007).

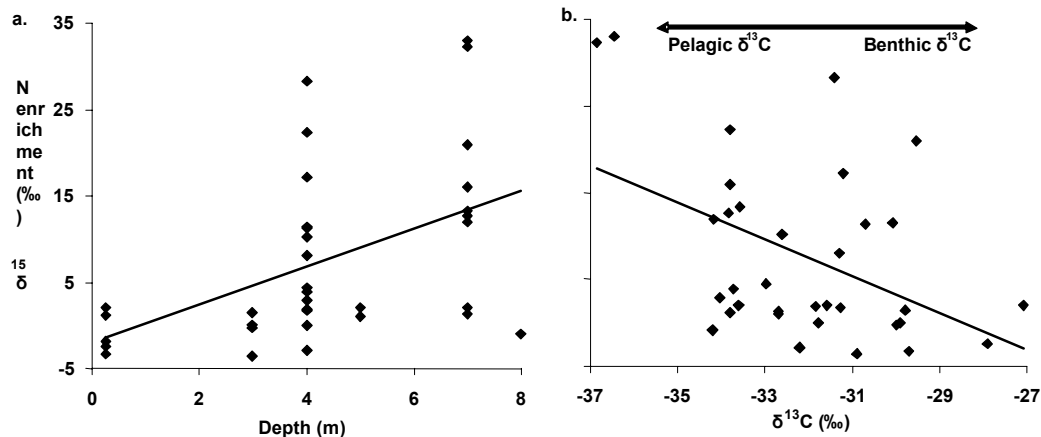


Fig. L8. $\delta^{15}\text{N}$ -tracer enrichment of chironomids versus a) depth and b) $\delta^{13}\text{C}$ background of chironomids in Lake E-5 following tracer additions during years 2002 through 2004. Step-wise linear regression indicates that date explains most of the variance in ^{15}N -tracer enrichment (see Fig. L3), while depth or ^{13}C can be used to explain an additional 10% of the variance ($p < 0.05$). For comparison, horizontal arrows represent inferred diet sources based on two-source $\delta^{13}\text{C}$ mixing models.

In addition to projects directly related to the LTER, other lake studies have focused on landscape linkages within watersheds, and within specific lakes. The Geomorphic Trophic Hypothesis project, led by A. Hershey, has examined effects of landscape topography on lake characteristics. The position of lakes on the landscape affects grayling growth and distribution (MacKinnon and Luecke 2007), patterns of biodiversity (Beatty and Hershey 2006), and biogeochemistry (Hershey et al. 2006). This study has also identified how the morphometry of lakes affects the spatial distribution of methane production (Hershey et al. 2006), trophic transfer within lake food webs, and the relative importance of benthic and pelagic production within a lake.

New insights on benthic-pelagic linkages allow us to generalize our results to other lake ecosystems. A simulation model of arctic lake food webs that explicitly includes both pelagic and benthic components indicates that excretion of nitrogen by benthic invertebrates rivals excretion rates attributed to zooplankton (Luecke and Hershey, submitted). Results from this simulation model indicate that the combined excretion from benthic and pelagic consumers can provide all of the nitrogen needed for primary producers in the lake (Fig. L9). Also, the presence of fish in deeper lakes like E-5 impacts phytoplankton production through the fish effect on invertebrate excretion rates, resulting in increased amounts of phytoplankton and reduced amounts of benthic chlorophyll in lakes with fish.

The combination of long-term monitoring, process-based studies, and whole-lake experiments provides a platform for synthesis of the physical, chemical, and biological interactions that define the structure and function of arctic lakes. Results of our research program demonstrate how regional and local meteorological events create the thermal structure of lake ecosystems. This thermal regime affects the distribution of nutrients as well as the rate of supply of nutrients to primary producers and, therefore, either increases or decreases the response of aquatic organisms to increased rates of nutrient additions. Results from these investigations suggest that the combination of climate warming and increased nutrient supply to lakes will enhance trophic connectivity and increase the degree of benthic-pelagic coupling in arctic lakes. This model of the linkages between climate, nutrient regimes, and food web interactions provides the foundation for future investigations of arctic landscapes.

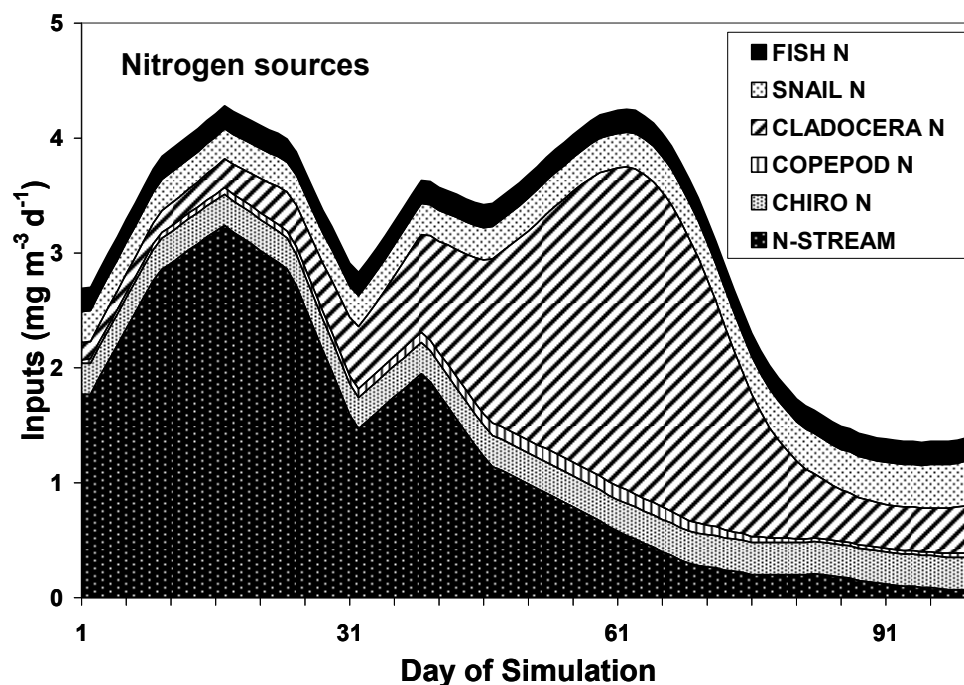


Fig. L9. Sources of dissolved inorganic nitrogen loading in arctic lake simulation model. Day 1 corresponds to mid-June (shortly after ice off). Nitrogen sources are dominated by stream inflows during first month of the simulations and by excretion from pelagic and benthic invertebrates after mid-July (Luecke and Hershey, submitted).

Table L-1. Lakes near the Toolik Field station that are part of the long term monitoring program. Small lakes are less than 5 m maximum depth and typically devoid of fishes, medium sized lakes have maximum depths of 5-10 meters, and deep lakes have depths of greater than 10 m.

Lake Size		
<u>Small</u>	<u>Medium</u>	<u>Large</u>
E-6	N-2	I-4
Fog-4	I-8	I-1
S-7	I-3	I-2
I-6 HW	I-Swamp	I-5
E-1	NE-9B	I-6
	S-11	I-7
	E-5	NE-12
		N-1
		Fog-2

5. LAND-WATER INTERACTIONS RESEARCH

The simple idea of a hydrological catchment as a study ecosystem has provided a clear framework of biogeochemical cycling within and between ecosystems for several decades. Yet it has proved an extraordinary challenge to measure the outputs of energy and biochemical elements and relate them back to the underlying processes controlling the structure and function of the terrestrial ecosystem. We still understand little about the complex dynamics and rates of production of dissolved materials on land and their delivery to surface waters. For example, a review of 42 studies of DOC and DON concentrations and fluxes in temperate forests found that lab and field studies differed greatly in their results and that site-specific controls such as temperature or C:N ratios were rarely evident at regional scales (Michalzik et al. 2001). We do know that across biomes the climate and vegetation influence the production of materials moving from land to water, and precipitation and hydrology are strong drivers of material exports and can govern the response of receiving surface waters. Using our conceptual model of these controls (Figure LW-1), we are asking research questions about each of them and synthesizing our observations in part by determining how these processes scale in space and time across landscapes. We have also begun to incorporate these concepts and measurements into mathematical models, necessary for extrapolations and predictions of how the arctic system operates and how it will respond to change. The sections below outline some background and highlights of our major research questions and results within the framework of land-water interactions.

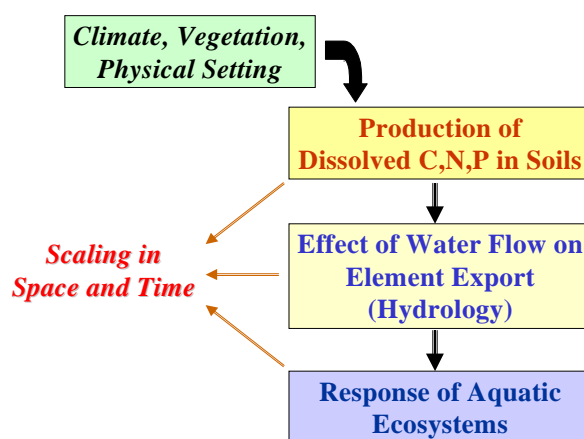


Figure LW-1. Conceptual model of controls on land-water interactions.

The main conclusions are: **(1)** Soil production and especially root production of dissolved materials that can be exported to surface waters is extremely high, but the net export is low and thus processing by microbes must be substantial; **(2)** Microbial community composition and activity are strongly linked and there are distinct and consistent patterns of microbial processing at key points in terrestrial and aquatic ecosystems across the landscape; **(3)** Interactions between different ecosystems along the toposequence of hillslopes are critical for understanding how process-level knowledge can be scaled-up to answer questions on catchment and regional biogeochemistry; and **(4)** Despite no evidence of increasing thaw depth near Toolik Lake, observed changes in the geochemistry of lakes and streams over time can only be explained by a melting of permafrost and thus systematic changes in thaw depth in the basin due to global warming.

a. Production and fate of dissolved materials on land.

Our initial research in land-water interactions for the Arctic LTER focused on carbon cycling, and set the stage for current research directions. We found that the C loss from the entire Kuparuk Basin via streams and lakes is around 4 g C m^{-2} of land surface per year, with almost one third of this loss as CO_2 and CH_4 released from surface waters directly into the atmosphere (Figure LW-2). This lateral loss of C is substantial and prior to this was

unaccounted for in terrestrial budgets. Globally, this movement of gases to the atmosphere from lakes and streams is about 25% of the total global C flux from land to the oceans through rivers.

On the basis of these findings we examined in detail the production rates of dissolved C in soils, and applied a ^{14}C tracer to intact tundra ecosystems. The findings were surprising in that the production of DOC from plant roots alone is extremely high, from 1-4 g C m^{-2} per day, whereas DOC export is only 2-3 g C m^{-2} per year! Our conclusion is that microbial processing

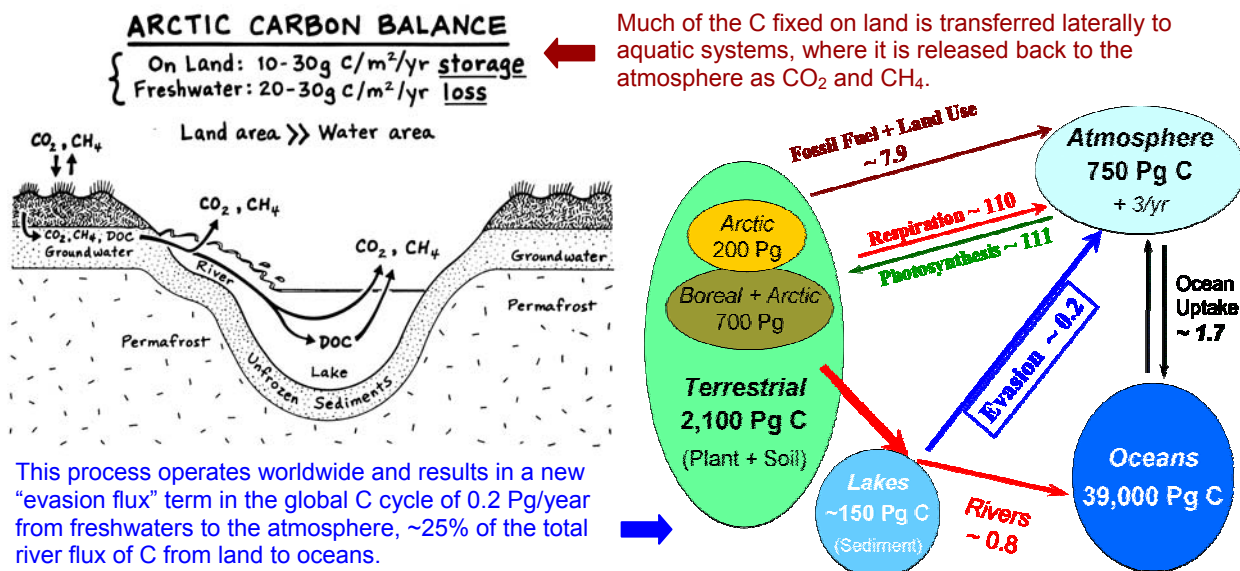


Figure LW-2. Schematic showing land-water transfer paths of C gases, and importance in the global C cycle (from (Kling et al. 1991, 1992; Kling 1995; Reeburgh et al. 1998).

of this C must be substantial, ~two orders of magnitude higher than the net catchment export (Judd and Kling 2002, Kling, Nadelhoffer, Sommerkorn, Rastetter unpublished). And this importance of microbial processing as DOM moves from land to oceans is not restricted to the Arctic; consider that in most terrestrial systems NPP is very large, 100s of g C m^{-2} per year, and yet the NEP is usually near zero and dissolved export averages only ~6 g C $\text{m}^{-2} \text{y}^{-1}$ worldwide (Hope et al. 1994). Thus the huge difference in terrestrial C production and aquatic export must be due mainly to microbial processing in soils. Given this strong biogeochemical influence across landscape scales, we can ask questions about the spatial pattern of microbial processing – where are the control points, and what microbes are responsible.

b. Microbial processing across the landscape.

The influence of land-water transfers of nutrients and organic matter is a dominant aspect of aquatic ecology; microbial transformations of these materials underlie production, respiration, and atmospheric gas-exchange in ecosystems. But consideration of how these processes are linked and interact across the landscape is relatively new and requires an integration of concepts in microbial and landscape ecology. For example, we must consider the congruence of ecotones and spatial boundaries of ecosystems with the rates of microbial activity, as well as the biogeographical diversity of microbes and the time scales that microbial populations adapt by changing their physiology and by changing population frequencies. As described below, we found several distinct patterns of microbial species and processing rates in terrestrial and aquatic ecosystems across the landscape.

Arctic ecosystems differ consistently in landscape position, plant species composition, litter biochemistry, and biogeochemical cycling rates. To test the idea that these ecosystems contain distinct microbial communities that differentially transform dissolved organic matter (DOM) as it moves downslope from dry upland to wet lowland tundra, we studied soil microbial communities in upland tussock, stream-side birch-willow, and lake-side wet sedge tundra (Figure LW-3). Using phospholipid fatty acids and 16s-rRNA analyses, we found that microbial community composition was distinct among tundra ecosystems, with

Landscape Diversity and Microbial Dynamics

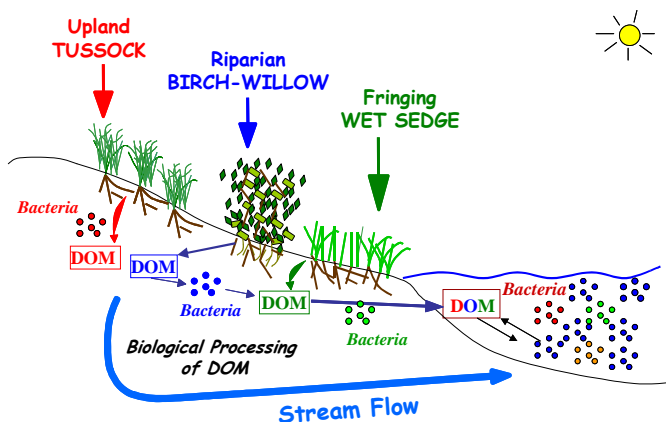


Figure LW-3. Conceptual model of landscape and microbial diversity.

C - Processing varies by Compound and Community

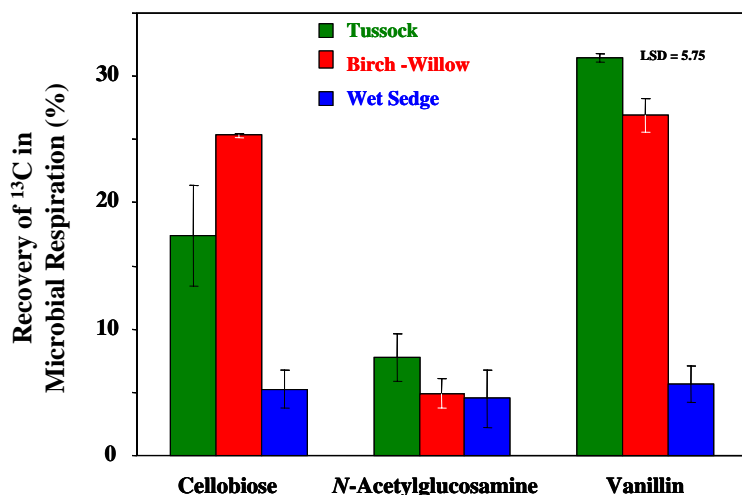


Figure LW-4. Rates of C processing of ^{13}C -labelled compounds representing cellulose, chitin, and lignin in soils varied by compound and by the location on the landscape (vegetation communities).

tussock tundra containing a significantly greater abundance and activity of soil fungi (Judd et al. 2006, Zak and Kling 2006). We also added compound-specific ^{13}C isotope tracers and made measurements of extracellular enzymes involved in cellulose, chitin, and lignin degradation to examine rates of microbial activity. Although the majority of ^{13}C -labeled substrates rapidly moved into soil organic matter in all tundra soils (i.e., 50 to 90% of applied ^{13}C), microbial respiration of labeled substrates in wet sedge tundra soil was lower than in tussock and birch-willow tundra (Figure LW-4 ; Zak & Kling 2006). Despite these differences,

wet sedge tundra exhibited the greatest extracellular enzyme activity. Thus it is apparent that topographic variation in plant litter biochemistry and soil drainage shape the metabolic capability of soil microbial communities, which, in turn, influence the chemical composition of DOM across the arctic tundra landscape.

In addition to discovering these patterns of community composition and activity, we tested an ongoing debate in ecology that revolves around how species composition and ecosystem function are related. To address the mechanistic controls of this relationship, we manipulated the composition of DOM fed to aquatic bacteria to determine effects on both bacterial activity and community composition. Sites along terrestrial to aquatic flow paths were

chosen to simulate movement of DOM through catchments (Figure LW-3) and DOM was fed to downslope and control bacterial communities. Bacterial production was measured and DOM chemistry and bacterial community composition (using denaturing gradient gel electrophoresis of 16S rRNA genes) were characterized following incubations. Bacterial production, DOC-specific bacterial production, and DOC consumption were greatest in mesocosms fed soil water DOM; soil water DOM enhanced lake and stream bacterial production by 320-670% relative to lake and stream controls (Judd et al. 2006). But the really novel finding was that adding upslope DOM to stream and lake bacterial

DOC Chemistry Drives Microbial Species Composition

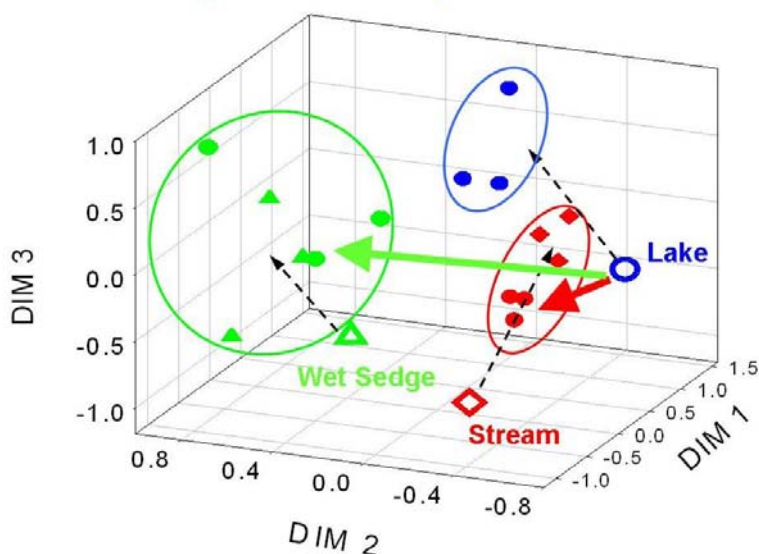


Figure LW-5. Changes in bacterial community composition in experimental and control mesocosms. Multidimensional scaling shows the direction of change in bacterial community composition from the beginning (initial inoculum, large symbols at arrow tail) to the end (small symbols at arrow head). Symbol shape represents the source of the bacterial inoculum (circle = lake; diamond = stream; square = wet sedge soil water), and symbol color indicates the DOM source (blue = lake; red = stream; green = soil water). Note that the “control” community for comparisons was the ending, not the beginning, community.

communities resulted in significant changes in bacterial community composition relative to controls. In these experiments the bacterial community composition converged based on DOM source regardless of the initial inoculum (Figure LW-5). In other words, when lake bacteria were fed soil or stream DOM, the lake community assemblage shifted to resemble the species present in the soil or the stream (green and red arrows in Figure LW-5). Clearly the soil and stream bacteria were already present in the lake in undetectable numbers, but when exposed to soil or stream DOM these populations had a metabolic advantage and grew to replace the originally-dominant lake bacteria. These results demonstrate that shifts in the supply of natural DOM were followed by changes in both bacterial production and community composition, suggesting that changes in function are likely predicated on at least an initial

change in the community composition. In similar experiments we also examined how photo-oxidation of DOM affected microbial activity and DOM processing along these dominant hydrological flow paths. The impacts of DOM photo-oxidation depended in part on DOM source, but were also due to the relatively rapid shifts in bacterial community composition to groups better able to consume photo-products or tolerate harmful radicals (Judd et al. 2007). Overall, these results indicate that variation in DOM composition of soil and surface waters influences bacterial community dynamics and, in turn, different communities control rates of carbon processing in set patterns across the landscape.

These landscape-level interactions were also observed between different aquatic ecosystems. In earlier work of the LTER, we showed that in a connected series of lakes and streams there was consistent and directional (downslope) processing of materials that produced spatial patterns in many limnological variables, and these patterns were coherent over time

(Kling et al. 2000). That is, the interactions of material processing in both lakes and rivers are critical for understanding the structure and function of surface waters, especially in a landscape perspective. In recent research we have expanded these ideas to show that the processing of DOM by microbes, and the species of microbes present, vary consistently as water moves through a network of streams and lakes in the Toolik catchment. For example, in Toolik Lake itself the rate of bacterial activity was related to shifts in the source (terrestrial versus phytoplankton) and lability of DOM, and the bacterioplankton communities were composed of persistent populations present

Bacterial Communities change Seasonally

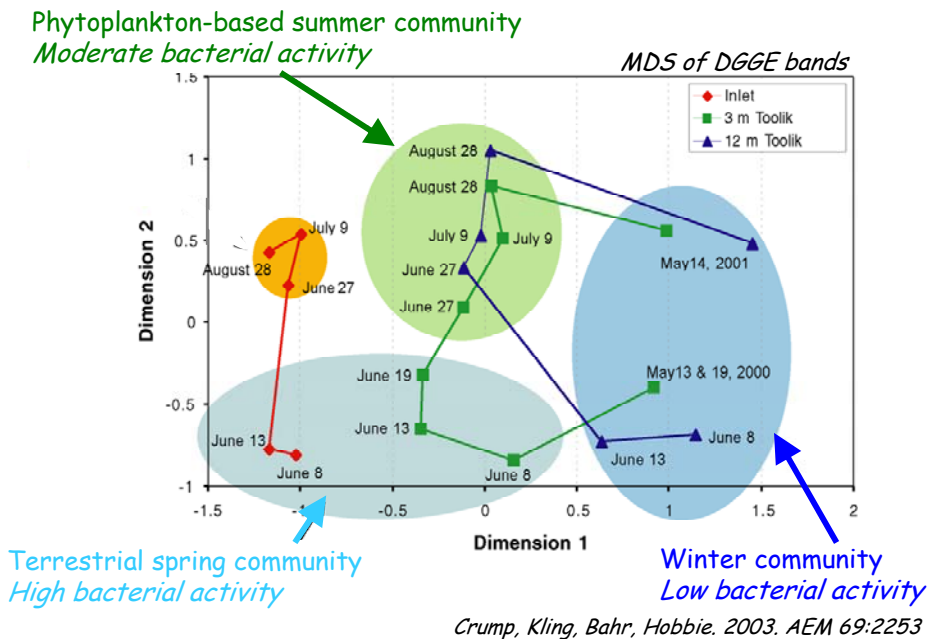


Figure LW-6. Multidimensional scaling calculated from DGGE banding patterns, showing consistent shifts in bacterial productivity and community composition in Toolik Lake.

Nearby sites have similar microbial communities

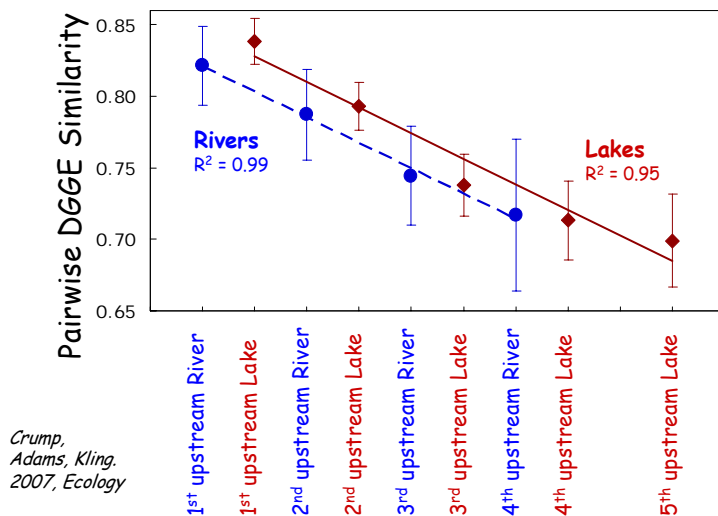


Figure LW-7. Average pairwise similarity values for DGGE banding patterns plotted against the degree of landscape separation. This separation is a categorical variable representing the number of upstream lakes or inlets separating two sites. X-axis values of 1-L mean that comparisons are made between a lake and its closest upstream lake, and 1-S compares a lake and its closest inlet stream. X-axis values of 2 represent a separation of two upstream lakes or two lake inlets. Error bars indicate standard error of all possible combinations within a category.

throughout the year and transient populations that appeared and disappeared (Figure LW-6; Crump et al. 2003). Shifts in community composition, measured by denaturing gradient gel electrophoresis (DGGE) of 16S rRNA genes, were associated with an annual peak in bacterial productivity driven by the large influx of labile terrestrial DOM associated with spring runoff. A second shift occurred after the terrestrial DOM flux declined and as the summer phytoplankton community developed.

Bacterioplankton community composition was also compared across 10 lakes and 14 streams within the Toolik catchment. Both lake and stream systems shared bacteria species (OTUs from DGGE analysis) and

stream communities changed with distance from the upstream lake, suggesting both dispersal of species between lakes and streams as well as inoculation and dilution with bacteria from soil waters or hyporheic zones (Crump et al. 2007). At the same time, similarity in lake and stream communities shifted gradually down the catchment (Figure LW-7). We found evidence that dispersal influences bacterioplankton communities via advection and dilution (mass effects) in streams and via inoculation and subsequent growth in lakes. We also found that the spatial pattern of bacterioplankton community composition was strongly influenced by interactions among soil water, stream, and lake environments. Overall these results reveal large differences in lake-specific and stream-specific bacterial community composition over restricted spatial scales (< 10 km) and suggest that geographic distance and connectivity influence the distribution of bacterioplankton communities across a landscape.

c. Controls on biogeochemical processes and catchment export.

One of the most critical issues in ecosystem research today is understanding how, exactly, do we apply our mechanistic or process-based knowledge of ecosystem function generated at small scales, such as a m^2 plot, to larger scales such as an entire catchment, region, or biome. There are myriad concerns and approaches related to issues of “ecological scaling”, but in our LTER we have focused on hillslopes as the “missing scale” required to transfer detailed process information to larger and larger areas (Figure LW-8). The toposequence of a hillslope represents the major ecosystem types and landscape morphology of an entire catchment, yet can be studied in depth and cohesively (e.g., Giblin et al. 1991). For example, we can monitor soil water chemistry from the hilltop to valley bottom through time, and relate the

A Hillslope as a Model Landscape

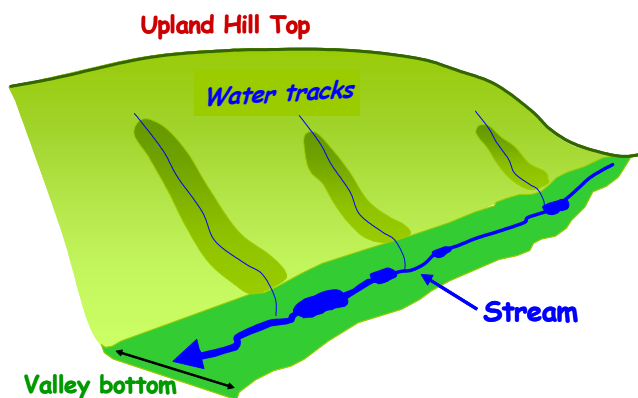
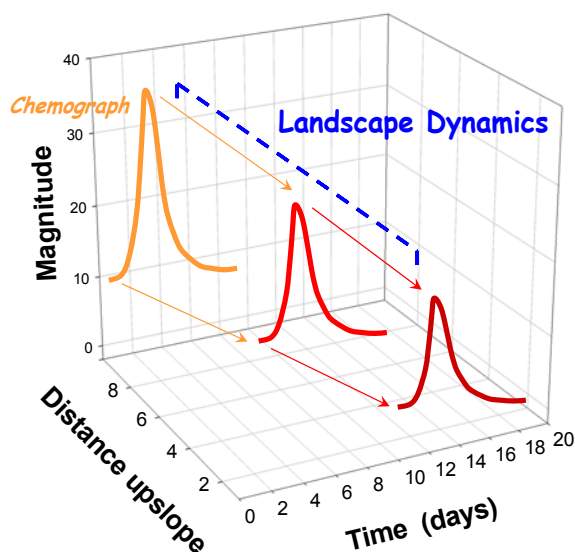


Figure LW-8. The hillslope (above) as a representative landscape model, with landscape components represented by the toposequence from upland heath to mid-slope tussock tundra to valley wet sedge vegetation. Landscape dynamics (right) can be represented by changes in patterns or processes (e.g., soil water chemistry) moving from upslope to downslope and through time.

Controls on biogeochemical processes and catchment export



observed patterns to soil, plant, and microbial processes. The pattern of DOC concentration in soil waters on the hillslope in 2005 (Figure LW-9) shows early and late summer peaks at mid-slope, slightly elevated concentrations at the footslope near the valley floor throughout the summer, and no evidence of major transport of DOC from upslope to downslope during the summer. Our interpretation of this pattern is that most DOC consumption occurs at the site of its production in the soil, which is consistent with the idea presented earlier that large amounts of

DOC processing occur before DOC leaves the catchment. Preliminary data suggest that the same patterns (and interpretation) occur for other dissolved materials such as nitrogen and phosphorus, and the next step is to examine the specific processes and rates at the landscape points where concentrations are high or they change rapidly.

Hillslope Patterns of DOC

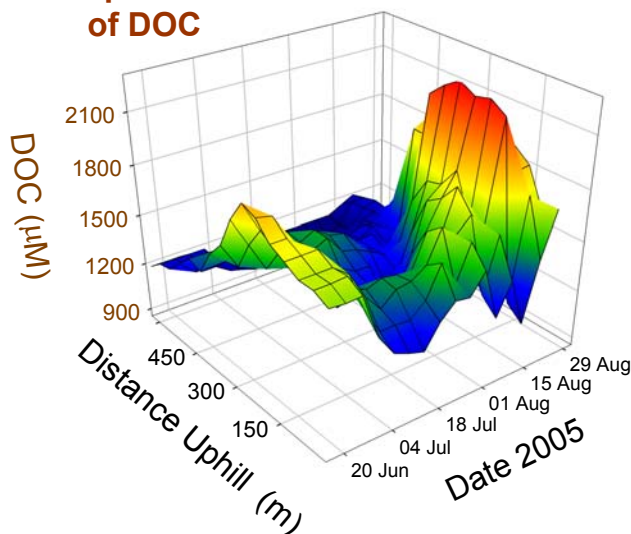


Figure LW-9. Plot showing the concentration of DOC in soil waters along the toposequence at Imnavait Creek through the summer of 2005 (X-axis). The stream is located at the bottom of the graph, and the hilltop is at the top of the graph (Y-axis).

these interactions. And through this research we are developing the methodology to link plot-scale biogeochemical models with realistic hydrological models, in order to better simulate hillslope processes. In the future, we hope to scale this hill-slope model so it can be driven with coarse-scale spatial data to project our knowledge of hill-slope processes to the Pan Arctic and into the next century.

Although the mass of C or nutrients processed on the hillslope may be much greater than that transported downslope and into streams and lakes, the materials transported have both great impacts on the functioning of receiving surface waters and can be substantial relative to the net C storage on land. Modeling of these landscape interactions based on a spatially linked, transect model indicates that hillslope interactions such as the downslope movement of nutrients and water may account for a 30% increase in C sequestration in tundra ecosystems over the next century (Figure LW-10; Rastetter et al. 2004).

Through monitoring and experimental manipulation, we are collecting the data needed to better model

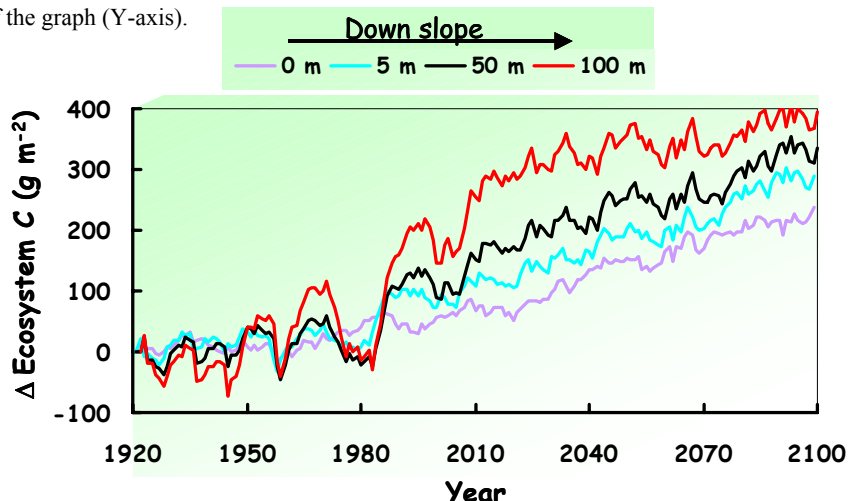


Figure LW-10. Model-simulated changes in ecosystem C stores along a hillslope transect (tussock tundra). Responses to increasing CO₂ and temperature over the next century are enhanced downslope by the movement of nutrients and water.

d. Permafrost melting and biogeochemical impacts on terrestrial and aquatic ecosystems.

Despite clear evidence of arctic warming, from the loss of sea ice to shifts in vegetation and species ranges, many measurements throughout the Arctic, including at Toolik Lake, show a

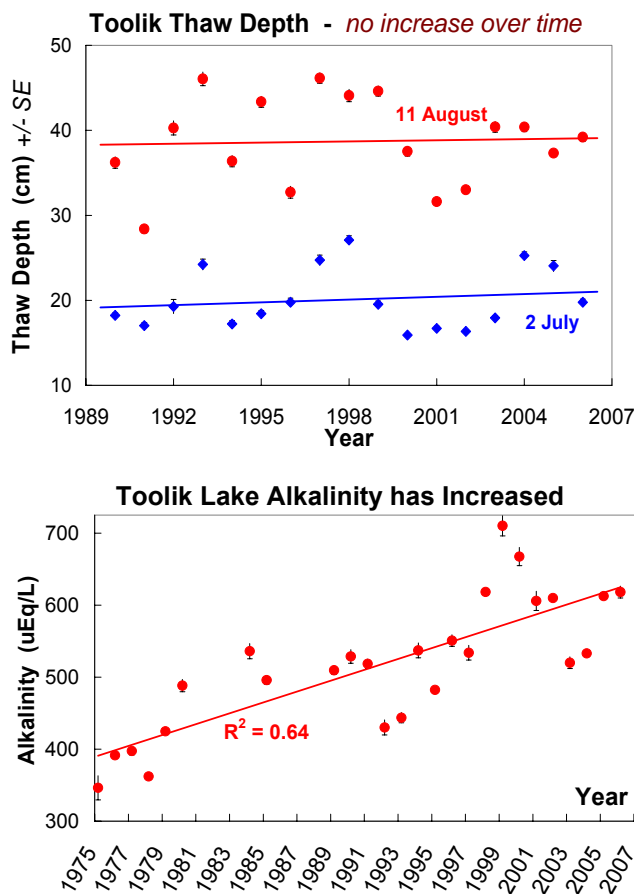


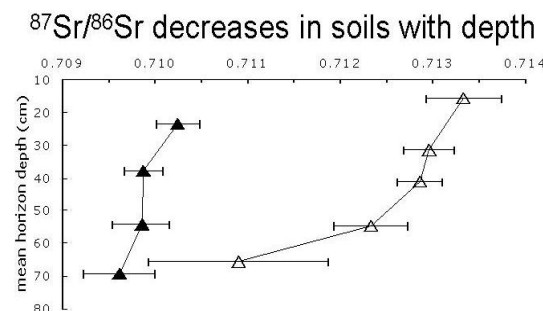
Figure LW-11. **Top** - Summer thaw depth in July and August in the Tussock Watershed near Toolik Lake. **Bottom** - Mean summer alkalinity in Toolik Lake.

related to changes in thaw depth, although the thawing may be confined to the unfrozen zones underneath streams and lakes rather than to the entire upland catchment.

The first piece of evidence we have to build this conclusion is that the carbonate concentrations in the soils increase with depth because the deeper soils are more mineral rich and they have been frozen so that less weathering has occurred (Keller et al. 2007). The second piece of evidence is that the ratio of strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) in soils decreases with depth near

the Arctic LTER (Figure LW-12). This means that as rainwater flows through deeper and deeper soils it will pick up the soil signature and the strontium isotopic ratio in the water will decrease. Finally, we observed just such a decrease in strontium isotope ratio in the stream entering Toolik

Lake (Figure LW-11). At the same time, we have measured substantial increases in the alkalinity of Toolik Lake since 1975, and these changes are unrelated to processes in the lake and appear instead to be caused by increased weathering of mineral soils in the catchment (Figure LW-11). This is puzzling given the fact that the depth of summer thaw has not increased over time to expose more mineral soil. However, these measurements of the maximum depth of summer thaw in soils are traditionally made using steel probes, which are limited in their use to upland terrestrial environments. To overcome this limitation we used a new approach to show that changes in the geochemistry of surface waters must be



Streamwater $^{87}\text{Sr}/^{86}\text{Sr}$ decreases over time

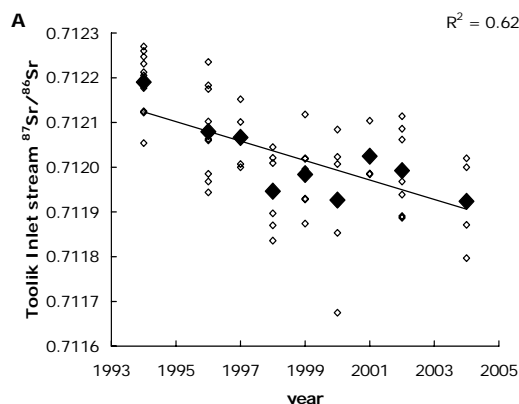


Figure LW-12. **TOP** - Strontium isotope ratios in older (filled) and younger (open) soils. **Bottom** - Strontium isotope ratios in the inlet stream to Toolik Lake over

Lake over the last 10 years (Figure LW-12). The implication is that water flowpaths in the basin have progressively deepened and are now in contact with previously frozen soils of different chemistry. Because thaw depths of terrestrial sites have not changed during that time period, it is likely that the unfrozen thaw bulb found underneath streams and lakes has actually expanded, and the deeper thaw here contributes most to the altered chemistry. Our results also suggest that increasing thaw depth will lead to increasing Ca supply to soils and streams, as well as spatially variable increases in P and K supply (Keller et al. 2007). It may be that such changes in stream chemistry caused by permafrost thawing are more widespread in the Arctic than currently believed, which can be tested using this new geochemical method at other sites in arctic and boreal regions with permafrost.

6. SITE MANAGEMENT

a. Overall management structure.

The research aims of the Arctic LTER project require collaboration among a diverse group of ecologists with a broad spectrum of backgrounds, skills, and talents. For the sake of efficiency and to promote more effective planning we began our LTER research in 1987 by dividing into three major groups focused on major components of the landscape, i.e., terrestrial, streams, and lakes. In the mid-1990s we added a fourth group that reflected our growing interest in linkages, the "land-water" now the "landscape interactions" group. At present, although many of the individual investigators are involved in research with more than one group, this structure has proved highly effective for the planning and implementation of field research, especially large, whole-system experiments and integrated surveys. Research plans and priorities are developed at an annual winter meeting of all senior investigators, research assistants, and students, held in Woods Hole, at which the four subgroups meet separately and plenary discussions of overall project priorities are held. Ad hoc meetings of individual groups are also held during the summer, at Toolik Lake, and occasionally groups will meet during the winter.

The lead PI of the project is John Hobbie, who will retire gradually from this role during current funding period (2005-2010). Gus Shaver is gradually taking over Hobbie's responsibilities and will take the lead in developing plans for our next renewal proposal as lead PI (2011-2016). An Executive Committee consisting of Hobbie (chair), representatives of each of the four research groups (currently Shaver, Peterson, Luecke, and Kling), and one additional person (currently Giblin) also meets at least twice a year, once in the fall and once during the winter plenary meeting. The purpose of the fall meeting is to review the previous summer's work, to review the current state of the project's budget, and to begin discussion of any changes in priorities, funding allocations, or new opportunities that might emerge in the coming year. At the fall meeting we also set the agenda for the winter meeting and often choose a theme. At the winter meeting the Executive Committee meets before and after the plenary sessions to review the agenda, consolidate priorities and reconcile conflicts in plans developed by the four research groups, and again review the budget. Throughout the year, the Executive Committee responds to requests for information about the project, prepares annual reports and other communications, and interacts with the LTER Network office and with NSF. At least one member of the Executive Committee (usually Hobbie and/or Shaver) attends every Network Coordinating Committee meeting (recently renamed the Science Council meeting) to ensure continuity in our network participation; both Shaver and Hobbie have served on the Network Executive Committee.

Key project personnel include the four full-time, senior assistants associated with the four research areas, and a half-time assistant who works with Hobbie to manage the project. These assistants work with the Executive Committee to do most of the day-to-day project management and coordination of field and lab research within the four research groups, and play a particularly important role in information management. One of them, Jim Laundre, is the project's senior Information Manager and attends the annual Network Information Management sessions.

b. Field site management.

The land on which most of the LTER research is carried out is owned by the US Bureau of Land Management (BLM), which grants permits to researchers to work there. Additional permits are required by the Alaska Department of Fish and Game for our research on fish. We work closely with these agencies to ensure that the permitting process runs smoothly. These

agencies are very helpful, for example in creating the Toolik Lake Research Natural Area that includes the entire headwaters region of the Kuparuk River.

Toolik Field Station (TFS), where most of the field research is based, is a facility of the Institute of Arctic Biology of the University of Alaska Fairbanks (UAF); it also operates under lease of its land from BLM (only the 17-acre camp itself is covered). Much of the support for TFS comes through a cooperative agreement between UAF and NSF's Office of Polar Programs (OPP); research projects with NSF support, including the LTER project, also receive "user-day" support from OPP in the form of daily use fees paid to TFS through NSF's arctic logistics contractor, VECO Polar Resources.

LTER scientists work closely with TFS management to ensure that research needs are met. During the summertime a "chief scientist" meets daily with camp management to discuss immediate issues and 2-3 times each summer general meetings are held with all camp personnel invited. LTER scientists also attend annual winter planning meetings as members of the TFS Steering Committee; Dr. M.S. Bret-Harte, an LTER scientist at the University of Alaska, is Associate Scientific Director of TFS. One particularly valuable service provided by TFS is its GIS and mapping service. The GIS manager and his assistant provide a wide range of custom maps for researchers and incorporate all known research activities into a Toolik GIS. This GIS is useful for many purposes including research planning and "zoning" to avoid conflicting land use by multiple projects. In 2006 TFS added personnel to their staff with responsibilities for general project support and for building an environmental monitoring program that incorporates all research at TFS, not only LTER. This service has already proved useful, for example, in collecting samples or data when LTER researchers are not in camp, and in the fabrication of apparatus for LTER and other projects. We are working closely with TFS to build a new, expanded environmental monitoring data base.

c. Collaborating projects and interactions with LTER Network.

Opportunities for collaboration were a primary consideration in designing the ARC LTER research, especially its long-term experiments. The collaborating projects include those that work directly on LTER sites and experiments, and projects that use the facilities at TFS and collaborate in synthesis papers. Often the LTER project will encourage a particular interaction by inviting visitors to work at Toolik Lake with supplemental or core research funds, in anticipation of their eventually obtaining independent funding (two examples are the successful development of the herbivory and soil food web project by L. Gough and J. Moore, which began with annual LTER supplemental funding, and the LTER study of microbial Dynamics by B. Crump and G. Kling). The ARC LTER project has been particularly successful in attracting young investigators in the past 10 years, by encouraging those who were trained at Toolik Lake as postdocs and graduate students to return there as principal investigators with their own funding and continuing research on LTER experiments (Syndonia Bret-Harte, Byron Crump, Laura Gough, Sarah Hobbie, George Kling, Loretta Johnson, and Martin Sommerkorn have all followed this route). A list of collaborating projects is provided in Section 12.

Cross-site and Network collaborations are also strongly encouraged, and are supported with supplemental and other funds where possible. Over the past ten years a growing exchange of researchers between TFS and Abisko Field Station in Sweden has developed, involving both students and investigators from the University of Copenhagen, Wageningen Agricultural University, Free University of Amsterdam, Sheffield, Durham, and Edinburgh; this has led to several publications, theses and a metaanalysis of responses to tundra experiments (e.g., van

Wijk et al. 2003, Williams et al. 2006, Clemmensen et al. 2006, Cornelissen et al. in press). In the past three years we have participated in several major international synthesis activities including the Arctic Climate Impacts Assessment (ACIA) in which Hobbie and Shaver contributed to the Aquatic and Terrestrial chapters (Callaghan et al. 2005, Wrona et al. 2005); working with the International Tundra Experiment (ITEX) network we have developed two metaanalyses of plant growth and community responses to warming (Arft et al. 1999, Walker et al. 2006).

7. INFORMATION MANAGEMENT AND TECHNOLOGY

a. Overall Strategy and Structure.

Information management in the Arctic LTER has two principal aims. The first is to maximize data **access** both within the project and to other researchers. We try to maximize data access by rapidly adding new data sets to the data base (usually before publication) and by making all of the data sets available for downloading by anyone; the only requirement is that NSF and the Arctic LTER project be acknowledged in any use of the data. The second aim is to optimize data **usability** and **integration** for within-site synthesis and modeling, regional and long-term scaling, and multisite or global comparisons and syntheses. This is achieved by making multiple kinds of measurements on the same sites (often the same small plots), usually at about the same time. Careful planning at the research design stage is required to ensure that any single set of measurements is easily linked to other measurements.

The structure of our information management system parallels the overall management structure of the project (Site Management section). A Senior Research Assistant, Jim Laundre, is the overall project information manager with responsibility for overseeing the integrity of the Arctic LTER information system. There are four major components to the information system, linked to the terrestrial, streams, lakes, and landscape interactions research components. Information management is a primary responsibility of the four full-time research assistants (including Laundre) associated with each of these four research components. While each of the four assistants maintains the data in their area, all are in frequent communication on overall data compatibility and metadata standards (three work at the MBL in Woods Hole, one is at the University of Michigan). Each of these assistants is also heavily involved in the actual research design, day-to-day management, and data collection within their area. The four research assistants work closely in the field with investigators, technicians, and students to ensure quality control and appropriate documentation. Overall guidance is provided by the PI Steering Committee while Laundre attends the LTER Network Information Manager's meetings and makes sure we are kept up to date and compatible with Network data standards.

Each year at our annual winter meeting in Woods Hole we review the status of the information system and ways of improving its accessibility and ease of use. At this meeting we focus in particular on the upcoming summer season and on how to design our research for optimum integration of diverse data sets. All project personnel including postdocs, graduate students, and occasional REU students participate in these discussions. See <http://ecosystems.mbl.edu/ARC/Datatable.html> for details of Arctic LTER's information management system.

b. Availability of Datasets.

Datasets of the Arctic LTER project are available without restrictions and can be downloaded by anyone from the Arctic LTER web site <http://ecosystems.mbl.edu/ARC/>. We ask only that the LTER project and the principal investigator responsible for the data set be informed and that NSF and the Arctic LTER be acknowledged in any papers published in which the data are used. Recent statistics of web site use are summarized in Table 4-1.

Data from the large-scale experiments and from routine monitoring are available online as soon as the data are checked for quality and, where necessary, transformed for presentation in standard units and scales. Many data sets, such as weather observations, stream flow, flower counts, and data that do not require a great deal of post-collection chemical or other analysis, are

available within 3-6 months of collection. Other data, particularly from samples requiring chemical analysis in our home laboratories, may take up to two years before they appear on-line. We also encourage others working on the LTER sites but not funded by the LTER project to contribute their datasets to our online database. For example, the NSF-OPP funded “Belowground Dynamics” project and the NSF-OPP “ITEX” project use the ARC LTER web server as their archival site.

In addition to datasets on our web server the Arctic LTER also participates in the LTER Network’s ClimDB and HydroDB information systems. These centralized databases provide access to meteorological and hydrological data from all the LTER sites.

c. Format of Datasets.

Research investigators, assistants and students who collect the data are responsible for data analysis, quality control, and documentation. This insures that the data are checked and documented by those most familiar with the data. While investigators may use any software for their own data entry and analysis, we expect that all documentation and datasets that are submitted conform to the Arctic LTER formats (<http://ecosystems.mbl.edu/ARC/Datatable.html>). The metadata and data are submitted using Arctic LTER’s new Excel based metadata form. For researchers who do not use Excel a rich text form is available with the data being submitted as comma delimited ASCII. Submitted files are checked for conformance by the four research assistants. Once files are accepted, they are placed in the appropriate data directories on the web. An Excel macro is used to parse the metadata form and to generate html, xml and data files need for accessing the data via the web. The xml file conforms to the LTER network’s “EML Best practices” level 4 (<http://cvs.lternet.edu/cgi-bin/viewcvs.cgi/emlbestpractices/#dirlist>). The xml file is uploaded to the LTER Network Office metacat server via a harvest list. Uploaded files are then available from the LTERNET data catalog (<http://prairie.lternet.edu:8080/knb/>).

d. Geographic Information Systems, Mapping, and Remote Sensing.

Geographic information from the Toolik Lake region is extensive, detailed, and linked to several key global and regional data bases. Because much of this first-class information system was developed with funding independent from the Arctic LTER project, we have focused our efforts on insuring access to this extremely valuable database and on optimizing its usability for our needs. Where appropriate, we have contributed small amounts of funds and personnel support to guarantee this access and usability. Links to the key databases are provided on the Arctic LTER web site at <http://ecosystems.mbl.edu/ARC/>; these include:

- The *Circumpolar Geobotanical Atlas*, developed by Dr. Donald (Skip) Walker and colleagues at the Alaska Geobotany Center, University of Alaska (<http://www.arcticatlas.org>), features a nested, hierarchical series of maps of arctic ecosystems at scales ranging from 1:10 (1 m²) to 1:7,500,000 (the entire Arctic), with multiple data layers at each scale including vegetation, soils, hydrology, topography, glacial geology, permafrost, NDVI, and other variables. Much of the development of this hierarchical system is based on original work done by Walker and colleagues at Toolik Lake and Imnavait Creek, with multilayer maps of these areas at 1:10, 1:500 (1 km²), 1:5000 (25 km²), and of the Kuparuk River basin at 1:25,000 and 1:250,000.
- The *Toolik Field Station GIS* (<http://www.uaf.edu/toolik/gis>) was developed with support from NSF-Office of Polar Programs to help manage and support research based at the Field Station including LTER research. This GIS is maintained by a full-time GIS and Remote

Sensing Manager, Andrew Balser, and includes a multilayer GIS based largely on the Geobotanical Atlas data described above, combined with landownership information, roads and pipelines, and disturbances (e.g., Fig. 3-2). Particularly important for our purposes is a detailed location map of research sites including all of the LTER experimental plots and sample locations in the upper Kuparuk region. The GIS includes a map of Inupiaq place names with annotations of historic use of the land by the Inupiaq people, along with an Inupiaq dictionary of plant and animal names and other common words.

e. General site information and publications.

General information about the Arctic LTER project is provided on our web site (<http://ecosystems.mbl.edu/ARC/>) including site descriptions, past proposals and other documents, a site bibliography including publications based on project research (Table 4-2), educational opportunities, contact information for site personnel, and links to related sites. This information is updated about once a year, or whenever major changes occur.

f. Future Plans.

Currently all our legacy metadata have been converted to Ecological Metadata Language (EML) but only at EML Best Practices level 2/3 (no attribute EML). In bringing the files up to level 4, the files will be reviewed and where appropriate consolidated into multi-year files. Differences in methods and personnel will require that some years remain separate. For some datasets we are also investigating using a relational database for storing and retrieving subsets of data. Especially appropriate would be climate data and routine measurements.

Plans are also underway to work with the Toolik Field Station GIS manager to generate EML files for some of the basic site GIS files. This would include the research locations and layers with vegetation, topography, streams and lakes.

As mention in the Site Management section, Toolik Field Station started an environmental monitoring program in 2006 and will be taking over some of the basic climate and environmental measurements, e.g. precipitation chemistry. These legacy databases will be transferred and housed at UAF. Jim Laundre will be working closely with the Toolik Field Station Information manager during this transfer.

Table 4-1. For the year 2006, each column shows month-by-month sums of hits outside of MBL on all Arctic LTER web pages and on data files only (excluding web-crawler hits). Data requests are also received via email to the Information Managers. These typically number 6-12 per year.

Month	Hits on Arctic LTER Web Site		Hits on Arctic LTER Data Files	
	All Hits	Outside MBL	All Hits	Outside MBL
1	25263	24546	192	168
2	29028	28630	648	614
3	28868	28313	434	427
4	30585	29855	354	343
5	28937	27368	700	689
6	25511	24730	174	165
7	26129	25271	219	160
8	24061	23227	176	172
9	26068	25389	256	253
10	31396	30138	375	345
11	31517	30633	120	119
12	34142	33592	126	126

Table 4-2. Publications of the Arctic LTER project, 1998-2007

<i>Publication type or journal</i>	<i>Published 1998-2003</i>	<i>Published or accepted 2004-2007</i>
Ph.D. theses	2	7
Masters theses	6	6
Books or book chapters	13	7
Advances in Coastal and Ocean Engineering		1
Advances in Water Research	1	
Ambio		17
Annual Reviews of Ecology and Systematics	1	
Applied and Environmental Microbiology	1	
Archiv für Hydrobiologie	1	
Arctic, Antarctic, and Alpine Research	2	3
Biogeochemistry	3	1
BioScience	6	
Boundary Layer Meteorology	1	
Canadian Journal of Fisheries and Aquatic Sciences	2	2
Canadian Journal of Forest Research	1	
Climatic Change		1
Ecography		1
Ecological Applications	1	2
Ecological Modeling	1	1
Ecological Monographs	1	
Ecology	9	6
Ecology Letters		1
Ecosystems	5	2
Environmental Biology of Fishes	1	
Environmental Science and Technology		3
Freshwater Biology	4	7
Geochimica et Cosmochimica Acta		1
Geophysical Research Letters	1	1
Global Biogeochemical Cycles	5	
Global Change Biology	7	2
Global Change Science	1	
Hydrobiologia	1	1
Hydrological Processes		2
Journal of Climate		2
Journal of Ecology	6	5
Journal of Evolutionary Biology	2	
Journal of Fish Biology		1
Journal of Geophysical Research	8	1
Journal of Hydrometeorology	2	2
Journal of North American Fisheries Management	1	
Journal of Plankton Research	1	
Journal of the North American Benthological Society	7	
Lake and Reservoir Management		1
Landscape Ecology		(1 submitted)
Limnology and Oceanography	3	5
Nature	2	2
New Phytologist	2	1
Oecologia	2	4 (1 submitted)
Oikos	4	2 (1 submitted)
Pedobiologia		1
Plant And Soil	3	
Polar Geography	1	
Polar Research	1	
Proceedings National Academy of Sciences		2
Science	2	
Soil Biology and Biochemistry	2	1
Soil Biology and Biochemistry	1	
Transactions American Fisheries Society	1	1
Verh. Int. Verein. Limnol.	1	2
Water Resources Research	1	1
TOTAL JOURNALS	109	89 (3 submitted)

8. EDUCATION AND OUTREACH

The Arctic LTER project maintains a multifaceted education and outreach program. In addition to the training of more than 60 graduate and undergraduate students in 2004-2007 (Table 5-1), every summer we bring one to three journalists to Toolik Lake as part of the Marine Biological Laboratory's Science Journalism Program (Table 5-2). Over the past six summers we have developed a very popular Schoolyard LTER program based at Barrow, Alaska, in association with the Barrow Arctic Science Consortium. In 2003, 2004 and 2006, we produced a field course for students and journalists, and in 2007 we are working with University of Alaska to produce an undergraduate "Field Course in Arctic Science". As part of our outreach program we regularly brief Federal and State agencies associated with land management on the North Slope of Alaska including the Bureau of Land Management (BLM), the Arctic National Wildlife Refuge (ANWR), the Alaska Department of Fish and Game, and the Alaska Department of Natural Resources (DNR). We cooperate closely with the University of Alaska Fairbanks in the management and development of the Toolik Field Station, which is owned by the University's Institute of Arctic Biology. Finally, we serve on a wide range of advisory and planning committees including US Arctic Research Commission (Hobbie), and the Steering Committees for the US Study of Environmental Arctic Change (SEARCH; Shaver and Peterson) and the NSF Arctic Systems Science Program (Peterson and Shaver). Shaver and Hobbie have helped to write chapters in the international review of climate change in the Arctic, the Arctic Climate Impacts Assessment (ACIA 2005), under the auspices of the International Arctic Research Committee (IARC).

All of these activities have continued to grow in 2004-2007, with the addition of a new program of support for graduate students as a result of an agreement (signed September 2003) between Brown University and the Marine Biological Laboratory, which for the first time ever allows MBL scientists to serve as principal advisors to Brown graduate students. Specific goals for our education and outreach program thus include:

- *REUs and graduate students:* We continue to support at least two REU students each year with LTER supplemental funds, and two to six others in association with collaborating NSF grants. REU students are selected as the result of a national search each year and come from a wide range of states and institutions (Table 5-1). We continue to promote the training of graduate students with support on collaborating grants, and we continue to encourage our foreign collaborators to send their students to us for a summer at Toolik Lake, as we have in the past. To promote communication among these students, every summer we help organize a weekly seminar series "Toolik Talking Shop", and at the end of the summer we organize a poster session for REU students. Graduate students, and occasionally REU students, are invited to our annual winter workshop in Woods Hole to present their results and to participate in planning for the following summer's research.
- *Science Journalism Course:* In this course, journalists spend a week at the MBL in Woods Hole to learn about ecology through lectures, field work and laboratory experiments, then travel to Alaska for two weeks of "hands on" field experience. A wide range of newspaper, magazine, radio, and film media are represented (Table 5-2).
- *Arctic ecology course:* In 2003, 2004, and 2006 we organized a course based on the NSF BioComplexity project, "Land-water Interaction at the Catchment Scale: Linking Biogeochemistry and Hydrology" as a joint effort of the International Arctic Research Center (University of Alaska Fairbanks) and the Marine Biological Laboratory. The courses, *Arctic*

Ecology and Modeling (2003), *Arctic Climate and Terrestrial Ecosystems* (2004) and *Arctic Hydrology and Terrestrial Ecosystems* (2006) were intended to provide graduate students and early-career scientists with an overview of the controls of ecosystem variability in northern Alaska, from the Alaskan interior to the Arctic, and an illustration of the interplay between data collection and modeling. Each course also gave students an understanding of the scientific underpinnings of the controls and feedbacks of climate-related changes in Arctic ecosystems, and it included first-hand exposure to ongoing research. In May-June 2007, with new funding as part of the NSF-IPY program, we will be working with University of Alaska, Fairbanks to produce a new course in Arctic Science, based primarily at Toolik Field Station.

- *Schoolyard LTER*: The Arctic LTER Schoolyard project, based in Barrow, AK, began in May 2002 and has had six very successful years. Directed by the Barrow Arctic Science Consortium (BASC; <http://www.arcticscience.org/aboutBASC.php>), it is designed for Barrow students (mostly Native Iñupiat Eskimo) in grades K-12, their teachers, and local residents. The project consists of two activities, a field experiment to demonstrate the effects on tundra vegetation of warmer air and soil temperatures and “Schoolyard Saturday,” a weekly series of lectures and field demonstrations by visiting and resident scientists. (<http://www.arcticscience.org/schoolyardProject.php>).
- *Federal and state management agencies*: We will continue our practice of regular briefings of BLM, ANWR, DNR, and Alaska Fish and Game officials; usually this consists of visits to their offices in Anchorage and Fairbanks and occasional tours of our research sites. We work particularly closely with the BLM and Alaska Fish and Game offices in association with the annual permitting process. The Alaska Fish and Game office has used our data and advice in the past to set angling policies and fish catch regulations. Our contacts with Alaska DNR have increased in frequency lately as the DNR has been engaged in a reassessment of winter off-road travel. Each year we invite representatives from these agencies to attend our winter meeting.
- *Research planning and organization*: We continue our long-term participation in national and international research planning and oversight organizations including the Arctic Research Commission, SEARCH, ARCSS, and ACIA, and we continue to help with the long-term management and organization of the University of Alaska's Toolik Field Station.

Table 5-1: LTER Students 2004-2007

Ph.D. Degree Completed

- Boelman, Natalie, Ph.D. 2006. Relating spectral vegetation indices to plant physiological and ecosystem processes at multiple spatial scales. Lamont-Doherty, Columbia University, New York, NY
- Burkart, Greta, Ph.D. 2006. Energy flow in arctic lake food webs: the role of glacial history, fish predators, and benthic-pelagic linkages. Utah State University
- Cherry, Jessie, Ph.D. 2006. Arctic hydroclimatology, Lamont-Doherty, Columbia University, New York, NY
- Evans, Mary Anne, Ph.D. 2007. Phytoplankton ecology of Arctic lakes. University of Michigan
- Gettel, Gretchen, Ph.D. 2006 Rates, importance, and controls of nitrogen fixation in oligotrophic Arctic lakes, Toolik, Alaska. Cornell University
- Judd, Kristi, Ph.D. 2006. Dissolved organic matter dynamics in an Arctic catchment. University of Michigan
- Keller, Katy, Ph.D. 2006. University of Michigan, Geochemistry of streams, soils, and permafrost and the geochemical effects of climate change in a continuous permafrost region, Arctic Alaska, USA. University of Michigan

M.S. Degree Completed

- Burris, Melinda, M.S. 2006. The life history, morphological, and behavioral changes of two Arctic daphnids to kairomone from the invertebrate predator *Heteroscope septentrionalis*. University of North Carolina, Greensboro
- Cappelletti, Carl M.S. 2006. Photosynthesis and respiration in an Arctic tundra river: Modification and application of the whole-stream metabolism method and the influence of physical, biological and chemical variables. University of Vermont
- Greenwald, M.J., M.S. 2007. Hyporheic exchange and biogeochemical processing in arctic tundra streams. Rubenstein School of the Environment and Natural Resources, University of Vermont.
- Johnson, Cody M.S. 2004. Coexistence and vertical distribution of two copepods *Cyclops scutifer* and *Diaptomus pribaifensis* in an oligotrophic Arctic Lake. University of North Carolina, Greensboro
- MacKinnon, Peter, M.S. 2006. Effects on growth of age-0 arctic grayling in tundra streams. Utah State University
- Holland, Victor, M.S. 2006. Infection of slimy sculpin (*Cottus congatus*) by the Cestode *Schistocephalus* in the presence and absence of Lake Trout (*Salvelinus namaycush*) in Arctic Alaskan lakes. University of North Carolina, Greensboro

Expected to finish in 2007

- Johnson, David, Ph.D. The role of herbivory on individual plant growth, community and ecosystem dynamics of moist acidic tussock and dry heath tundras under increased nutrient availability, University of Texas, Arlington
- Parker, Stephanie, Ph.D. Effects of natural disturbance on Arctic stream communities, University of Alabama
- Alexander-Ozinskas, Marselle, M.S. Controls on N accumulation and loss in Arctic tundra ecosystems, Brown University
- Yelen, Lauren, M.S. Microbial communities in soils, University of Michigan

Ongoing Ph.D.students 2004-2007

- Adams, Heather, University of Michigan
- Allen, Angela, Brown University
- Belshe, Fay, University of Florida
- Hicks, Caitlin, University of Florida
- Johnson, Cody, Utah State University
- Koop-Jacobsen, Ketil, Boston University
- Lee, Hanna, University of Florida
- Rantala, Heidi, University of Alabama
- Simpson, Rod, Colorado State University
- Whittinghill, Kyle, University of Minnesota
- Wyant, Karl, Colorado State University

Ongoing M.S.students2004-2007

- Bailey, Alex, University of North Carolina, Greensboro
- Benson, Bridget, University of California Santa Barbara
- Boby, Leslie, University of Florida
- DeMarco, Jenny, University of Florida
- Green, Curtis, University of North Carolina, Greensboro
- Heatherly, Tom, University of Alabama
- LaRouche, Julia, University of Vermont
- Moulton, Carol, University of Texas, Arlington
- Parsons-Field, Avrey, University of California Santa Barbara
- Smith, Robyn, University of California Santa Barbara

Undergraduate Research Assistants 2004-2007:

Cheng, YiWei, Georgia Institute of Technology
Duling, Andrew, University of Vermont
Garcia, Andres, University of Northern Colorado,
Northeastern University
Knight, Jeff, University of Texas Arlington
Martin, Beverly, University of Alabama
Moon, Brian, University of Texas Arlington
Morse, Nathaniel, University of Vermont
Varns, Theodore, University of Alaska Fairbanks

Foreign Students 2004-2007:

Clemmensen, Karina , University of Copenhagen
Deslippe, Julie , University of British Columbia
Lang, Simone , Free University Amsterdam
Suzuki, Nozomi, Tokyo Institute of Technology
Matsui, Yohei, Tokyo Institute of Technology

REU Students 2004-2007

Bayer, Skylar, Brown University
Bernhardt, Beth, Lawrence University
Cook, Jenna, University of Alabama
Day, Natalie, Lewis and Clark College
Dzul, Maria, University of Michigan
Falso, Paul, Allegheny College
Forrest, Alyse, Middlebury College
Graham, Elizabeth, University of Michigan
Huang, Julia, University of Florida
Hudson, Benjamin, Brown University
Juice, Stephanie, Cornell University
Larsen, Ashley, University of Michigan
Layn, Aaron, University of California Santa Barbara
Powers, Joseph, Michigan Technological University
Reistetter, Joe, Beloit College

Table 5-2: Science Journalism Program

2004: John Carey, *BusinessWeek*
 Rebecca Clarren, Freelance Science Writer
 Elizabeth Grossman, Freelance Science Writer
 Eugene Russo, Freelance Science Writer

Articles:

“Baked Alaska,” by Rebecca Clarren, Salon.com, September 2004

2005: James D. Bruggers, The Courier-Journal
 Hannah Hoag, Freelance Science Writer
 Kristan Hutchison, The Antarctic Sun
 Mike Stark, The Billings Gazette
 Jeff Tollefson, Santa Fe New Mexican

Articles: “Canary in the Mine,” by Mike Stark, *The Billings Gazette* - 11/22/2005 (also appeared in *Helena Independent Record*)

2006 Marc Airhart, Freelance Science Writer, from Austin, Texas
 Molly Murray, *The News Journal*, Wilmington, Delaware
 Anton Caputo, *San Antonio (TX) Express Journal*
 Mary Engel, *Los Angeles Times*
 Jim Metzner, Pulse of the Planet radio series, Accord, NY

Articles: “In Alaska: Studying global warming,” by Molly Murray, *The News Journal*, October 23, 2006.

Blogs: Molly Murray: <http://www.delawareonline.com>

Anton Caputo: <http://blogs.mysanantonio.com/weblogs/environment/2006/08/>

Jim Metzner: http://pulseplanet.com/sci-diaries/sd_jim.html

Broadcast: In production for summer 2007: Four Pulse of the Planet’s Science Diaries on grayling research (Heidi Golden) and the soil emissions experiment done by Robert Rhew’s team from Berkeley.

2007 Anne Bolen, Managing Editor, *GeoTimes*
 Peter Thomson, Acting Senior Producer, PRI’s Living on Earth

9. FUTURE PLANS

Overall we expect that the research of the Arctic LTER project will continue to evolve as new opportunities arise and as results of our current research lead to new insights and new hypotheses. We expect that our current themes of landscape linkages, regional and PanArctic syntheses, and predictions of future states of arctic ecosystems will continue to serve a useful heuristic purpose in focusing our research activities, and that our current management framework of lakes, streams, terrestrial, and land-water interactions research will continue to be useful (Fig F-1). Over the next three years of the LTER IV project we have the following specific goals:

1. Increase the pace of our synthesis activities as part of the LTER Network's "Decade of Synthesis" including:
 - a. Complete the ARC site synthesis volume: This volume is currently in outline form, with drafts of several chapters written. The outline has been submitted to the publishers, Oxford University Press, for review.
 - b. Continue and expand our efforts in PanArctic syntheses: Within the past five years we have completed several focused syntheses, including metaanalyses of controls on arctic plant growth and community composition (van Wijk et al. 2003, Walker et al. 2005), and a PanArctic litter decomposition experiment (Cornellissen et al. in press). We also were active participants in the Arctic Climate Impacts Assessment (ACIA 2005), coauthoring two chapters of the main assessment and 17 related papers on terrestrial and aquatic ecosystems. Currently, several ARC investigators, students, and postdocs are preparing for an international meeting on "**High Latitude Terrestrial and Freshwater Ecosystems: Interactions and Response to Environmental Change**", to be held at Abisko, Sweden in September 2007; a main objective of the meeting is to develop a conceptual model of C cycling in arctic catchments including the linkages that are the focus of much of our current work. Finally, members of the ARC steering committee are actively involved in planning of current national and international arctic syntheses including SEARCH (Study of Environmental Arctic Change), AON (Arctic Observatory Network), and ISAC (International Study of Arctic Change).
 - c. Continue and expand efforts in LTER network-level and cross-site syntheses: We have participated in several of these in the past (e.g., Waide et al. 1999, Knapp and Smith 2001, Peterson et al. 2001, Suding et al. 2005) and are currently engaged in a multisite comparison of the effects of shrub expansion on ecosystem processes (Knapp et al. submitted). We look forward to continued collaboration in these efforts as they develop.
2. Prepare for the ARC LTER 2010 renewal incorporating the LTER ISSE plan:
 - a. One of the main new components of the LTER Network initiative, Integrated Science For Society and the Environment (ISSE) is a greatly expanded role for social science research at LTER sites. We have already begun moving in this direction, using annual supplemental funds to begin developing a new study of perceptions of climate change and its effects on Native Alaskan Inuit communities. Our initial efforts are focused on the Inuit community of Kaktovik, on the north coast of Alaska about 150 miles from Toolik Lake; the work is led by Dr. Gary Kofinas of University of Alaska.
 - b. A second new component of the ISSE effort is to develop a common conceptual framework for interpreting and understanding research at diverse LTER sites. This

framework is built around the concept of disturbance regimes (pulse and press, anthropogenic and nonanthropogenic); we are working with the network to link this framework with our ongoing research and with our future monitoring and experimental plans (e.g., Figure F-1, F-2).

- c. Third, we are actively expanding education activities of the ARC LTER. Much of this is made possible by the growth of the Toolik Field Station itself, including recent additions of meeting/classroom space and living quarters. As part of the AON activities described above, in 2007 we will begin teaching a field course in Arctic Ecology. Assuming greater funding becomes available, we also hope to expand our interactions with the schools at Barrow, Alaska as part of our Schoolyard program.
 - d. Finally, recent improvements to Toolik Field Station include the capacity for year round operation, making it possible for heated instruments and communications even in midwinter. Our new AON observations will run year-round starting in 2007-2008 and we are just beginning to define the activities as part of the ARC LTER that will take advantage of this new capacity.
3. Prepare for collaboration with new, regional and global research programs including IPY (International Polar Year) and NEON (National Environmental Observatory Network):
 - a. The Arctic Observatory Network (AON) currently consists of 27 projects funded as part of the US contribution to the International Polar Year (IPY). The projects include research on the arctic atmosphere, oceans, and land as well as cyberinfrastructure (<http://www.eol.ucar.edu/projects/aon-cadis/>). At least 4 of these projects are either based at Toolik Lake or are planning significant activity there. One project, a collaboration of several ARC investigators at the MBL and UAF, involves the establishment of 2-3 eddy correlation towers for development of a time series of observations of C, water, and surface energy balance. There are many opportunities for collaboration of ARC with the AON network including the testing of models based on our detailed process-level research and results of our long-term experiments. One of the objectives is development of a PanArctic flux data base, and we are actively engaged in setting this up in a way that allows optimum use and application of the >20 years of LTER research. The IPY began in March 2007 and will continue for 2 years; like LTER, however, most of the IPY-AON activities are expected to continue indefinitely.
 - b. The National Environmental Observatory Network (NEON; <http://www.neoninc.org/>) will be a network of 20 regional sites throughout the US where long-term, multivariable observations are maintained for many years. Although the NEON program has not yet started it is expected to begin establishing sites in 2008; so far Toolik Lake is included among the Core Sites chosen in the initial NEON design review. We are hopeful that NEON research will begin at Toolik Lake within the next 2-3 years. If so Toolik Lake will be the only site where LTER, IPY, and NEON overlap, creating a particularly powerful suite of research opportunities.
 4. Continue to attract new collaborating research projects with new investigators and new skills/interests. LTER research and its applications are enriched greatly by collaborations with independently-funded projects that complete their research on LTER sites and long-term experimental plots. The spectrum of collaborating projects is constantly changing; in the

next few years we are particularly interested in increasing the number and diversity aquatic projects. Current priorities include:

- a. Aquatic research projects, especially in the areas of hydrology, trophic interactions, and land-water interactions.
- b. Terrestrial projects in birds, mammals, and insects.
- c. Microbial communities, functions, and diversity
- d. Develop and expand modeling capabilities especially in
 - i. large-area land/water/atmosphere interactions
 - ii. coupled element cycles in heterogeneous landscapes

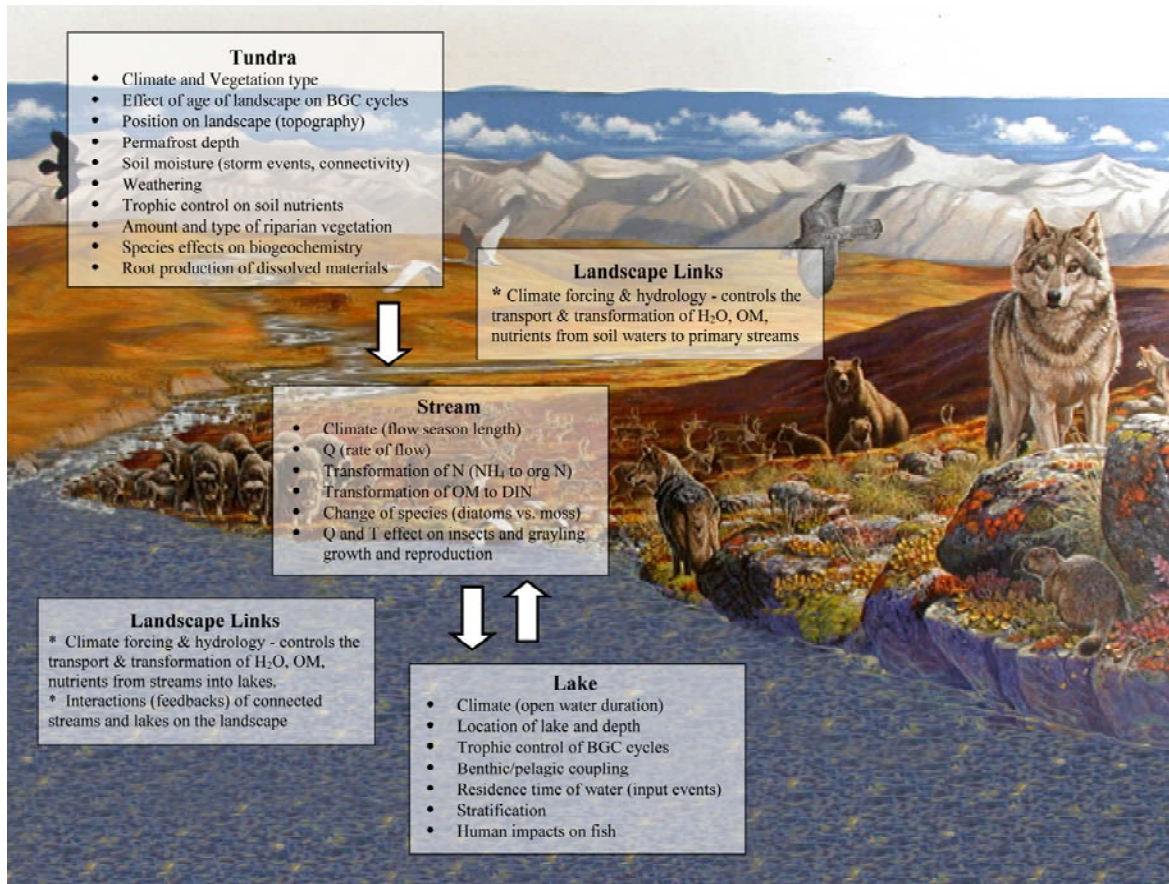


Figure 2-3. The conceptual framework of the Arctic LTER project with a background of the foothills and mountains at Toolik Lake, Alaska (modified from the U.S. Postal Series Number 5, Nature of America). The large boxes are the three components of the landscape. The bullets inside the boxes are the factors and linkages within ecosystems that affect the formation, transformation, and movement of water, nutrients, and organic matter (OM). The two smaller boxes are the linkages between components. The bullets inside the boxes are the factors that control the transport and transformation of between components. BGC is biogeochemical; OM is organic matter; N is nitrogen; DIN is dissolved inorganic nitrogen.

Figure F-1. The current conceptual framework of the Arctic LTER project (from our 2004 proposal).

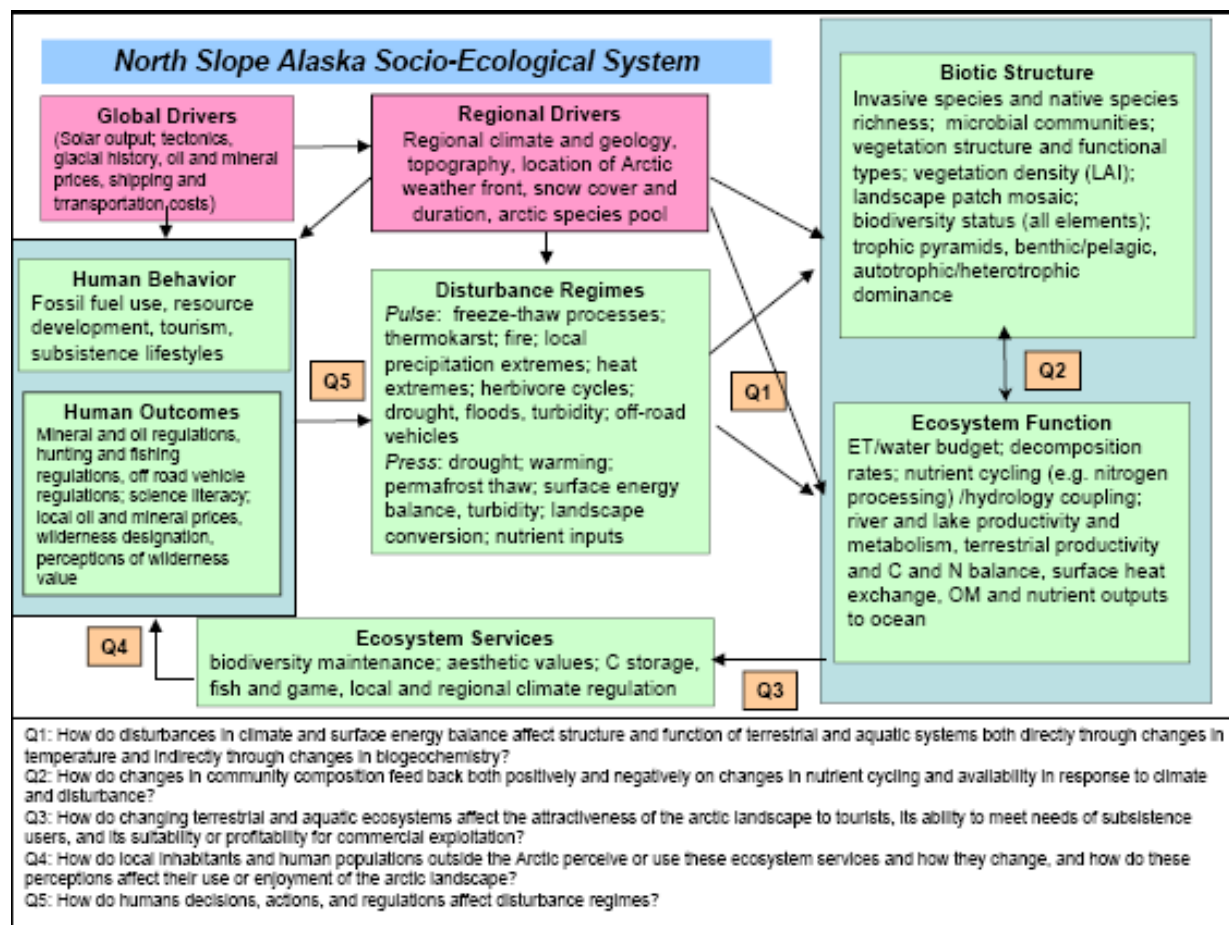


Figure F-2. The Arctic LTER in the ISSE framework. In northern Alaska, the main kinds of disturbances related to human use of the landscape include those resulting from subsistence life styles, tourism, hunting and fishing, and oil and mineral resource development. Key features of the natural disturbance regimes are those related to surface energy and water balance, especially the formation and thawing of the continuous permafrost that underlies the entire landscape, and flooding and droughts effects on aquatic systems. Climate warming is a press disturbance that has already started in this region. Herbivore cycles (both large and small mammals) are also important disturbances; fires are currently rare but may become more common and frequent. Humans affect these disturbance regimes through physical disruption of the permafrost-soil-vegetation-atmosphere energy equilibrium, by changing surface water flows and patterns of snow accumulation, and by hunting and fishing. This feedback loop indicates several potential points of collaboration with the LTER network.

10. CHRONOLOGY OF GRANT SUPPORT FOR ARCTIC LTER AND RELATED PROJECTS

LTER grants

NSF 8702328 An LTER Program for the Alaskan Arctic

John Hobbie (Principal Investigator)
\$2,419,499
9-1-87 to 2-28-93

NSF DEB 9211775 The Arctic LTER Project: Terrestrial and Freshwater Research on Ecological Controls

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
\$4,230,405
9-1-92 to 12-31-99

NSF DEB 9810222 The Arctic LTER Project: The Future Characteristics of Arctic Communities, Ecosystems, and Landscapes

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
\$4,498,703
12-15-98 to 11-30-05

LTER-related grants

1975

NSF-OPP 7512951 Aquatic Ecosystem Modeling and the Role of Bacteria in Alaskan Arctic Lakes

John Hobbie (Principal Investigator)
3-15-75 to 3-15-78
\$90,000

NSF OPP 7512949 Controls of Zooplankton Productivity in Large Arctic Lakes Of Alaska

W. John O'Brien
\$34,000
5-1-75 to 9-30-77

NSF-OPP 7512945 Dynamics and Ecological Role of Sestonic Detritus in Alaskan Arctic Lakes

Michael Miller
3-15-75 to 3-15-78
\$60,000

NSF DEB 0423385 The Arctic LTER Project: Regional Variation in Ecosystem Processes and Landscape Linkages

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
W. John O'Brien (Co-Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
George Kling (Co-Principal Investigator)
\$2,533,360
12-1-04 to 11-30-07

1976

NSF OPP 7607929 Collaborative Research on Aquatic Ecosystem Modeling and The Role of Bacteria in Alaskan Arctic Lakes

John Hobbie (Principal Investigator)
\$52,000
4-1-76 to 6-30-78

NSF OPP 7607931 Controls of Zoobenthos in North Slope Lakes – Fish Predation in *Nitella* Beds

Samuel Mozley
\$60,000
3-15-75 to 3-15-78

NSF OPP 7680652 Collaborative Research on Controls of Zooplankton Productivity in Large Arctic Lakes of Alaska

W. John O'Brien
\$20,000
1-1-77 to 6-30-78

ERDA-DOE #EE-77-03-1525. Research on dynamics of tundra ecosystems and their potential response to energy resource development.
Gaius Shaver (Co-principal investigator and subcontractor.)
6-76 to 5-79

NSF OPP 7680650 Role of Zooplankton in North Slope Tundra Lakes Role of Zooplankton in North Slope Tundra Lakes
James Haney
\$12000
1-1-77 to 6-30-78

1977

NSF OPP 7706656 Workshop on Arctic Alaska Limnology to Be Held in Woods Hole, Massachusetts During May, 1977
John Hobbie (Principal Investigator)
\$29,500
4-15-77 to 9-30-78

NSF OPP 7722564 Nitrogen Nutrient Relationships, Arctic Lake Process Studies (Alps)
Vera Alexander (Principal Investigator)
\$27,500
5-1-78 to 10-31-79

NSF OPP 7722994 Controls of Arctic Zooplankton, Arctic Lake Process Studies (Alps)
W. John O'Brien (Principal Investigator)
\$25,200
5-1-78 to 10-31-79

NSF OPP 7723475 Phosphorus in Arctic Lakes, Arctic Lake Process Studies (Alps)
Robert Barsdate (Principal Investigator)
\$26900
5-1-78 to 5-31-79

NSF OPP 7723879 Arctic Streams and Arctic Bacteria, Arctic Lake Process Studies (Alps)
John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
\$131,462
5-1-78 to 10-31-81

NSF OPP 7723883 Microbial Degradation of Organic Compounds, Arctic Lake Process Studies (Alps)
J. Robie Vestal (Principal Investigator)
\$9000

5-1-78 to 10-31-79
1978

NSF OPP 7827574 Microbial Degradation of Organic Compounds in Arctic Waters, A Component of Project Alps (Arctic Lake Process Studies)
J. Robie Vestal (Principal Investigator)
\$28000
5-1-79 to 9-30-81 \$28000

NSF OPP 7828041 Controls of Arctic Zooplankton Production: a Component of Project Alps (Arctic Lake Process Studies)
W. John O'Brien
\$51,320
5-1-79 to 10-31-81

EPA R804152010 Effect of Petroleum Hydrocarbons on Microbial Populations in an Arctic Lake
Robert Barsdate

ERDA E 11-1-2989 Effect of Petroleum Hydrocarbons on Microbial Populations in an Arctic Lake
John Hobbie

1979
U.S. Army Research Office DAA629-76-6-0296 Revegetation of Alaskan disturbed sites by native tundra species.
Gaius Shaver (Subcontractor and co-principal investigator.)
5-97 to 4-82
5-82 to 4-85

NSF OPP 7900815 Nitrogen Cycle Process Studies in Arctic Lakes and Streams, A Component of Project Alps (Arctic Lake Process Studies)
Vera Alexander vera@sfos.uaf.edu (Principal Investigator)
\$65086
5-15-79 to 8-31-81

NSF-DEB 7905842 Mobile Carbon Pools in Arctic Tundra Plants
F. Stuart Chapin (Principal Investigator)
Gaius Shaver (Subcontractor and Principal Investigator.)
\$207,339
5-15-79 to 10-31-82

1980

NSF DEB-80-04174 Recovery of nutrients from senescing plant tissues: Its controls and its role in nutrient cycling.

Gaius Shaver (Principal Investigator)

Jerry Melillo (Co-Principal Investigator)

\$155,075

7-1-80 to 12-31-82

U.S. Army CRREL DACA89-80-M-1453 Baseline studies in arctic plant growth: Effects of latitude and annual climatic variation.

Gaius Shaver (Principal Investigator.)

6-80 to 11-80

6-81 to 6-82

6-82 to 6-83

6-83 to 6-84

1981

NSF OPP 8102875 Arctic Lake Process Studies -- a Synthesis

John Hobbie (Principal Investigator)

Bruce Peterson (Co-Principal Investigator)

\$81,653

8-15-81 to 11-30-83

1982

NSF-DEB-8205344 The Relationship of Relative Growth Rate of Plants to Ecosystem Processes in Alaskan Tundra

F. Stuart Chapin (Principal Investigator)

Gaius Shaver (Subcontractor and Co-principal Investigator.)

\$500,000

7-1-82 to 6-30-86

NSF OPP 8219260 Collaborative Research on Responses of Arctic Freshwater Ecosystems to Increased Nutrients and Changes in Predator Abundance

John Hobbie (Principal Investigator)

\$389,000

8-15-83 to 1-31-85

1983

NSF OPP 8320544 Response of Arctic Freshwater Ecosystems to Environmental Stress

John Hobbie (Principal Investigator)

Bruce Peterson (Co-Principal Investigator)

\$1,529,808

6-1-84 to 11-30-89

1984

DOE-U8406034. Nutrient cycling on river floodplains in Arctic Alaska: Variation in biogeochemistry and response to disturbance.

Gaius Shaver (Principal Investigator)

7-84 to 12-86

1985

NSF -DEB 8507493 Nutrient Cycling in an Arctic Landscape: Interactions Between Ecosystems Along a Riverside Toposequence

Gaius Shaver (Principal Investigator)

\$816,577

9-15-85 to 8-31-89

1986

1987

NSF OPP8722015 Changes in Arctic Freshwaters

John Hobbie (Principal Investigator)

Bruce Peterson (Co-Principal Investigator)

\$1,423,722

3-15-88 to 8-31-91

1988

NSF DEB 8806635 Biogeochemical diversity in the Arctic landscape: Element transport and the spread of disturbance effects.

Gaius Shaver (Principal Investigator)

Knut Nadelhoffer (Co-Principal Investigator)

Edward Rastetter (Co-Principal Investigator)

Anne Giblin (Co-Principal Investigator)

\$365,299

9-15-88 to 8-31-91

DOE-19X-SC968V Response of northern ecosystems to global climate change.

Gaius Shaver (Subcontractor.)

10-88 to 9-89

1989

NSF-DEB 8904503 International Conference on "Physiological Process Studies in the Arctic: Implications for Ecosystem Response to Climate Change held on August 3-6, 1989 in Toronto, Canada."

F. Stuart Chapin terry.chapin@uaf.edu (Principal Investigator)

James Reynolds (Co-Principal Investigator)

Gaius Shaver (Co-Principal Investigator)

\$49,830

7-1-89 to 6-30-90

NSF DEB 8918273 The Controls of Sulfur Storage in Lake Sediments by Interactions among the Carbon, Iron, Oxygen and Sulfur Cycles

Anne Giblin (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Brian Fry (Co-Principal Investigator)
\$899,726
5-15-90 to 4-30-94

1990

NSF BSR-9019055. Global Change and the Carbon Balance of Arctic Ecosystems: The Importance of Carbon/nutrient Interactions.

Gaius Shaver (Principal Investigator)
Knut Nadelhoffer (Co-Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
Anne Giblin (Co-Principal Investigator)
\$1,272,358
11-1-91 to 10-31-96

NSF OPP 9024188 Freshwater Systems

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
Linda Deegan (Co-Principal Investigator)
\$2,547,508
8-1-91 to 1-31-96

1991

1992

NSF ANT 9214961 Attaining Ecological Understanding at the Regional Level: The Kuparuk River as a Model Arctic System

John Hobbie (Principal Investigator)
\$117,682
9-15-92 to 8-31-94

1993

NSF DEB 9307888 Recovery of Terrestrial Ecosystems from Major Disturbance: Constraints Due to Carbon/Nutrient Interactions

Edward Rastetter (Principal Investigator)
Jerry Melillo (Co-Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
\$850,000
8-1-93 to 7-31-97

NSF ARC 9318529 Attaining Ecological Understanding at the Regional Level: The Kuparuk River as a Model Arctic System

John Hobbie (Principal Investigator)
\$569,642
6-1-94 to 5-31-99

1994

NSF ARC 9400722 Controls of Structure and Function of Aquatic Ecosystems in the Arctic

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
Linda Deegan (Co-Principal Investigator)
\$2,726,000
6-15-94 to 5-31-99

NSF ARC 9415411 Primary Production in Arctic Ecosystems: Interacting Mechanisms of Adjustment to Climate Change

Gaius Shaver (Principal Investigator)
Edward Rastetter (Former Principal Investigator)
\$1,131,500
4-15-95 to 6-30-02

NSF DEB 9416807 Investigating Controls on the Benthic Flux of Nitrogen and Phosphorus from Lake Sediments: A Comparative Ecosystems Approach

Anne Giblin (Principal Investigator)
\$200,000
11-1-94 to 10-31-98

1995

NSF ARC 9509613 Multiple Resource Interactions and Ecosystem Function

Edward Rastetter (Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
\$400,000
10-1-95 to 9-30-00

NSF DEB 9509348 RUI: Landscape Control of Trophic Structure in Arctic Alaskan Lakes

Anne Hershey (Principal Investigator)
Michael Miller (Co-Principal Investigator)
John Pastor (Co-Principal Investigator)
Michael McDonald (Co-Principal Investigator)
Carl Richards (Co-Principal Investigator)
\$200,000
11-1-95 to 10-31-98

NSF ANT 9522061 Ecological Responses to Increases in Carbon Dioxide Concentration and Temperature: A Global Change Study at Abisko, Sweden

John Hobbie (Principal Investigator)
Jerry Melillo (Former Principal Investigator)
\$215,842
9-1-95 to 8-31-99

American Geophysical Union: Travel grant to attend NATO workshop on Disturbance and Recovery of Arctic Terrestrial Ecosystems, Rovaniemi, Finland. September 1995

Gaius Shaver
\$2,200
9-95

1996

NSF ARC 9614038 Modeling Canopy Carbon and Energy Balances in the Pan- Arctic: Scaling from Leaf to Region

Edward Rastetter (Principal Investigator)
Gaius Shaver (Co-Principal Investigator)
Mathew Williams (Co-Principal Investigator)
\$285,707
9-1-96 to 8-31-00

NSF-DEB-9615563 Global Change and the Carbon Balance of Arctic Ecosystems: The Importance of Carbon/nutrient Interactions in Soils.

Gaius Shaver (Principal Investigator and Co-Principal Investigator)
\$743,000
4-97 to 3-00

NSF ARC 9615949 Key Connections in Arctic Aquatic Landscapes

John Hobbie (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Linda Deegan (Co-Principal Investigator)
Anne Giblin (Co-Principal Investigator)
\$2,977,554
5-1-97 to 4-30-02

NSF ARC 9615986 Collaborative Project: Effects of Climate-Landscape Interactions on Carbon Storage in Arctic Alaska

George Kling
\$65,941
9-1-96 to 8-31-99

NSF ARC 9622157 Development Of A Linked Hydro-Biogeochemical Model For An Arctic Watershed

Anne Giblin (Principal Investigator)
\$115,024
4-15-96 to 3-31-99

NSF-DEB 9628860 Nitrogen Uptake, Retention and Cycling in Stream: An Intersite N-15 Tracer Experiment

Jackson Webster (Principal Investigator)
Bruce Peterson (Co-Principal Investigator)
Judith Meyer (Co-Principal Investigator)
Patrick Mulholland (Co-Principal Investigator)
\$1,135,057
9-1-96 to 8-31-01

1997

NSF DEB 9711626 MMIA: Terrestrial Biospheric Responses to Atmospheric Deposition and Application to Integrated Assessment

Edward Rastetter (Principal Investigator)
Ronald Prinn (Co-Principal Investigator)
A. David McGuire (Co-Principal Investigator)
Xiangming Xiao (Co-Principal Investigator)
\$400,000
1-15-98 to 12-31-02

NSF OPP-9732281 The Response of Carbon Cycling in Arctic Ecosystems to Global Change: Regional and Pan-Arctic Assessments

John Hobbie (Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
Mathew Williams (Co-Principal Investigator)
\$1,000,000
4-15-98 to 3-31-05

NSF ARC 9714327 LEXEN: Ecology of Microbial Systems in Extreme Environments: The Role of Nanoflagellates in Cold and Nutrient-Poor Arctic Freshwaters

John Hobbie (Principal Investigator)
Mitchell Sogin (Co-Principal Investigator)
\$300,000
9-15-97 to 8-31-01

1998

1999

NSF ARC 9902695 Collaborative Research: Moist Acidic Versus Nonacidic Tundra: Why does the Vegetation Composition Differ and What Are The Consequences for Ecosystem Carbon Storage?

Sarah Hobbie (Principal Investigator)

\$225,141

5-1-99 to 4-30-03

NSF ARC 9911681 Developing Process-Level Understanding of Controls on Belowground Carbon and Nutrient Dynamics in Tundra Ecosystems

George Kling (Principal Investigator)

Knut Nadelhoffer (Former Principal Investigator)

Edward Rastetter (Co-Principal Investigator)

\$1,653,896

2-15-00 to 1-31-04

NSF OPP-9911278 Aquatic Ecosystem Responses to Changes in the Environment of an Arctic Drainage Basin

John Hobbie (Principal Investigator)

Bruce Peterson (Co-Principal Investigator)

Linda Deegan (Co-Principal Investigator)

Anne Giblin (Co-Principal Investigator)

Joseph Vallino (Co-Principal Investigator)

\$4,563,868

7-1-00 to 6-30-07

2000

NSF ARC 0002369 Collaborative Research: Modeling Hydrologic Processes in the Arctic: A Watershed Approach for Regional and Global Climate Models

Marc Stieglitz (Principal Investigator)

Colin Stark (Co-Principal Investigator)

\$283,890

9-1-00 to 8-31-03

NSF DBI 0084048 FSML: An Analytical Laboratory for Examination of Land Use Change and Its Consequences for Aquatic Ecosystems

Anne Giblin (Principal Investigator)

Christopher Neill (Co-Principal Investigator)

\$173,889

9-1-00 to 8-31-03

NSF DEB-0087046 LTER Cross Site 2000: Interactions between climate and nutrient cycling in arctic and subarctic tundras

Gaius Shaver (Principal Investigator)

Mathew Williams (Co-Principal Investigator)

\$318,000

10-1-00 to 9-30-05

NSF DEB-0089585 Turnover and Retention of Nitrogen in an Arctic Watershed: Links to Organic Matter Accumulation and Response to Climate

Gaius Shaver (Principal Investigator)

Knut Nadelhoffer (Co-Principal Investigator)

Edward Rastetter (Co-Principal Investigator)

Anne Giblin (Co-Principal Investigator)

\$1,110,892

9-15-01 to 8-31-05

NSF DEB 0090202 RUI: A Geomorphic-Trophic Hypothesis for Arctic Lake Productivity

Anne Hershey (Principal Investigator)

W. John O'Brien (Co-Principal Investigator)

Stephen Whalen (Co-Principal Investigator)

Chris Luecke (Co-Principal Investigator)

Carl Richards (Co-Principal Investigator)

\$1,222,840

5-1-01 to 9-30-05

NSF OPP-0096523 Primary Production in Arctic Ecosystems: Interacting Mechanisms of Adjustment to Climate Change

Gaius Shaver (Principal Investigator)

\$533,119

1-1-01 to 12-31-04

2001

NSF DEB- 0108960 Species-, Community-, and Ecosystem-Level Consequences of the Interactions Among Multiple Resources

Edward Rastetter (Principal Investigator)

Gaius Shaver (Co-Principal Investigator)

\$417,946

7-15-01 to 6-30-05

2002

NSF DEB 0212749 Collaborative Research on the Effects of Plant Species and Functional Types on Diversity, Ecosystem Function, and Ecosystem Response to Perturbation in Arctic Tundra

Michelle Mack (Principal Investigator)

\$185,454

8-1-02 to 7-31-06 (collaborative research with Marion Bret-Harte)

NSF DEB 0213130 Collaborative Research on the Effects of Plant Species and Functional Types on Diversity, Ecosystem Function, and Ecosystem Response to Perturbation in Arctic Tundra

Marion Bret-Harte (Principal Investigator)

\$375,046

8-1-02 to 7-31-06

NSF ATM 0221835 BE/CBC: Land-Water Interaction at the Catchment Scale: Linking Biogeochemistry and Hydrology

Marc Stieglitz (Principal Investigator)

John Hobbie (Co-Principal Investigator)

George Kling (Co-Principal Investigator)

Joshua Schimel (Co-Principal Investigator)

Kevin Griffin (Co-Principal Investigator)

\$1,411,660

9-1-02 to 9-30-04

2003

NSF OPP-032740 Will Climate Change Affect Hyporheic Processes in Arctic Streams? An Assessment of Interactions among Geomorphology, Hydrology, and Biogeochemistry in Arctic Stream Networks

William Bowden (Principal Investigator)

James McNamara (Co-Principal Investigator)

Michael Gooseff (Co-Principal Investigator)

\$608,708

8-1-03 to 7-31-07

NSF OPP-0352897 Resource Allocation and Allometry of Plant Growth in the Arctic: Key Constraints on Change and Predictability of the Arctic System

Gaius Shaver (Principal Investigator)

\$892,302

5-1-04 to 4-30-08

2004

NSF ARC 0408371 Developing Process-Level Understanding of Controls on Belowground Carbon and Nutrient Dynamics in Tundra Ecosystems

George Kling (Principal Investigator)

Knut Nadelhoffer (Co-Principal Investigator)

\$802,340

9-1-03 to 1-31-07

NSF 0425045 Science Journalism Program for the Arctic

John Hobbie (Principal Investigator)

Christopher Neill (Co-Principal Investigator)

Pamela Clapp (Co-Principal Investigator)

Kenneth Foreman (Co-Principal Investigator)

\$164,073

5-5-04 to 4-30-07

NSF ARC 0425606 Collaborative Research: Aboveground and Belowground Community Responses to Climate Changes in Arctic Tundra

John Moore (Principal Investigator)

\$296,644

8-15-04 to 11-30-06

NSF ARC 0425827 Collaborative Research: Aboveground and Belowground Community Responses to Climate Change in Arctic Tundra

Laura Gough (Principal Investigator)

\$152,149

8-15-04 to 7-31-07

NSF ARC 0436118 Synthesis and Scaling of Hydrologic and Biogeochemical Data on the North Slope and Coastal Zones of Alaska: A Basis for Studying Climate Change

Marc Stieglitz (Principal Investigator)

Bruce Peterson (Co-Principal Investigator)

Robert Holmes (Co-Principal Investigator)

James McClelland (Co-Principal Investigator)

\$677,402

1-1-05 to 12-32-07

NSF ATM 0439620 BE/CBC: Land-Water Interaction at the Catchment Scale: Linking Biogeochemistry and Hydrology

Marc Stieglitz

\$1,009,967

1-1-04 to 8-31-07

NSF DEB 0444592 Loss and Retention of Nitrogen in an Arctic Landscape: Key Pathways and Process Regulation

Gaius Shaver (Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
Anne Giblin (Co-Principal Investigator)
\$912,000
1-5-05 to 12-31-07

2005

NSF DEB 0516041 Collaborative Research on Shrub-Snow Interactions in Alaskan and Canadian Tundra and their Potential for Positive Feedbacks to Vegetation and Climate Change

Michelle Mack (Principal Investigator)
\$186,000
8-15-05 to 7-31-08

NSF DEB 0516043 RUI: A Geomorphic-Tropic Hypothesis for Benthic-Pelagic Coupling in Arctic Lakes

Anne Hershey (Principal Investigator)
W. John O'Brien (Co-Principal Investigator)
Stephen Whalen (Co-Principal Investigator)
Chris Luecke (Co-Principal Investigator)
Roy Stine
\$855,999
8-15-05 to 7-31-08

NSF DEB 0516509 Collaborative Research on Snow-Shrub Interactions in Alaskan and Canadian Tundra and their Potential for Positive Feedbacks to Vegetation and Climate Change

Marion Bret-Harte (Principal Investigator)
Paul Grogan (Co-Principal Investigator)
\$471,000
8-15-05 to 7-31-08

2006

NSF ARC 0611995 Factors Controlling Seasonal Changes in the Structure and Function of Food Webs of Perennial Spring Streams in Arctic Alaska

Alexander Huryn (Principal Investigator)
Jonathan Benstead (Co-Principal Investigator)
\$541,347
9-1-06 to 8-31-09

NSF ARC 0612340 Science Journalism Program for the Arctic

John Hobbie (Principal Investigator)
Christopher Neill (Co-Principal Investigator)
Pamela Clapp (Co-Principal Investigator)
Kenneth Foreman (Co-Principal Investigator)
\$16,298
4-15-07 to 3-31-08

NSF ARC 0612595 Collaborative Research: Most Arctic Plants Obtain Nitrogen by Symbiosis with Fungi: Development of a Radical Concept Cooperative Project

John Hobbie
\$120,250
8-15-06 to 7-31-08

NSF ARC 0632139 IPY: Collaborative Research on Carbon, Water, and Energy Balance of the Arctic Landscape at Flagship Observatories and in a PanArctic Network

Gaius Shaver (Principal Investigator)
John Hobbie (Co-Principal Investigator)
Edward Rastetter (Co-Principal Investigator)
\$395,656
3-15-07 to 2-29-08

NSF ARC 0632264 IPY: Collaborative Research on Carbon, Water, and Energy Balance of the Arctic Landscape at Flagship Observatories and in a Pan-Arctic Network

Marion Bret-Harte (Principal Investigator)
Brian Barnes (Co-Principal Investigator)
Sergei Zimov (Co-Principal Investigator)
\$708,344
3-15-07 to 2-29-08

NSF DEB 0639790 LTREB: Collaborative Research: What Controls Long-term Changes in Freshwater Microbial Community Composition?

Byron Crump (Principal Investigator)
\$112,985
1-15-07 to 12-31-08

NSF DEB 0639805 LTREB: Collaborative Research: What Controls Long-term Changes in Freshwater Microbial Community Composition?

George Kling
\$69,351
1-15-07 to 12-31-08

2007

**NSF ARC 0701295 Collaborative Research:
Aboveground and Belowground Community
Responses to Climate Changes in Arctic Tundra**

John Moore (Principal Investigator)

\$135,214

8-31-06 to 7-31-07

11. ARCTIC LTER PUBLICATIONS 1998 to 2003

- Agren, G., G. R. Shaver, and E. B. Rastetter. 1999. Nutrients: Dynamics and Limitations. Pages 333-345 in Y. Luo and H. A. Mooney, editors. *Carbon Dioxide and Environmental Stress*. Academic Press, New York.
- Arft, A., M. Walker, P. Turner, J. Gurevitch, J. Alatalo, U. Molau, U. Nordenhaell, A. Stenstroem, M. Stenstroem, M. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, and G. Henry. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs* **69**:491-511.
- Arscott, D. B., W. B. Bowden, and J. C. Finlay. 1998. Comparison of epilithic algal and bryophyte metabolism in an arctic tundra stream, Alaska. *Journal of the North American Benthological Society* **17**:210-227.
- Arscott, D. B., W. B. Bowden, and J. C. Finlay. 2000. Effects of desiccation and temperature/irradiance on the metabolism of 2 arctic stream bryophyte taxa. *Journal of the North American Benthological Society* **19**:263-273.
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- Brown, J., G. W. Kling, K. M. Hinkel, L. D. Hinzman, F. E. Nelson, V. E. Romanovsky, and N. I. Shiklomonov. 2002. Arctic Alaska and Seward Peninsula. Pages 165-258 in J. J. Brown, K. M. Hinkel, and F. E. Nelson, editors. *The circumpolar active layer monitoring (CALM) program: Research designs and initial results. Polar Geography*.
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- Buzby, K., and L. A. Deegan. 2000. Inter-annual fidelity to summer feeding sites in arctic grayling. *Environmental Biology of Fishes* **59**:319-327.
- Buzby, K., J. Hobbie, L. Deegan, M. McDonald, and B. Peterson. 1999. Effects of fertilization on fish in Alaskan arctic tundra streams and lakes. Pages 99-112 in J. G. Stockner and G. Milbrink, (eds.) *Restoration of Fisheries by Enrichment of Aquatic Ecosystems*. Uppsala University, Uppsala, Sweden.
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