

## **The Arctic LTER: Regional Variation In Ecosystem Processes And Landscape Linkages**

**Intellectual Merit.** At Toolik Lake, Alaska, the ecology of tundra, streams, and lakes has been studied to gain an understanding of the controls of ecosystem structure and function: *the long-term goal is to predict the effects of environmental change*. Although there are now a number of well-studied ecosystems, it is clear that there is variability among ecosystems at the site because of such factors as differences in glacial age of the soils, differences in tundra vegetation, differences in the chemistry of water entering streams and lakes, differences in stream size and differences in size and depth of lakes. It is also clear that the movement of water and materials 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. A <sup>15</sup>N-labeling experiment will determine more explicitly the rates and forms of downslope N movement. Continuing long-term studies will 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 upslope 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.

**Broader Impacts.** The research addresses an important societal goal: the prediction of response of arctic ecosystems to environmental change. The data and insights are provided to federal and Alaska officials regulating the development of oil and gas on the North Slope.

A 20-person undergrad/graduate course is given jointly by the University of Alaska and MBL for 14 days in August. Undergraduates (2 REUs from LTER and 2-6 from collaborating NSF grants) spend 6-8 weeks in the field. There are 17 graduate students from 10 universities presently at work and several more are expected through the new Brown/MBL joint graduate program. Through the Science Journalism Course (MBL), several journalists visit Toolik Lake. The Arctic LTER sponsors a Schoolyard project at Barrow where most of the participants are Native Americans. Students (K-12) conduct and observe field experiments similar to those at Toolik Lake and residents hear talks on science topics by local and visiting scientists.

## TABLE OF CONTENTS

---

For font size and page formatting specifications, see GPG section II.C.

	<b>Total No. of Pages</b>	<b>Page No.* (Optional)*</b>
Cover Sheet for Proposal to the National Science Foundation		
Project Summary (not to exceed 1 page)	1	_____
Table of Contents	1	_____
Project Description (Including Results from Prior NSF Support) (not to exceed 15 pages) <b>(Exceed only if allowed by a specific program announcement/solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)</b>	50	_____
References Cited	12	_____
Biographical Sketches (Not to exceed 2 pages each)	20	_____
Budget (Plus up to 3 pages of budget justification)	30	_____
Current and Pending Support	37	_____
Facilities, Equipment and Other Resources	2	_____
Special Information/Supplementary Documentation	25	_____
Appendix (List below. ) <b>(Include only if allowed by a specific program announcement/ solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)</b>	_____	_____
Appendix Items:		

\*Proposers may select any numbering mechanism for the proposal. The entire proposal however, must be paginated. Complete both columns only if the proposal is numbered consecutively.

---

## **SECTION 1: Results of Prior LTER Support (BSR-8702338, DEB-9211775, 9810222)**

**Goals of Previous LTER Projects.** The Arctic LTER was first funded in 1987 but research at the site began in 1975. Since then, we have made use of descriptive studies of the organisms, of measurements of rates and controls, and of long-term experiments on tundra, streams, and lakes. The goals of prior LTER projects were:

- LTER I (1987) and LTER II. (1992). Understand how tundra, streams, and lakes function in the Arctic and predict how they respond to changes including climate change.
- LTER III (1998). Understand the present and predict the future characteristics of arctic communities, ecosystems, and landscapes based on knowledge of the controls of ecosystem structure and function by physical, climatic, and biotic factors.

**Publications from LTER Research.** Table 1 (Supplementary Documentation) lists 109 journal articles published or accepted, 15 journal articles submitted, 19 chapters in books, 6 theses and dissertations, and 10 other publications for the period 1998-2003. The published or accepted papers have appeared in 43 different journals; those with multiple publications include Science (2); Nature (2); Ecology, Ecological Monographs, or Ecological Applications (11); Journal of Geophysical Research (8), Global Change Biology (7), Journal of the North American Benthological Society (7), BioScience (6), Journal of Ecology (6), Ecosystems (5), Global Biogeochemical Cycles (5), Freshwater Biology (4), Oikos (4), Biogeochemistry (3), Limnology and Oceanography (3), Plant and Soil (3), Oecologia (2), New Phytologist (2), Journal of Evolutionary Biology (2), Canadian Journal of Aquatic and Fisheries Science (2), and Journal of Hydrometeorology (2).

**Data Sets and Data Set Use.** As described in Tables 2 and 3 (Supplementary Documentation), the Arctic LTER data base contains ~1400 data sets (72 MB). In 2003 there were 12,329 hits on the data sets from outside the MBL and 600 from within MBL.

**Education and Outreach.** As described in Section 5 of this proposal, we supported the training of 34 REU students, 6 Master's and Ph.D. students (17 students are currently in progress), 5 foreign graduate students, a Science Journalism program, a field course in "Arctic Ecology and Modeling", and a Schoolyard LTER program in collaboration with the Barrow Arctic Science Consortium (most participants are Native Americans).

**Terrestrial Research Accomplishments.** Achieving the goal of "Predictions of Future Characteristics" of arctic ecosystems depends on a solid core of basic, process-level understanding that comes from descriptive and monitoring studies and from annual harvests of long-term experimental plots. Since 1998 the products of our terrestrial research have included:

- **NPP and vegetation biomass:** We showed that nutrient availability consistently and strongly limits production and biomass of a wide range of tundras at Toolik Lake, and documented long-term (up to 20 years) differences in responsiveness among these tundras (Shaver et al. 1998, 2001, Gough et al. 2002, Gough and Hobbie 2003, Mack et al. submitted).
- **Species composition and effects on biogeochemistry:** The mechanisms of change in species composition include dramatic interspecies differences in branch demography and in stem secondary growth (Bret-Harte et al. 2001, 2002). High C:N ratios in shrub wood, combined with more efficient use of N in leaves, make shrubs much more efficient at N use when N availability is increased in acidic tundra (Shaver et al. 2001).
- **Biodiversity and niche partitioning:** Although all species of moist tundra are strongly N-limited, they differ dramatically in the forms of N that they take up from the soil, including

amino acids as well as inorganic N (McKane et al. 2002, Nordin et al. in press). Species richness is related to NPP and to N supply (Gough et al. 2000), and probably also to overall N uptake and efficiency of N use (Hobbie et al. 1999, Bret-Harte et al. in review).

- **Soils processes:** Our most surprising result of the past 6 years is that long-term N+P fertilization leads to an overall *decrease* in C stocks, at least in the upper organic mat, of moist, wet, and dry tundras (Mack et al. submitted, Shaver unpublished data), suggesting that decomposition is also nutrient-limited and that even large increases in C fixation in a warmer climate may not exceed C loss resulting from increased soil N mineralization. Decomposition is strongly affected by species composition and is highly variable among soil and community types (Hobbie et al. 2002, Hobbie and Gough 2002, submitted, Schmidt et al. 2002).
- **Soil food webs:** Long-term fertilization has shifted the balance between the fungal and bacterial pathways at Toolik Lake, confirming studies at other LTER sites (Doles et al. 2000, Moore and de Ruiter 2000, Chinn 2001). We developed simple models of the bacterial and fungal pathways to explore the consequences of the observed shift on the dynamic stability of the system (Moore et al. 2003).
- **Biogeochemical modeling:** We developed a new, general model of N fixation (Rastetter et al. 2001), and improved our existing models to account more fully for downslope N movement (Rastetter et al. in press) and for dissolved N losses (Rastetter et al. submitted).
- **Scaling up and regional synthesis:** NDVI is a good predictor of vegetation biomass and NPP, at least within ecosystem types (Boelman et al. 2003). Across ecosystems, we have shown that leaf area index and canopy N content are consistently correlated across a wide range of plant functional types (Williams and Rastetter 1999, Van Wijk et al. manuscript). In collaboration with the NSF-Arctic Systems Science program, we have used this information to develop large-area models of productivity and C cycling (Williams and Rastetter 1999, Williams et al. 2001) and hydrology (Steiglitz et al. 2003a, 2003b).
- **PanArctic synthesis:** To test our ability to extrapolate our knowledge from northern Alaska to the rest of the Arctic, we used meta-analyses and empirical comparisons to determine overall patterns of vegetation response to long-term manipulations in Sweden and Alaska (Shaver and Jonasson 1999, Graglia et al. 2001, Schmidt et al. 2002, Van Wijk et al. 2003) and the entire Arctic (Arft et al. 1999, Cornelissen et al. 2001). Other products include reviews of arctic biogeochemistry (Shaver and Jonasson 2001, Jonasson and Shaver 1999, Jonasson et al. 2000, 2001) and element interactions in northern ecosystems (S. Hobbie et al. 2002).
- **Network and global synthesis:** Within the LTER Network, we contributed to cross-site syntheses of controls on biodiversity (Gough et al. 2000, Gross et al. 2000), NPP (Knapp and Smith 2001), climate variability and ecosystem response (Hobbie et al. 2003), and temporal and spatial scaling (Rastetter et al. 2003). Finally, we contributed to global analyses of response of soils to long term warming experiments (Rustad et al. 2001), and we reviewed current global understanding of long-term responses to atmospheric and climate change (Canadell et al. 2000, Shaver et al. 2000).

**Stream Research Accomplishments.** Research on streams at the Toolik Lake LTER has focused on long-term perturbation experiments involving bottom-up and top-down controls of stream community structure, controls of in-stream processes of production and nutrient spiraling, and regional surveys of contrasting stream types in the foothills region of the North Slope of Alaska.

### *Fertilization Experiments.*

- After a lag of about 8 years, the biota responded to long-term fertilization of the Kuparuk River by an increased abundance of bryophytes which now dominate primary production, nutrient retention and insect habitat in the P-enriched segment of the river (Bowden et al. 1999).
- Tundra streams of 2<sup>nd</sup> to 4<sup>th</sup> order consistently respond to inputs of available phosphorus with increased primary and secondary production (Slavik et al. in press, Harvey et al. 1998, Benstead et al. submitted).
- The success of different bryophyte species as colonists in Arctic streams can be understood in terms of their individual physiological ecology (Arscott 1997). This information helps understand how these keystone species might respond as a consequence of climate change.
- Trophic cascades are not strong in these tundra stream ecosystems. Only at extraordinarily high densities did fish have a small effect on algal grazing insects, and grazing insects consistently had little effect on algal biomass (Golden and Deegan 1998).

### *Stream Processes*

- The new in-situ estimates of dissolved oxygen change suggest that respiration is much higher and that tundra streams are mineralizing much more terrestrially-derived organic matter than we had previously estimated (Bowden 1999).
- Nitrogen tracer additions have shown that ammonium seeping into tundra streams is rapidly taken up or nitrified. Nitrate uptake is less rapid unless phosphorus levels are artificially increased. Uptake distances are related to stream depth with smaller streams removing DIN and fine particulates most efficiently (Peterson et al. 2001, Wollheim et al. 2001).
- Nutrients and discharge strongly controls fish growth (Deegan et al. 1999) but have surprising little effect on annual survival (Buzby and Deegan in press). Grayling show high fidelity to summer feeding territories (Buzby and Deegan 2000). Their migration to lakes where they over winter provides a subsidy of nutrients and organic matter to lake ecosystems and a high quality food resource for lake char (Deegan et al. in prep.).
- Studies of hyporheic dynamics in arctic streams (Edwardson et al. 2003) showed that during the thawed season biogeochemical processing of organic matter in the hyporheic zone of streams is as important as in temperate streams.

### *Regional Surveys.*

- Streams on the North Slope are diverse, including mountain, glacial, spring and tundra stream types. These streams support a surprisingly wide range of macroinvertebrate biomass that nearly equals the global range of reported values (Huryn et al. submitted).
- The invertebrate communities within these habitats are structured by 3 primary factors of nutrient availability, substrate stability and freezing probability. Refugia from freezing are much more widespread than previously thought (Huryn et al. submitted).
- Climate change will impact on the tundra stream type most because warming will lead to perennial flow and higher nutrients inputs from the landscape (Huryn et al. submitted).

Synthesis. Tracer studies of nitrogen cycling in streams at the Arctic LTER site have stimulated LTER inter-site studies of N cycling at sites throughout the US ( LINX 1 and 2 projects) and an inter-biome synthesis of N retention and spiraling in headwater streams (Peterson et al. 2001). Work at the Pan-Arctic scale on related NSF-OPP-Arctic System Science projects has synthesized knowledge of nutrient and sediment export and river discharge to the Arctic Ocean (Holmes et al. 2000, Holmes et al. 2002, Peterson et al. 2002). These inter-biome and Pan-Arctic projects allow us to place the Toolik LTER stream work into the larger context.

**Lake Research Accomplishments.** Previous LTER research on arctic lakes has focused on: **(1) lake foodwebs**- especially how predators regulated populations and structure communities, **(2) the impact of nutrient loading** on primary producers and their subsequent impact on the rest of lake food webs, and **(3) landscape impact** on lake function and structure.

#### *Lake Foodwebs*

- Food web effects are largely determined by the presence of fish. In large lakes, Lake Trout play a keystone role in lake communities. They have direct effects on prey organisms by controlling the size and density of benthic invertebrates and fish (Merrick et al. 1991, Hanson et al. 1992), and have indirect impacts on habitat distribution of Slimy Sculpin (Hanson et al. 1992).
- In the absence of fish, crustacean zooplankton biomass increased by 3-8 fold, but the rate of zooplankton grazing on phytoplankton only doubled (Burkart and Luecke, unpublished data). This reduction in grazing appears to derive from a shift to less edible phytoplankton in fishless lakes. The presence of fish did not affect nutrient limitation of phytoplankton (Gross et al. submitted).

#### *Nutrient Loading*

- We have conducted three lake nutrient additions experiments: In a divided lake experiment, the phytoplankton response was rapid but the zooplankton response was variable by species and lagged in time (O'Brien et al. submitted). The response of benthic animals was also variable with snails increasing in density in the treated sector but chironomids failing to respond (Hershey 1992).
- In a whole lake experiment phytoplankton were greatly stimulated but the zooplankton declined (Bettez et al. 2002). This strong eutrophication response resulted in shifts of the algal assemblage to largely inedible taxa and dramatic declines in oxygen in deeper waters.
- In an ongoing low level nutrient addition to a shallow and deep lake phytoplankton nearly doubled and zooplankton also increased. It appears that zooplankton respond to modest increases in phytoplankton but not to major increases.
- An Arctic Lake Model was developed that heats, thermally stratifies, cools, and freezes simulated arctic lakes. Results showed these lakes to be very sensitive to nutrient loading because many arctic lakes do not mix after ice out (Barfield and O'Brien submitted).

#### *Landscape Impact*

- Kling et al. (1999) found considerable synchrony and connectedness in water chemistry in a chain of lakes that ultimately empty into the largest lake, Toolik Lake.
- In a survey of more than 100 lakes, Hershey et al. (1999, 2000) found that lake depth and outlet steepness determined the presence of fish which then had profound influences on the benthic and pelagic animal communities. The benthic fish, sculpin, had the greatest effect on zooplankton assemblages with arctic grayling having little impact. Physical and chemical variables explained very little of zooplankton distribution except species diversity increased with both lake depth and area (O'Brien et al., in press).

**Landscape Interactions Research Accomplishments.** The general topic of land-water linkages, and specifically the movement of C and nutrients from terrestrial ecosystems to streams, lakes, and oceans, is of critical importance to understanding how ecosystems function. Previous LTER research on land-water linkages focused on **(1) Production Of Materials** - how climate, vegetation, and physical setting act to control the production of materials such as carbon and

nutrients in soil waters, **(2) Linkages** – how hydrology in turn controls the linkage between material exported from soils to streams and from streams to lakes, and **(3) Impacts** – how exported materials impact the receiving water bodies. The major findings from measurements and process studies are:

*Production of materials:*

- Tundra ecosystems have a much greater potential to transport carbon in surface waters to the ocean, and gases to the atmosphere, than previously estimated (Kling et al. 1991, 1992; Kling 1995; Reeburgh et al. 1998). Recent experiments demonstrated that vegetation type and hydrologic flushing are the dominant controls on production and transport of this carbon in soils (Judd and Kling 2002).
- $^{14}\text{CO}_2$  addition experiments indicate that recent photosynthates are rapidly transferred to soil waters and are important substrates for dissolved carbon production in soils (King et al. 2002; Loya et al. 2002).

*Linkages:*

- We determined that gas flux from lakes to the atmosphere is likely underestimated by current models. This linkage is controlled as much by internal lake mixing as it is by atmospheric conditions (Eugster et al. 2003; MacIntyre et al. 2002).
- Using a process model that predicts hydrological export (Stieglitz et al. 1999) we showed that the way water is “connected” belowground may have a large impact on element transport and how terrestrial ecosystems function (Stieglitz et al. 2003).
- Monitoring of a series of lakes and streams indicated that the behavior of aquatic ecosystems is more dependent on surrounding ecosystems than previously thought. The response of streams and lakes to climate and disturbance was shown to rely on the proximity and the processes of other surface waters, and not solely on internal processing (Kling et al. 2000; Soranno et al. 1999).

*Impacts*

- We discovered that bacterial communities in Toolik Lake undergo rapid seasonal succession in part driven by spring runoff inputs of organic matter (Crump et al. 2003). In addition, experiments show that the chemical environment of soil and stream bacteria is most responsible for determining the community composition of microbes (Judd et al. In prep).
- Initial results from experiments and models indicate that broadly applied methods for determining primary production in aquatic ecosystems may be biased. This bias is due to the finding that “fixed-depth” incubations routinely used underestimate the true productivity rates when compared to incubations that are allowed to move through the underwater light field in response to internal waves (Evans et al., in prep.).

**Service to the LTER network.** During this grant period, Gus Shaver served on the LTER Executive Committee and was the lead author of the White Paper prepared for the LTER 20-Year Review. John Hobbie is currently serving on the LTER Executive Committee and also edited the BioScience 2003 Special Section on the US Long Term Ecological Research Network. Bruce Peterson helped organize the LTER Synthesis Projects LINX 1 and 2 (Lotic Intersite Nitrogen Experiments) that use a standardized approach to study nitrogen cycling in small streams from Alaska to the desert Southwest and Puerto Rico.

## SECTION 2. PROJECT DESCRIPTION

**Introduction and Goal.** The Arctic landscape consists of a mosaic of landscape components, that is ecosystems of tundra, streams, and lakes. Since 1987 the research emphasis of the Arctic LTER has been on the controls over structure and function of these ecosystems. It has become clear that there is variability amongst ecosystems at the site and that the ecosystems are tightly linked by the movement of water and materials. These linkages can occur within and across ecosystems (i.e., riffle to pools, benthic to pelage lake systems, or the movement of material down slope within tundra). It is obvious that we can not understand even a single ecosystem without considering its linkages to its surrounding environment and neighboring ecosystems.

There is, in addition, evidence for changes in structure and function of ecosystems due to perturbations of climate and resource development. To gain a predictive understanding of effects of environmental change we must look at the site at a larger scale of catchment and landscape. Accordingly, the goal of the Arctic LTER Project is now ***To understand changes in the Arctic system at catchment and landscape scales.***

Knowledge of the internal dynamics of landscape components is necessary but not sufficient to predict linkages among components or to predict changes at the landscape scale. *We believe that to fully understand both these within-ecosystem changes and changes at the landscape level requires knowledge of the linkages and interactions among ecosystems.* Accordingly, we propose to scale-up our study of this Arctic landscape by explicitly focusing on landscape linkages. Eventually, we would like to use the Arctic LTER site and the surrounding North Slope of Alaska as a model landscape for the study and prediction of large-scale, long-term change.

### **Questions.**

We have organized the research around three questions that build on one another.

- Q1. What are the linkages and how do they vary over the landscape?**
- Q2. How are linkages controlled and how will they change in future environments?**
- Q3. How will landscapes respond to environmental change?**

In **Question 1** we will continue much of our research on linkages within and across landscape components *under the contemporary environment*. Added research sites will extend our knowledge to different types of streams, different ages of soils, and lakes in older glacial landscapes. Additional measurements will include, for example, the transport of dissolved organic nitrogen (DON) in soil water.

Under **Question 2** (above), we will carry out experiments and make use of natural experiments to examine the *controls* of linkages. Further, we will explore linkages and controls *in future environments* through experiments and unusual situations. We will ask how ecosystem structure and function is controlled by perturbations and by the relative strengths of various linkages. Community structure will also respond to shifts in strengths of linkages. Some natural experimental situations are warm spring streams and lakes with high sulfate concentrations. Manipulation experiments include fertilization and heating of tundra plots.

Under **Question 3** (above), we will begin work on understanding and predicting how the overall landscape behaves. We need to know how the various system components (e.g., tundra, stream, lakes) interact in space and time. We need to understand linkages, and the changes in their strengths, to predict landscape change. We will work on developing and integrating models such as the hydrological and biogeochemical models for nutrient transfer and transformation along a

hillslope. In this research we are not promising a fully-integrated model that predicts future changes in the abundances or flow rates of materials or individuals, but we will continue to develop parts of such a model and integrate our results into the arena of current ecological thought.

## **SITE DESCRIPTION**

**Historic overview: climate and geologic setting.** In 1975 NSF Office of Polar Programs funded aquatic ecology research on the rivers and lakes of the northern foothills of the Brooks Range, Alaska. Toolik Lake (68°N, 149° W) was chosen because of its depth and accessibility; the road along the oil pipeline had just opened (Shaver 1996). In 1976 terrestrial ecologists began projects at the site. In 1987 the Arctic LTER project was funded. Today the Toolik Field Station of the University of Alaska Fairbanks (<http://www.uaf.edu/toolik/>) supports up to 100 scientists and includes modern laboratories and living quarters. It is open May through September. In 2003 there were 6,000 user days by scientists from 75 different institutions.

The Arctic LTER research site includes the entire Toolik Lake watershed and the adjacent watershed of the upper Kuparuk River, down to the confluence of these two watersheds (Fig. 2-1, 2-2). See details at <http://ecosystems.mbl.edu/ARC/>. This area is typical of the northern foothills of the Brooks Range, with no trees, a complete snow cover for 7 to 9 months, winter ice cover on lakes and streams, and no stream flow during the winter. Tussock tundra vegetation of sedges and grasses mixed with dwarf birch and low evergreens is the dominant vegetation type but there are extensive areas of drier heath tundra on ridge tops and other well-drained sites as well as areas of river-bottom willow communities (Walker et al. 1994; <http://www.geobotany.uaf.edu/arcticgeobot/index.html>).

The climate at the site is typical of Arctic regions, with a mean annual air temperature of about -10°C and low precipitation (45% of the 20-40 cm of precipitation falls as snow). During the summer the daily average air temperature is 7-12°C with the sun continuously above the horizon from mid-May to late July. Permafrost underlies the site to a depth of 200 m. An active layer thaws each summer to a depth of 28-47 cm (Hobbie et al. 2003).

The existing glacial tills that cover the hills near Toolik have three different ages, ~300,000 years, ~60,000 years, and 11,500-25,000 (Hamilton 2003; see Table 2-1, Fig. 2-2). Lakes in these different landscapes differ in their chemistry with the oldest lakes being very dilute with low amounts of inorganic ions and alkalinity (Kling et al. 2000). Soils are acidic in the 60,000 year surface and less acidic in the 10,000 year surface because of less leaching of the carbonate-rich glacial till (Walker et al. 1996). One consequence is that a different vegetation covers these two surfaces (for example, there is little or no birch in the non-acidic tundra; Gough et al. 2000).

**Sampling sites.** Instead of a single site, the LTER and associated projects have studied many sites; the intensively studied sites and their characteristics are listed in Table 2-1. Most of these are close to the Haul Road but some, for example, the springs surveyed by the stream project, were reached by helicopter.

## **OVERVIEW**

**Conceptual Background.** The use of a hydrological catchment as a study ecosystem is not new in ecology; it was developed in the 1960's when Bormann and Likens took advantage of the US Forest Service's monitoring of water flow in an experimental forest and developed budgets for

anions, cations, and nutrients (Likens et al. 1967). The studies soon went beyond budgets to ask how inputs of materials from the atmosphere and bedrock interacted with biota to store, transform, and eventual export as integrated outflow from the catchment. The abiotic processes, such as evapotranspiration and weathering, and the biotic processes, such as plant production and microbial decomposition, are tightly linked in a series of direct controls and indirect feedback loops. Despite the seemingly inexplicable complexity of a complete abiotic and biotic system, the measurement of the outflow from the entire system, for example, at the weir of a Hubbard Brook catchment, has proven to be a valuable tool for determining major processes and controls. Yet, new approaches continually force us to rethink our concepts. One recent example is the study of Perakis and Hedin (2002), which suggested that the export of organic nitrogen from forests is not well known and may be an important part of the functioning of the nitrogen cycle. Another example is the Arctic LTER study (Kling et al. 2000) that showed that the response of a series of lakes and streams to climate and disturbance was linked in part to the proximity and the processes of other surface waters.

Studies of processes within catchments are numerous as are the measurements of the export of inorganic ions, inorganic nutrients, and organic material. In streams, the concepts of the river continuum (Vannote et al. 1980) and the spiraling of nutrients and organic matter (Elwood et al. 1983) are particularly useful. Yet there are few mechanistic models that can predict the outflow of materials as an integrated result of the processes and interactions within the catchment. Early modeling studies were made by Cosby et al. (1985) for inorganic ions and Hornberger et al. (1994) for organic matter. Fisher et al. (2000) summarized the modeling work up to that date and later important studies were made by Lee et al. (2000), and Band et al. (2001). Macro-scale models of water and nutrient flux to the coastal zone are reviewed by Vörösmarty and Peterson (2000). They include models of river discharge, terrestrial mobilization, and in-stream processing and transport.

The linkages between land and water were the first part of the system to be studied. From the first studies of single catchments (e.g., Likens and Bormann 1974), the measurements have expanded to include a wide range of elements and compounds. Moreover, the measurements now encompass the movement from catchments, to streams, lakes, and oceans (Meybeck 1982). And catchments can no longer be treated as a single entity because we now realize that the heterogeneity within a single component creates distinct areas where major transformations occur. For this reason, Peterjohn and Correll (1984), Lowrance et al. (1984), and Van der Peijl and Verhoeven (2000) focused on ecotones or riparian zones. Heterogeneity is also found in lakes where top-down control of species, trophic cascades, and nutrient cycling may depend upon the species present (e.g., Brooks and Dodson 1965 and Carpenter et al. 1985).

Another approach, exploited from the beginning of catchment studies, is a comparative approach where biogeochemical cycling in a control or untreated catchment is compared with that in a disturbed catchment or with that in a catchment with a different vegetation (i.e., the clearcut catchments at Hubbard Brook or the conifer vs. deciduous catchments at Coweeta). From these and other studies, we now understand (Beaulac and Reckhow 1982, Lewis and Saunders 1989) that the export of materials is primarily linked to water flow and to landscape heterogeneity (i.e., differences in geologic setting, land use, vegetation type).

A final way to tease apart the various processes, their linkages, and their importance is to investigate natural sites where changes in biogeochemistry can be estimated over geologic time (space for time substitution). This approach has long been used for studying soil fertility and vegetation productivity (e.g., Crocker and Major 1955, Jenny 1980). Recent studies in tropical

forest systems, for example, have revealed several broad patterns of changes over four million years of ecosystem and landscape development in Hawaii (Hedin et al. 2003, Vitousek 2003), including predictable shifts in the balance of limiting elements that result from interactions of weathering, deposition, fixation, volatilization, and other processes. In boreal and arctic ecosystems, many of the key long-term controls appear to be related to patterns of N accumulation and turnover (e.g., Hobbie et al. 2000, Gold and Bliss 1995, Gold 1998, Shaver et al. 1992). In northern Alaska near Toolik Lake, where multiple advances and retreats of glaciers have created a four million year old chronosequence of landscapes (Figure 2-2), the Arctic LTER project has the opportunity to show how C, N, and P cycles interact both in space and over long time periods to regulate landscape biogeochemistry.

**Conceptual Diagram.** (Fig. 2-3) Landscape linkages are the potential communications between components of the landscape. The manifestations of linkages are the flow of elements, energy, and organisms across the landscape. Their pathways are defined by the topology of the landscape and their currencies are the fluxes of water, nutrients, energy, organic matter and migrating organisms. The regulation of these currency exchanges resides with the processes within landscape components that control rates of weathering, primary and secondary production, decomposition, and water flow.

**Monitoring And Experiments.** The LTER project will continue to monitor for many environmental factors and ecological processes (Table 2-2). The details of methods and protocols for chemistry and sampling are available at the Arctic LTER web site. Experiments and modeling and synthesis activities for the project are summarized in Table 2-3 and described in detail in the following sections on research in each component.

## TERRESTRIAL RESEARCH

**Rationale.** Terrestrial ecosystems dominate the landscape of northern Alaska, covering most of the area and accounting for the majority of its productivity and element cycling (Williams et al. 2000, 2001, LeDizes et al. 2003). Almost all of the water and elements that enter aquatic systems must pass through terrestrial systems first (Rastetter et al. in press, Steiglitz et al. 2003), thus making the link between terrestrial and aquatic systems one key to our research: *How do terrestrial systems control inputs to aquatic systems?* A second key is the fact that terrestrial ecosystems of the Arctic are extremely variable in relation to topography (Fig. 2-4), often differing by an order of magnitude or more in productivity or various measures of C or N cycling over distances of only a few meters (Billings 1973, Giblin et al. 1991, Shaver et al. 1996, Jonasson et al. 2001). At the same time these terrestrial ecosystems are all in contact with the same soil water, which generally stays close to the surface because continuous permafrost prevents deep drainage as the water moves downslope (Shaver et al. 1991, Figs. 2-4, 2-15). Because adjacent ecosystems along toposequences differ so dramatically in both species composition and biogeochemistry, yet are clearly linked by downslope soil water movement, this leads to the obvious question: *How does the transport of elements in soil water between adjacent terrestrial ecosystems affect the function of those ecosystems, and how is this transport controlled?*

**Overview of monitoring and long term experiments.** Terrestrial research of the Arctic LTER includes experimental and descriptive studies of the effects of climate, biota, geology and geomorphology, and fluxes of water and nutrients on tundra ecosystems. The research design incorporates these controls through a combination of comparisons among sites that differ in their

biota and their geology and geomorphology with long-term manipulations of climate and nutrient inputs (Table 2-4). Over the past 21 years we have developed a suite of experiments in which contrasting tundras, dominated by different plant functional types and located on different geologic surfaces, are subjected to identical manipulations of nutrient inputs (with N and P fertilizers), air temperature (plastic greenhouses), light (shading), and other treatments such as herbivore exclusion (Fig. 2-5). Comparisons among treatments within a tundra type lead to insights about the interactions of climate and nutrient fluxes in regulating their composition and biogeochemistry (Chapin et al. 1995, Shaver et al. 1998, Gough et al. 2002, Gough and Hobbie 2003). Comparisons among sites teach us how geology and geomorphology affect ecosystem structure and function (Shaver and Chapin 1991, Shaver et al. 1996, Gough et al. 2000). Comparisons of plant functional types in response to this common suite of manipulations teach us how differences in species function affect overall ecosystem characteristics (Hobbie et al. 1999, Chapin and Shaver 1996, Shaver et al. 2001, Bret-Harte et al. 2000, 2001). Finally, comparisons of decomposition and other soil processes among sites and experiments teach us how vegetation composition interacts with soils and how overall C and N cycles are regulated (Giblin et al. 1991, Johnson et al. 2000, Hobbie et al. 2002, Weintraub and Schimel 2003).

Over the next six years, we will maintain our existing suite of long-term experiments and comparisons, with periodic major harvests as in the past (Table 2-3, 2-4). Because these ecosystems continue to respond to our treatments, with each harvest we gain new insights about ecosystem regulation and we expect to continue to do so as long as the experimental plots continue to change. We also will continue long-term monitoring of plant growth and flowering in relation to weather variation (Shaver et al. 1986). With complementary funding from related grants, we will continue process studies (below). Simulation modeling and cross-site comparisons will be a major, continuing effort. *The major difference between the research we plan for 2004-2010 and our previous work is that we plan to shift our focus, placing a greater emphasis on linkages between landscape patches rather than on their internal regulation and responses. We also will be taking a broader, regional approach, placing our work at Toolik Lake in the context of the larger landscape of the North Slope of Alaska.*

### **New activities.**

**Glacial Chronosequence and Regionalization Studies:** The headwaters of the Kuparuk River, including our existing study sites in the Toolik Lake and Innnavait Creek watersheds, include a range of surface ages from ~10,000 to >300,000 years since deglaciation (Fig. 2-2). We already know that these surfaces differ widely in their species composition, productivity, biomass turnover, and soil nutrient availability (Walker et al. 1996, Gough et al. 2000, Hobbie et al. 2002, Oswald et al. 2003a, 2003b). The next task is to define more clearly how they differ in terms of the linkages among terrestrial ecosystems within them, and in terms of element losses to aquatic systems. We will do this by intensifying our monitoring of soil chemistry and water movement in the Toolik-Innnavait region (Tables 2-1 to 2-3). In the larger region, we will join forces with the survey efforts of the aquatics and landscapes interactions groups to sample other surfaces of different geology and age, in particular the older surfaces of the Anaktuvuk (~1 M y) and Gunsight Mountain (2-4 M y) glaciations in the nearby Sagavanirktok River valley.

**Innnavait toposequence and watershed studies:** The major new activity for 2004-2010 will be an intensive study of element and water movement through a first-order watershed, Innnavait Creek, 10 km northwest of Toolik Lake (Fig. 2-1). This watershed has a long history of research. Some of the first long-term fertilizer plots on the North Slope were set up there in 1976 (Shaver and Chapin 1986, 1995), and a major, integrated study of "Landscape Function and Disturbance in

Arctic Tundra" was focused on Imnavait Creek in the mid-1980s (Oechel 1989, Reynolds and Tenhunen 1996). Perhaps most important to our theme of linkages is that continuous hydrologic monitoring and process research has been maintained there since the 1970s, making Imnavait Creek by far the most thoroughly-studied small watershed in the Arctic (Kane et al. 1989, Hinzman et al. 1996, 1998, Steiglitz et al. 1999, 2000, 2003). Arctic LTER researchers have monitored Eriophorum flowering there since 1976 (Shaver et al. 1986) and have sampled its stream and ponds periodically for over 20 years (LTER data base). Over the past three summers (2001-2003) we have returned to Imnavait Creek with support from two new NSF grants (DEB-0089585 and ATM-0120468). Over the next six years the terrestrial LTER group will work with these two projects to develop the landscape linkages theme, with primary responsibility for the chemical, climatic, and hydrologic monitoring, for maintaining the data base, and for promotion of synthesis of research in this watershed. To do this we will work closely with the Landscape Interactions group (described below). The major new components of this work include:

- Monitoring of inputs and outputs of water, N, and other elements in the Imnavait watershed including precipitation, atmospheric deposition, N fixation, and stream flow and stream chemistry (Arctic LTER data base).
- Monitoring of C, N, and P chemistry in soil water along toposequences in the Imnavait watershed, to determine downslope transport of these elements and their inputs to streams (Tables 2-1 to 2-3).
- A <sup>15</sup>N-labeling experiment to determine more explicitly the rates and forms of downslope N movement (collaboration with DEB-0089585).
- Process studies, to be completed with separate funding, such as soil incubation experiments to determine temperature and moisture controls on leaching losses of elements.
- Toposequence and watershed models (described below).

**New long-term experiments.** Our existing suite of experiments (Table 2-4) has been extremely successful at identifying the environmental controls and quantifying species, community, and ecosystem responses to them in the Toolik Lake region. One reason for their success is that the manipulations we apply represent dramatic changes in nutrient availability, temperature, light, and other factors; the downside of this approach, however, is that such treatments are often well outside the range of expected environmental changes. It is now time to start experimenting with more moderate manipulations. Accordingly, we will add low-level N+P fertilizer treatments to our portfolio in 2004, monitoring them with annual observations of species changes and periodic harvests (every 5-7 years) as part of our overall efforts. Finally, we will work with the Landscapes Interactions group to develop a soil water flushing (water addition and removal) experiment that will serve as the focus for process studies on water-nutrient transport interactions.

**Gaps in our general understanding of tundra ecosystems:** We have made significant progress toward characterizing tundra soil communities over the past 6 years through annual sampling of invertebrate components (Doles 2000, Moore et al. 2003) and preliminary sampling of microbial community structure. Coincident with nutrient additions and the concomitant changes in the plant communities is a shift in the balance between the fungal and bacterial pathways of the soil communities (Moore and de Ruiter 2000, Chinn 2001). Our models of the bacterial and fungal pathways indicate that the observed shifts are less stable than native communities. Our goal for 2005-2010 is to obtain independent funding for this work and to integrate these findings more closely with ongoing soil research, soil-plant interaction studies, and landscape linkage studies.

Synthesis and Modeling: Simulation models, developed over the past 25 years of research at Toolik Lake, will be used to integrate the results of field experiments and to develop and test predictions about linkages and long-term changes (e.g., McKane et al. 1997a, 1997b, Hobbie et al. 1998, Clein et al. 2000, Rastetter et al. 2003). The two models of particular interest to the terrestrial group include the General Ecosystem Model (GEM, Rastetter et al. 1991) and the Multiple Element Limitation (MEL, Rastetter & Shaver 1992). In a recent application, we coupled GEM to a hillslope hydrology model (Steiglitz et al. 1999) to examine whether the downslope movement of inorganic N influenced how moist tussock tundra along a 100 m transect responded to changes in CO<sub>2</sub> and climate (Rastetter et al. in press). We also recently adapted the MEL model to examine the effects of dissolved organic N losses on long-term responses to changes in CO<sub>2</sub> and climate (Rastetter et al. in review). Finally, we have begun to develop versions of these models for analysis of the effects of plant community change on element limitation and biogeochemistry (Herbert et al. 1999, in press, Rastetter and Ågren 2002). All three of these developments are key to the application of these models to our three core questions.

**Link to conceptual framework and three core questions.** For the terrestrial group in 2005-2010 the major shift will be one of emphasis, from a focus on the internal regulation of tundra ecosystems as a mosaic of relatively isolated patches to a focus on the exchanges of water and materials that link them with each other and with streams and lakes. We will contribute to answering our three core questions in the following ways:

- 1) **What are the linkages and how do they vary over the landscape?** The terrestrial group contributes to answering this question by directly measuring the concentrations and production rates of mobile forms of C, N, and P in soil and how they change in relation to vegetation composition, geology and geomorphology, and to changes in climate, nutrient, and water fluxes in long-term experiments. We use the understanding that results to develop longer-term predictions of change using simulation models and to develop hypotheses about responses to environmental variation that we do not actually observe in the field. The perspective is that linkages among terrestrial ecosystems and between land and water are strongly influenced by vegetation and soils, which are functions of landscape age, landscape position, and climate. The key linkage to be studied over the next 6 years is the flux of elements dissolved in soil water, and the controls over that flux.
- 2) **How are linkages controlled and how will they change in future environments?** The terrestrial group addresses this question through a combination of measurements and modeling. Integrated, multi-variable monitoring of multiple sites and long-term experimental treatments provides a direct view of interactions and responses among key linkages and their controls. We also use models such as GEM and MEL to quantify these interactions in the context of whole-system budgets and to develop long-term predictions of change.
- 3) **How will landscapes respond to environmental change?** Integrated measures of landscape- and catchment-level change in relation to climate and weather variation come from monitoring of variables like stream flow and stream chemistry. We will also use comparisons of whole catchments and toposequences along the glacial chronosequence and in relation to major variation in geology and geomorphology, in collaboration with the streams group. Although logistic and funding requirements preclude whole-catchment experimentation for direct observation of overall system changes at this time, we can use the new versions of the GEM and MEL models to compare predicted changes in linkages along toposequences and in catchments with the variation we observe in our regional comparisons.

## **STREAMS RESEARCH**

**Background.** Streams are the primary pathways for transport of water and materials across the landscape thereby linking land to lakes, large rivers, and the ocean via a complex network (Fig. 2-3, Wiens 2002, Gomi et al. 2002). The extent to which streams process nutrients and organic matter depends in large part on when and how these materials enter stream ecosystems (Dent et al. 2001, McClain et al. 2003). In the Arctic during snowmelt, hydrological transport processes are more important than in-stream processing for controlling export. However as the season progresses, a number of ecological and biogeochemical mechanisms interact with hydrology and geomorphology to process materials as they follow distinct land-stream-lake transport pathways. As in streams everywhere, epilithic bacteria and primary producers (diatoms and bryophytes) assimilate carbon and nutrients while decomposition on the stream bottom and in the hyporheic zone releases inorganic nutrients for further transport and recycling (Poole 2002, Edwardson et al. 2003, Slavik et al. in press). The decomposition of fine and coarse particulate organic matter is linked to the availability of inorganic nutrients for decomposers (Grattan and Suberkropp 2001, Stelzer et al. 2003, Benstead et al. submitted). Diverse groups of insects play important roles by grazing algae, shredding coarse particulate organic matter and filtering fine particulate organic matter (Power and Dietrich 2002, Peterson et al. 1985). Growth and successful reproduction of fish is determined in part by landscape characteristics that affect nutrient inputs and discharge (Fig. 2-6, Fausch et al. 2002, Deegan et al. 1999). In arctic streams, climate is the master controller of future changes because all processes will be affected by a longer flow season, changes in the dynamics of snowmelt, and increased variability in summer discharge (Oswood et al. 1992; Rouse et al. 1997).

**Rationale.** Because of their role in linking land to other aquatic ecosystems, streams may serve as loci for amplifying or damping the propagation of disturbance across the landscape (Reiners and Driese 2001, Grimm et al. 2003). In addition, water and material fluxes may exhibit non-linear responses to the predicted changes in the environment including climate variability (Dent et al. 2002). Our prior stream research has focused on the structure and function of stream reaches and on surveys of stream types in the foothills of the North Slope. Our knowledge of controls of ecosystem structure and function at the reach scale is comprehensive and has prepared us to develop new predictive knowledge of linkages among landscape components at the watershed scale. We now propose to scale-up our study of arctic streams to encompass stream networks while explicitly focusing on linkages to terrestrial and lake components of the landscape (Reiners and Driese 2001, Gupta and Cvetkovic 2002, Wiens 2002). Water, nutrients, energy, organic matter and migrating organisms are all exchanged in the landscape network. These exchanges are regulated by weathering, decomposition, water flow, and primary and secondary production within and among different landscape components. The new focus for the streams component of this renewal proposal is the quantification of these inputs from upslope ecosystems (in collaboration with the terrestrial and landscape interactions groups) and the acquisition of a predictive understanding of how these inputs alter stream ecosystem structure, how they are in turn altered by metabolism and physical forces as they travel through stream networks, and in what form they are ultimately exported to lakes.

**Sites.** Our network of research sites includes 1) long-term studies on the Kuparuk River, Oksrukuyik Creek, Hershey Creek, 2) eight stream reaches (2-6 order) that we have intensively studied with <sup>15</sup>N tracers, 3) approximately 50 sites within the Upper Kuparuk drainage, and 4)

selected mountain, glacial, spring and tundra stream types throughout the foothills region of the North Slope (31 streams, Table 2-1).

**Monitoring.** Stream monitoring sites include the Kuparuk River reference and fertilized, Oksrukuyik Creek, and Hershey Creek. These sites are sampled several times each summer (Table 2-2). Spring, mountain, glacial and tundra streams will continue to be sampled via helicopter several times each summer. A new effort includes synoptic sampling of over 50 sites on tributaries within the Upper Kuparuk watershed (Fig. 2-7). These will be sampled once or twice each year for all forms of carbon, nitrogen, phosphorus, major ions, algae, insects and fish (Table 2-2). The Kuparuk River grayling population is monitored through intensive mark-recapture studies during the summer in the mainstem and during the fall migration into overwintering lakes (Fig. 2-6B).

**Long-Term Experiment.** The flagship stream experiment is the Kuparuk River fertilization that has continued for 20 consecutive years (Peterson et al. 1985, Slavik et al. in press). Phosphate is added to elevate the concentration by 10 micrograms per liter immediately downstream. For the first 7 years algal growth, microbial activity, insect abundance and fish growth were all stimulated. In subsequent years, bryophytes gradually became dominant and caused a large increase in primary production and marked changes in insect community structure. This is one example of a non-linear ecosystem response to environmental change. Experiments in Oksrukuyik Creek (Harvey et al. 1998) and Hershey Creek (Benstead et al. submitted) have confirmed the reproducibility of the dominant fertilization effects in tundra streams from 2<sup>nd</sup> to 4<sup>th</sup> order. The Kuparuk River fertilization experiment will continue with an emphasis on the evolution of community structure and the impact of extreme events such as floods and droughts.

**Models.** The new Tundra River Ecosystem Model (TREM) combines data from the long-term monitoring and P addition experiment on the Kuparuk River with data describing climate variability (solar radiation, temperature and discharge) to predict stream ecosystem structure and phosphorus cycling in tundra rivers (Fig. 2-8, Wan and Vallino submitted). TREM is being used to forecast changes in tundra streams expected under GCM projections for this century. The structure of TREM was inspired by the SISTM (Stable Isotope Stream Tracer Model) developed through our intensive studies of nutrient spiraling (Wollheim et al. 2001). The SISTM model has proven itself a useful synthesis tool at Toolik and in the LTER cross-site LINX projects. An arctic Habitat Template Model (HTM, Scarsbrook & Townsend 1993, Biggs et al. 1998) was developed from detailed analysis of macroinvertebrate community structure in different types of arctic streams (Hury et al. submitted). Frequency of disturbance, probability of winter freezing and phosphorus supply are the primary determinants of community composition (Fig. 2-9). The arctic HTM provides guidance about changes in stream communities expected as climate evolves thereby facilitating the application of TREM and SISTM. In our new research we will link the TREM model with a GIS-based stream-network hydrology model developed over the past 2 years (Wan and Vallino, submitted) to scale up our reach-based model to predict transport and processing throughout the stream network. Synoptic sampling of the 50 Upper Kuparuk sites will provide data for testing the linked transport and processing model (Fig. 2-7).

**Question 1. What are the linkages and how do they vary over the landscape?**

Stream reach structure and function are strongly molded by the characteristics of the surrounding landscape (Wiens 2002). We need to quantify the linkages between upslope sources and streams and between streams and receiving systems, and determine how these links vary over the landscape. We will continue our surveys of stream reaches in diverse settings to further define

these linkages. We will also collaborate with the terrestrial and landscape interactions groups and use outputs from hillslope and small catchment models to drive our stream network model.

**1A. How do landscape attributes affect stream ecosystem structure?**

*Approach*-We will continue our surveys of the biogeochemistry, structure and function of contrasting stream types and upper Kugaruk River stream network (Table 2-1). The chemistry of seepage inputs to streams from riparian ecosystems will be measured using stream-side wells and conservative tracer additions. The relationships between landscape attributes (e.g., glacial age, vegetation, slope), seepage inputs and stream reach structure will be determined using survey data, existing GIS data layers, and expertise at the Toolik Lake GIS facility (Fig. 2-7).

**1B. How do stream reaches of different physical and biological structure transport and transform nutrients and organic matter prior to export?**

*Approach* – The effect of stream reach and network structure on nutrient and organic matter processing will be assessed in the upper Kugaruk stream network (Fig. 2-7). Influences of physical and chemical drivers on stream primary production and respiration will be investigated through season-long monitoring of whole-stream metabolism and multivariate analysis of drivers (e.g., discharge, temperature, nutrients and light). We will measure the uptake and mineralization of organic matter using dextrose (<sup>13</sup>C tracer), or tundra-vegetation leachate in small streams. Coarse particulate organic matter decomposition (litterbags) and fine particulate organic matter decomposition (O<sub>2</sub> consumption) and transport will be measured (Georgian et al. 2003). Nutrient diffusing substrata will reveal spatial patterns of nutrient limitation while *in-situ* P and N uptake experiments will determine the effect of location within the network on spiraling distances (Fig. 2-10). Growth rates of insects will be measured with *in-situ* chambers and cohort analysis. Grayling length/weight frequency analysis and RNA:DNA ratios (calibrated with measured growth rates from the Kugaruk) will be used to measure growth rates of fish (Arndt et al. 2002, Smith and Buckley 2003). These studies of the spatial patterns of processes will provide data for calibration of the stream network model.

**Question 2. How are linkages controlled and how will they change in the future?**

We must acquire more knowledge of how perturbations alter stream ecosystem structure because structure controls the processing of organic matter and nutrients within stream networks. One example is how climate warming may change the volume of the hyporheic zone which controls nutrient regeneration (Edwardson et al. 2003). Our prior research suggests that the structure of arctic stream communities is responsive to landscape setting, climate and nutrient supply. Recent GCM projections of rapid climate change underline the pressing need for forecasting changes in the function of streams in the arctic landscape. These change in stream structure and function will affect transport and transformation of materials across the landscape and ultimately affect lakes and coastal oceans.

**2A. Will permafrost thaw affect stream network structure and function?** Thawing of permafrost affects hyporheic volume, stream network structure as water tracks become incised, the probability of perennial flow in stream channels, and P supply due to increased soil volume.

*Approach*: We will assess the seasonal extent of the thaw zone beneath stream channels with ground penetrating radar to quantify hyporheic volumes in the upper Kugaruk network and at sites of perennial springs in collaboration with Bowden, Gooseff, McNamara, and Bradford (OPP award -0327440). The function of stream reaches with widely different hyporheic volumes will be assessed by measurements of nutrient concentrations and uptake, chlorophyll, *in-situ* respiration, and insect community structure.

**2B. Will projected temperature increases affect stream ecosystem structure?** Climate warming will alter rates of processing and the distribution of organisms changing stream structure and function.

*Approach:* To the potential affects of warming, we will use ‘space for time’ substitution, continued long-term monitoring and modeling. We will examine how organic matter processing and food web structure differs in cold and warm perennial spring streams vs. tundra streams. Because a longer season may alter life history characteristics of stream insects, we will determine if species that reproduce once a season are able to reproduce more often in streams with longer growing seasons. We will continue to monitor our long-term sites and use bioenergetic modeling to determine how a warmer will affect grayling growth and survival.

**2C. Will changes in discharge affect stream ecosystem structure?** We have found that discharge is a dominant factor determining stream structure and function (Fig. 2-6A, 2-9). Since climate models predict a longer open water season, higher late summer precipitation and more flood events for the Toolik region, we expect major impacts on arctic streams.

*Approach:* We will study the impact of disturbance regime on stream productivity and community structure by comparing stream reaches with different hydrologic characteristics. Finally, we will test the TREM model by using data from Oksrukuyik Creek to see if the changes in community structure predicted by the model for high and low flow years are reflected in the long-term monitoring and fertilization experiment data.

### **Question 3. How will landscapes respond to environmental change?**

Understanding controls and the effects of perturbations on how materials move across the arctic landscape is the long-term goal of the LTER. This long-term goal will be achieved by linking models of all landscape components and all material fluxes in one all-encompassing model. A final synthesis is beyond the scope of this renewal but we will progress toward such a synthesis by sequentially linking tundra, hillslope transport, stream network and lake models for one or two constituents at a time. This level of synthesis seems achievable within the next decade.

*Approach:* We will experimentally field test the stream network model using <sup>15</sup>N tracer and bulk nutrient-addition experiments to follow the uptake, transformation and export of nitrate as it passes through stream networks encompassing several stream orders. Study of long-distance transport is feasible using nitrate because prior research has shown that nitrate uptake distances range up to 10 km in tundra streams (Wollheim et al. 2001). We will use output from hillslope models as input to streams and then predict how processing within the stream network will affect output to lakes and larger rivers. If we can validate the network model, we will be closer to understanding and predicting linkages from land to streams to lakes.

We will use the results of our extensive stream surveys, the stream-network model, and space-for-time substitution to predict the physical and biotic structure of future stream networks. The arctic Habitat Template Model (Huryn et al. submitted) suggests that arctic stream communities are structured primarily by nutrient availability, substrate stability (disturbance regime) and freezing probability. If we can specify how these drivers respond to climate change we can predict stream community structure and then use the network version of the TREM model to compute stream network processing of inputs from land and export to lakes.

## **LAKES**

**Rationale.** Results of long term research of lakes in the Arctic LTER indicates that landscape age, lake morphometry, and food web structure contribute to our understanding of the variation in primary productivity and patterns of trophic transfer in arctic lake ecosystems. This variation

in productivity derives from differences in biogeochemistry inherent in the diverse mosaic of landscapes around the Toolik Lake LTER site. In this proposal we plan to focus efforts on the landscape-to-lake linkages that define how this terrestrial patchiness controls patterns of productivity in arctic lakes. The proposed research has three dominant themes: 1) examining 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, 2) understanding the role of watershed-stream-lake linkages in regulating transformations in water chemistry and patterns of productivity, and 3) development of a lake-watershed model to assess landscape linkages to lake function and to predict impacts associated with potential changes in landscapes due to global change.

**Overview of monitoring, long term experiments, and new initiatives.** Research on lakes in the Arctic LTER has focused on how food web structure influences the biogeochemical cycles that define patterns of productivity and trophic transfer. We propose to continue with these monitoring activities to assess how climate patterns influence lake function (Table 2-2). We will expand on these activities by increasing sampling in seepage and drainage lakes (Table 2-1). We will continue monitoring lake production processes and components of biogeochemistry and will enhance these activities by including explicit comparisons of benthic and pelagic production in these systems and by investigating effects of short term storm and mixing events on productivity patterns (Table 2-2). We will continue the low-level fertilization experiment on lakes on the older landscape surface to assess impacts of landscape disturbances expected during the next 50 years (Table 2-3). Results from this fertilization experiment will be compared to results of previous fertilizations conducted in lakes on newer landscapes. Each of these research components will be integrated into the enhancement of the Arctic Lakes Model to better assess effects of changing climate and landscape cover on lake ecosystem function.

**Question 1. What are the linkages and how do they vary over the landscape?** Lakes show significant variations in their chemistry which seem to be determined by their position in the landscape, the size of the watershed, and whether they are seepage or drainage lakes. We propose to continue analysis of base ions and alkalinity in lakes in the Arctic LTER site emphasizing contrasts between drainage and seepage systems. This contrast will allow us to assess the importance of lake drainage patterns to terrestrial subsidies in lake productivity (Pace et al. 2004). Drainage lakes chosen for the study are part of the inlet series of lakes (I-series) along the major stream inflow to Toolik Lake. A number of seepage lakes dominated by groundwater inflows are present in the Toolik Lake region (S-series lakes and NE-9b). Large differences in biogeochemistry of these drainage and seepage lakes are apparent (Fig. 2-11). Research on I-series lakes (Kling et al. 2000) has shown that lake and stream processing of materials affects biogeochemistry. Lakes receive inputs that incorporate effects of stream processing. The lakes then further impact linkages to downstream ecosystems by producing DOC and POC. We propose to extend this evidence of linkages to processes of biological production by conducting investigations in conjunction with the Land-Water Interactions group on how these differences in biogeochemistry impact primary and secondary production of organisms in lakes. We will coordinate efforts with the Streams Group to assess how lake biogeochemical processing impacts outflow stream ecosystem function. Our continued monitoring of primary productivity in Toolik Lake as alkalinity changes will provide insight into linkages between landscape contributions of alkalinity and arctic lake productivity (Kling et al. 2000).

Stream inflows into lakes dominate the linkage between local landscapes and lake processes. Short-term storm events can have dramatic and lasting impacts on lake productivity (see Fig. 2-19), but these effects appear to be modulated by hydrologic conditions of the local landscape, lake morphometry, and thermal stratification in the receiving lake. We will work with the Landscape Interactions group to assess effects of storm events in two lakes in the I-series. Lake morphometry will be measured using hydroacoustic technology, lake thermal stratification will be monitored with thermistor chains established with each lake, and event samplers will assist in collection of water chemistry and hydrology information. Dye studies will be conducted to assess location of inflow plumes. These studies will be coordinated with estimates of primary production designed to assess small scale spatial and temporal differences in productivity.

One of the dominant linkages defining arctic lake ecosystems is the exchange of materials between benthic and pelagic regions of the lake (Vadeboncoeur et al. 2002). We propose to examine how variation in major ions, DOC, POC, and nutrients affects benthic and pelagic production and material exchange in four study lakes (Cole et al. 2002). Two of the lakes will be in the I-series to represent lakes in a drainage system. These lakes are relatively deep and characterized by high light and low nutrient and DOC concentrations. Two seepage lakes will also be investigated to compare production processes in both drainage and seepage systems. Seepage lakes tend to be shallow, and have higher DOC and nutrient concentrations. Most of the seepage lakes do not contain fish and thus have different benthic and pelagic communities. This design will allow us to assess the importance of fish as integrators of benthic and pelagic components of food webs (Vander Zanden and Vadeboncoeur 2002). Benthic and pelagic primary production, nutrient release from sediments, secondary production of benthic and pelagic invertebrates and fish will also be measured. Fish production will be estimated using pit-tagged individuals to estimate individual growth rates. Mark recapture techniques provide estimates of population size. Seepage lakes tend to have higher levels of primary production with benthic producers dominating (Giblin, unpublished research). Results of these studies will allow us to evaluate how the ratio of benthic to pelagic production varies with lake type, lake morphometry, DOC and nutrient concentrations. Results from these investigations will be added to the matrix of lake characteristics (landscape age, lake depth, and food web structure) that determine lake productivity in arctic ecosystems.

**Question 2. How are linkages controlled and how will they change in future environments?**

Although primary production and chlorophyll a levels in lakes in the Toolik lake region are very low, productivity varies widely across the region ranging from ultra-oligotrophic to nearly mesotrophic. Both mesocosms, and whole lake experiments, have shown that primary productivity is strongly nutrient limited. (See previous section). The large differences in the role of watersheds in controlling lake chemistry can be seen in the tremendous variation of lake water in the region which spans differences in alkalinity, cations and sulfate that are as large as seen in the rest of North America. The underlying reason for this variability is differences in soils that range in age from only 10,000 to >300,000 years old in just a few kilometers.

We are presently conducting a set of long-term experiments to assess impacts of low level fertilization on lake ecosystems on the older glacial-age surfaces. These lakes on older landscapes have lower concentrations of nutrients and base cations and should be more sensitive to changes in nutrients compared to previous fertilization experiments conducted on recently glaciated surfaces (see previous results). This low level of fertilization is similar to increases in nutrient loading anticipated from natural weathering processes associated landscape age and with

anticipated warming of the arctic (see Landscape Interaction section). We propose to continue our low-level fertilization experiment on Lake E-5 and E-6 for the next three years, assess impacts on pelagic and benthic linkages in these lakes and two reference lakes (Fog-2, Fog-4), and then observe the recovery of these lakes once the fertilization is discontinued. We will continue our measurements of pelagic and benthic primary production, estimate secondary production of benthic invertebrates and zooplankton, grazing rates of zooplankton, sedimentation rates, and estimates of fish production (Vadeboncoeur et al. 2001). Continued analysis of stable isotopes of C and N will allow us to assess trophic linkages among benthic and pelagic organisms (Vander Zanden, and Rasmussen. 1999).

Preliminary results of the first two years of this low level fertilization will shape the research focus on the work proposed. Benthic primary production is of the same magnitude as pelagic primary production in all lakes, and exceeds pelagic production in shallow lakes (Fig. 2-12). Carbon isotope analyses indicated that pelagic zooplankton and benthic invertebrates had little overlap in food resources (Fig. 2-13). This separation of benthic and pelagic trophic pathways converged for deep-water chironomids where isotopic analyses indicated a mixture of benthic algae and sedimenting phytoplankton as dominant food resources. Diet and isotopic analyses for fish indicated a mixture of chironomids and snails as dominant food resources. Interestingly as Lakes E-5 (deep) and E-6 (shallow) received more nutrients the separation of pelagic and benthic pathways was enhanced. Pelagic production of phytoplankton and zooplankton increased in response to nutrient additions, but benthic production remained unchanged. These differences are apparent in the uptake rates of  $^{15}\text{N}$  added as a tracer in our fertilization study (Fig. 2-14). We propose to enhance our assessment of pelagic-benthic linkages by improving measurement of sedimentation rates (Sarnelle 1999) and release of nutrients from sediments under various light and temperature regimes. We also plan to study the impacts of different zooplankton assemblages on nutrient recycling and sedimentation (Schindler et al. 1993; Vanni 2002).

Longer term changes in landscape perturbations such as climate change will impact nutrient and organic matter inputs because of permafrost melting, tundra sloughing events, and extensions of growing seasons. Results of over twenty years of research documents a general increase in alkalinity, base cations and sulfate in many of the lakes in the Toolik region (Fig. 2-11). This increase is seen in lakes in all of the geologic surfaces and has occurred without significant land use changes providing an opportunity to assess effects due to changes in temperature or hydrology. These differences in base cations and alkalinity are likely linked to the input of nutrients, especially P, into lakes. Benthic GPP, nitrification and benthic N fixation is frequently higher on lakes located on younger glacial surfaces. Our proposed research will allow us to assess the strength of these relationships and solidify our understanding of the links between cations, alkalinity and production in arctic lakes.

**Question 3. How will landscapes respond to environmental change?** Our empirical data from a variety of lake types and food webs will be used to calibrate model simulations to assess impacts of climate change on arctic lakes. An arctic lake model (ALM) has been developed to heat, thermally stratify, cool, freeze and thaw arctic lakes of different sizes and morphometries (Barfield and O'Brien, submitted). The model uses daily weather variables as inputs to drive a dynamic one-dimensional model to predict depth gradients of light, heat, and dissolved oxygen. Thermal structure is modeled using 0.5m discrete depth increments according to the temperature eddy diffusion equations of Henderson-Sellers (1985). The model grows phytoplankton in each depth cell based on external nutrient loading and internal recycling

processes. In our proposed research we will expand this model to include benthic producers, zoobenthos and zooplankton, and fish. Zooplankton consume phytoplankton and grow based on established relationships (Luecke et al. 1996). Large zooplankton are consumed by fish based on arctic grayling selectivity information (Hughes 1992; O'Brien and Showalter 1993). Benthic primary production will be modeled based on photosynthesis-irradiance curves from lakes associated with different landscape surfaces. Benthic primary production will be subject to mortality from grazing benthic invertebrates (Gettel in prep). The model will include information on rates of sedimentation, benthic nitrogen fixation and denitrification for each depth cell. Growth dynamics of benthic animals and fish will allow predictions of secondary production over the range of lakes present on landscape in the region.

The goal of this modeling exercise is to predict how changes in climate and lake inflow chemistry affect overall rates of primary productivity and the ratio of pelagic to benthic production. Simulation runs will allow us to assess our degree of understanding of the processes regulating variation in production and community composition observed in the lakes of the Arctic LTER. Eventually we plan to aggregate our model output with other component models from the Terrestrial, Landscape Interactions, and Streams Groups to derive a spatially explicit simulation tool to predict nutrient transformations, patterns of productivity, and relevant gas fluxes across the arctic landscape.

## LANDSCAPE INTERACTIONS

**Rationale.** As mentioned in Section 1 (Landscape Interactions Research Accomplishments), our LTER focus has been on understanding (1) the production of materials on land such as organic matter and nutrients, (2) the linkage of the transfer of these materials between land and surface waters as controlled by hydrology, and (3) the impacts of these materials on receiving water bodies. Probably the most important *conceptual* advance resulting from this work is the realization that linkages of material flows or of processes within ecosystems, and between ecosystems, is of much greater importance and prevalence than previously understood. For example, on land we viewed the system rather simply as the production of dissolved materials in all soil waters, followed by the flushing of those materials from soils to streams by hydrological flows. But we know now that the interaction between how materials are produced at different places on the terrestrial landscape (e.g., along a toposequence), and how hydrology connects or isolates those places really determines the amounts and timing of material movement into streams (Stieglitz et al. 2003). In lakes we viewed the inputs of nutrients from streams during storm events as important controllers, but really it is the interactions between those inputs and the internal lake linkages (e.g., benthic-pelagic coupling or cross-thermocline mixing) that determine how the system functions and reacts. A third example is at the landscape scale, where we now realize that internal processing within lakes and streams is additive in nature across the aquatic landscape, and these linkages collectively determine how individual systems respond to climate or other perturbations. In this renewal we will not abandon the studies of specific processes or linkages, but instead we will complement that process-based research with a greater focus on how specific linkages operate *and interact* both within and between ecosystems. The long-term goal in the "Landscape Interactions" research is to assemble this array of processes and linkages into a framework for understanding how rapid or sustained disturbances, such as climate change or anthropogenic impacts, will affect the structure and function of terrestrial or aquatic ecosystems. This synthesis will occur mainly through the development of conceptual and mathematical models that are described below and elsewhere in this proposal.

Overview of monitoring and long-term experiments. We monitor three catchments intensively in this research (Table 2-1, 2-5). In the Tussock and Imnavait Watersheds we monitor soil water chemistry and primary stream flow and chemistry in order to connect the production of DOM and nutrients on land to their transformation and transport on the way to streams (Research Question 1). In the 3<sup>rd</sup> catchment, we monitor the chemistry and biology of a series of connected streams and lakes that collectively flow into Toolik Lake, and we monitor Toolik Lake intensively during storm events. This monitoring allows us to understand how aquatic systems are functionally linked across an entire landscape, and provides information on the relative importance of internal processes versus external inputs especially in lakes (Research Question 1). We began a long-term tracer experiment using <sup>14</sup>C in tussock and wet sedge communities in 2000 (Table 2-3, 2-5), and a new water addition-removal experiment is proposed for this research (Question 2). These experiments provide information for all three of our Research Questions described below.

## **Major Research Questions and Future Landscape-Interactions Research**

### **Q1. What are the linkages and how do they vary over the landscape?**

Linkages and processing of DOM along a toposequence. On land we will continue the measurements on soil water chemistry and soil water movement (using our hydrology model) at different places along the toposequence, which correspond to differences in vegetation and flowpaths (Fig. 2-15). We will expand on this research based on recent results that indicate that there are consistent differences in soil water chemistry, microbial species composition, and organic matter processing as materials move from the upland tussocks to the riparian birch-willow to the lowland wet sedge communities (Judd et al. in prep; Fig. 2-16). However, it remains unclear exactly how these aspects of organic matter transformations are linked along a toposequence, and which aspects dominate in the control of these transformations (see Q2). For example, does the microbial species composition in the soil determine both the soil water chemistry and the DOM and SOM processing rates, or is it the opposite, where the soil water chemistry determines the species and the biochemical transformations? Continued monitoring of soil water chemistry, coupled with *new activities* of determining microbial species composition and microbial processing rates will allow us to advance our understanding of these questions in the next six years.

Soil weathering and its linkage to surface-water chemistry. It is clear that the Arctic is responding to recent global warming (see Brown et al. 2002 for changes in thaw depth), and one consequence may be increased rates of weathering and changes in surface water chemistry. One of the *new activities* in this research will be to continue our initial investigations showing that depth of weathering is a dominant control on surface water chemistry (Fig. 2-17). There are consistent down-profile patterns of Ca, Na, and strontium isotopes in soils that correspond with outputs of these materials in stream waters throughout the summer season. This research examines the mechanistic side of the changes in alkalinity that has been observed in lakes, and will thus link to the lakes research as well as to our understanding of landscape biogeochemistry.

Interactions of aquatic ecosystems at larger scales. At the landscape scale, our LTER research has shown that current concepts of aquatic ecosystems within a landscape can be placed in a broader context by including the spatially-dependent processing of materials in both lakes and streams taken together (Kling et al. 2000). Studies of the series of connected lakes that flow into Toolik Lake showed that there are distinct spatial and temporal patterns in chemical variables. These patterns are determined in part by the effect of increasing catchment area feeding into

lakes further downslope, and in part by the systematic processing of materials in lakes and in the stream segments between lakes. These results (Kling et al. 2000) illustrate that over small geographic areas, and somewhat independent of lake or stream morphometry, the consistent and directional (downslope) processing of materials helps produce spatial patterns that are coherent over time for many limnological variables. *Future research* in this area will concentrate on working with the Lakes Group to expand our measurements to quantify the rates of biological production (bacteria, algae, invertebrates, and fish) from several stream and lake segments within the Inlet Series of Toolik Lake. In parallel to the measurements made on soil waters under different types of vegetation along a toposequence, we will also measure the chemistry, rates of organic matter processing, and bacterial species moving from the headwaters to Toolik Lake.

## **Q2. How are linkages controlled and how will they change in future environments?**

The most important controls on processes that link parts of ecosystems or different ecosystems include: the rates of production and decomposition of organic matter and nutrients; movements of soil water down a toposequence on land; movements of water from soils into riparian zones and into stream water; and both the horizontal inflows of water into lakes and the vertical movements of water, nutrients, and organisms in the lake (Fig. 2-15).

One of the fundamental questions in ecology is how do systems respond to external influences, whether the influence is due to climate forcing, species immigration, or inputs of nutrients and organic matter. In the proposed research we will examine this question using research on both terrestrial and aquatic systems.

Controls on production of dissolved materials. We will continue the measurement of production of dissolved materials from roots and soil organic matter (SOM) in different habitats through a  $^{14}\text{CO}_2$  addition experiment (Fig. 2-18). The *new activities* in this research will augment our understanding of how water flow and soil saturation contribute to the production of dissolved materials (and thus the land-water linkages of DOM and nutrients) by beginning a “water removal and addition” experiment in a wet sedge community. These communities are the final buffer or control point in the movement of material from land to surface waters, and it is critical to understand how increased or decreased water saturation will affect this movement. We will divert water from one part of the wet sedge meadow to another to accomplish this experiment (see also the Terrestrial section). This experiment will also help to integrate the upland experimentation and plot-level research with the riparian and aquatic investigations relating to the controlling forces of water flow between systems.

Relative strengths of storm events and internal processing in lakes. We found that the linkage between storm events and lake function in Toolik Lake was surprisingly strong (Fig. 2-19, 2-20). This figure shows how a wind event can impact primary production in the lake, and we have other data (not shown) indicating that storm-water inflows can have similar impacts. The research has illustrated how such periodic forcing events can rapidly change the trajectory of system functioning, and can have long-lasting affects.

*Future research* in this area will be coordinated with the Lakes component, and will expand measurements to other lakes with different morphometry and residence times in order to develop an understanding of the patterns of response of lake ecosystems to these periodic, external forcing events.

## **Q3. How will landscapes respond to environmental change?**

Empirical studies on the processes of production, decomposition, and water flow will continue to add to our knowledge base of ecosystem processes, but the real question for prediction of change is how do various system components interact in space and time to

influence system behavior across a landscape? Our conceptual approach to answering this question is derived by integrating two ideas, first that in time there is a characteristic *synchronicity between drivers and processes*, and second that in space there is a *variable “connectivity” of patches on the landscape*. This approach is guided by observations that drivers and processes are often asynchronous in their operation; e.g.: (a) storm events flush N in soil waters at rates exceeding the maximum uptake rates of plants; (b) microbial activity in soils can be rapid, yet the decomposing SOM pool turns over 10 to 1000 times more slowly; and (c) plant photosynthesis varies on timescales of minutes to hours, while the labile N pool that ultimately supports C fixation has a residence time in soils of years to decades (Stieglitz et al. 2000). The spatial counterpart of this temporal view says there is a “connectivity” of drivers, processes, and system components on the landscape. Landscape heterogeneity tends to be patterned (e.g., along a toposequence), but our hypothesis is that the importance or impact of this landscape heterogeneity is governed by whether these components are functionally connected or separated by groundwater flow. When rainfall saturates the ground, the uplands and lowlands of a catchment are hydrologically connected. The lack of such a connection is not surprising for huge drainage areas where precipitation events are localized, but our findings show that many smaller catchments periodically lose this connectivity during drier conditions (Stieglitz et al. 2003). Thus, in addition to the static spatial heterogeneity of the system, there is an overlay of dynamic heterogeneity such that the products of weathering or biological processes in soil waters are often isolated before being transported downslope.

New research in this proposal includes three steps to advance our ability to predict how tundra landscapes will change in the future. **First**, we will continue our development of hydrological and biogeochemical models to upgrade plant and microbial processes and the spatially-explicit routing of water on the landscape. Results from the chemical and hydrological monitoring described above, plus our new water addition-removal experiment, will guide these developments. **Second**, we will begin to integrate these two models to make predictions of hydrological outputs of C and N (initially) from the study catchments. The monitoring results, including databases of climate, discharge, and chemistry, will be used to test the models. **Third**, mostly heuristic simulations will determine exactly how our conceptual controls and driving processes interact, and what impacts these interactions have on the linkages between upland and lowland and aquatic ecosystems. This approach is designed to test our overall hypothesis that landscape heterogeneity and “connectivity” interact to control the rates of production, consumption, and final transfers of biogeochemical materials on the landscape.

## **INTEGRATION OF MAJOR ACTIVITIES**

Over the next decade, we will continue to build an integrated perspective of the Arctic landscape and develop a quantitative understanding of the linkages among tundra, streams, and lakes. These linkages are mediated by the movement of water and entrained materials down hill slopes, through the riparian zone, into streams and lakes, interacting with the stream bed and lake sediments, and eventually transported out of the landscape in major rivers. We have already begun development of the models necessary to describe these linkages for the three major components of the Arctic landscape, the terrestrial tundra, the streams, and the lakes. Ultimately we will develop a fully linked model that ties these three components together by scaling the individual models to an appropriately coarse scale using the techniques laid out by Rastetter et al. (1992, 2003, in press) and Williams et al. (1997). The aim of this scaling is to develop an aggregated representation of the landscape components that embodies their essential function,

but does not retain so much detail that their linkage in an integrated landscape model becomes impossible.

During this grant period, we will use the development of the component models as our major integrating tool. As mentioned in Table 2-3 and described in detail in the description of the terrestrial, streams, lakes, and landscape links studies, we already have working models for terrestrial (GEM and MEL), streams (TREM), lakes (ALM), and landscapes (TOPMODEL, BIOGEOCHEMICAL MODEL, ROOTS MODEL). Thus, we are well-beyond the startup phase of the model development and can use the models to identify gaps in knowledge, identify budgets that do not balance, and find process controls that are incomplete.

It is also true that the movement of water and materials from one component to another, already well-studied at the Arctic LTER, is by its nature an integration of all the processes and fluxes of the system. The budgets and models we develop have to be able, at a minimum, to reproduce these fluxes so we do have a natural test of the quality of our understanding.

Integration and planning of the project is carried out at the annual March meeting of the P.I.s, Postdocs, graduate students, and research assistants of the LTER and related projects. Additional planning and integration meetings are held during late June at Toolik Lake when the leaders of the component groups are all present.

## RESPONSE TO COMMENTS OF JULY 2001 SITE REVIEW

The following numbered responses correspond to the numbered recommendations of the site review team that visited Toolik Lake in July 2001, as communicated to Arctic LTER investigators in a September 19, 2001 letter from H. Gholz, NSF LTER Program Director.

- 1. Program integration.** We now invite most graduate students to our annual winter meeting, and spend more time at that meeting on coordinating within-site activities. We have articulated a data management strategy and approach that emphasizes data *access* and data *integration* and have communicated that to site personnel (proposal section 4). The site data base receives a lot of internal use and there are no restrictions at all for external users. We have developed an intranet capability but thus far it has not been extensively used, probably because other forms of communication are not viewed as limiting by project personnel.
- 2. Centralize the role of integrative hydrologic modeling.** Since 2001 a number of our P.I.s have begun work on two new projects, closely linked to the LTER, in which hydrology is central: NSF-ATM-0221835 (Marc Stieglitz lead PI) and NSF-DEB-0089585 (G. Shaver lead PI). These two projects are both focused on our watershed/toposequence research in Innavaik Creek, and are developing linked hydrologic-biogeochemistry models.
- 3. Expand sampling to the winter.** In spring 2003 there was extended sampling of Green Cabin Lake, and we worked with Dr. Mathew Sturm to measure snow distribution before the spring melt. In 2002 and 2003 we sampled in May the end-of-winter conditions in a long list of lakes, and in 2003 our soil chemistry and hydrology measurements extended into mid-September. The major period of interest is the periods of freezing and thawing in fall and spring; these are the largest hydrologic and surface energy balance events of the year.
- 4. Expand outreach.** In 2002 we started a Schoolyard program with the Barrow school that funds LTER-type activities for students as well as a public lecture series by scientists. We are continuing the Science Journalists program (NSF funded) to bring journalists to Toolik. We have instituted a summer field course aimed at demonstrating for advanced college students how mathematics and ecology combine to study the arctic climate and land-water interactions. We continue to meet regularly with State and Federal management agencies.

**5. Site Management and Cross-Site Research.** The Arctic LTER has membership on the University of Alaska Fairbanks' Toolik Field Station Steering Committee and attends its meetings each December. We work closely with the Station Management to set priorities for expansion and new equipment, and to evaluate performance of Station personnel. We have established close connections with the field station at Abisko (Sweden) and have exchanged students, postdocs, and technicians in field research annually for 7 years. Shaver was awarded an LTER Cross-Site grant (NSF-DEB-0087046) to develop comparisons with Abisko, leading to several review papers written with Abisko researchers, and to a metaanalysis of results of long-term experiments at the two sites (van Wijk et al. 2003). A new award to Shaver (NSF-OPP 0352897) will support research at Abisko, Zackenberg (Greenland), and on Svalbard (Norway) starting in summer 2004. Barrow provides a site for comparative research but so far there is no organized program to interact with; we have made several visits to Barrow over the past two years and collaborate with the Barrow Arctic Science Consortium in our Schoolyard LTER project.

**Table 2-1.** Sampling sites within the Arctic LTER site. For details of location and description see <http://ecosystems.mbl.edu/ARC/>

<b>Terrestrial</b>	
Toolik Lake area	Multiple sites on Itkillik I and Itkillik II aged surfaces and outwash (10,000-60,000 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 Oksrukyuk Creek and Sagwon; toposequence on Itkillik II surface and outwash in northern foothills
<b>Streams</b>	
Kuparuk River	4 <sup>th</sup> order, oligotrophic, clear-water tundra stream; 25 km in length from origins to Dalton Hwy. crossing (143 km <sup>2</sup> area); draining surfaces 60,000 to 780,000 yr old.
Oksrukuyik.	3 <sup>rd</sup> order, oligotrophic, clear-water tundra stream; 12 km in length from origins to Dalton Hwy. crossing (73.5 km <sup>2</sup> area); tributary of the Sagavanirktok River. ~300,000 yr old surface
Hershey Creek	2 <sup>nd</sup> 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 <sup>2</sup> watershed encompassing the headwaters of the Kuparuk River; predominantly underlain by older Sagavanirktok aged surfaces (125,000 to 780,000 yr old), with extreme headwaters draining Itkillik I - aged surface (~50,000 yr old).
Extensive Surveys	Several sites from the Colville, Kuparuk, Sagavanirktok and Sadlerochit drainages, representing Mountain, Glacier, Tundra and Spring streams.
<b>Lakes</b>	
Toolik Lake	25 m deep lake, 1.5 km <sup>2</sup> , 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 10,000 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
<b>Landscape Interactions</b>	
Tussock Watershed	1 ha watershed with a primary stream and weir; ~100,000 yr old surface
Imnavait Watershed	2.2 km <sup>2</sup> watershed with weir on primary stream weir on one of many distinct water tracks; >300,000 yr surface.
<b>Climate and Hydrology</b>	
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
Oksrukyuk Creek	Stream gauge, temperature at Dalton Highway crossing
Sag River Valley	Climate Stations at Sag toposequence and Sagwon

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

<b>Ecosystem and Linkage</b>	<b>Monitoring and Process</b>	<b>Frequency of Sampling</b>
<b>Terrestrial</b>	<i>Protocols and methods at:</i> <a href="http://ecosystems.mbl.edu/arc/data_doc/terrest/Terrestmethods.html">http://ecosystems.mbl.edu/arc/data_doc/terrest/Terrestmethods.html</a>	
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
<b>Streams</b>	<i>Protocols and methods at:</i> <a href="http://ecosystems.mbl.edu/ARC/data_doc/streams/streamsdefault.htm">http://ecosystems.mbl.edu/ARC/data_doc/streams/streamsdefault.htm</a>	
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 <sub>3</sub> , NH <sub>4</sub> , 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 <sup>th</sup> order river	Monitoring in stream network feeding Kuparuk River. Flow, temperature, conductivity, alkalinity, SRP, TDP, PP, NO <sub>3</sub> , NH <sub>4</sub> , 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 <sub>3</sub> , NH <sub>4</sub> , 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
<b>Lakes</b>	<i>Protocols and methods at:</i> <a href="http://ecosystems.mbl.edu/ARC/data_doc/lakes/lakedefault.htm">http://ecosystems.mbl.edu/ARC/data_doc/lakes/lakedefault.htm</a>	
Benthic/pelagic linkages	Four study lakes Benthic and pelagic 1 <sup>o</sup> 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)
<b>Landscape Interactions</b>	<i>Protocols and methods at:</i> <a href="http://biology.lsa.umich.edu/~gwk/protocol_v2.pdf">http://biology.lsa.umich.edu/~gwk/protocol_v2.pdf</a>	
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 in 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

**Table 2-3.** The experiments to be carried out and the modeling and synthesis to study linkages within and between various ecosystem components.

<b>Ecosystem Component And Linkage</b>	<b>Experiments and sampling</b>	<b>Modeling and Synthesis</b>
<b>Terrestrial</b>		
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 topequence	( <sup>15</sup> NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> addition experiment at 4 locations along Imnavait topequence	New model of N transport
Belowground C inputs	Root production and C inputs in fertilized sites in wet sedge and tussocks using <sup>14</sup> 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
<b>Streams</b>		
Productivity and community/nutrient supply	Phosphate continual addition to 10 ppb level final concentration	TREM, SISTM, Habitat Template Model
<b>Lakes</b>		
<sup>14</sup> C 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
<b>Landscape Interactions</b>		
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 <sup>14</sup> C as tracer	Roots model - OM and nutrient production by roots

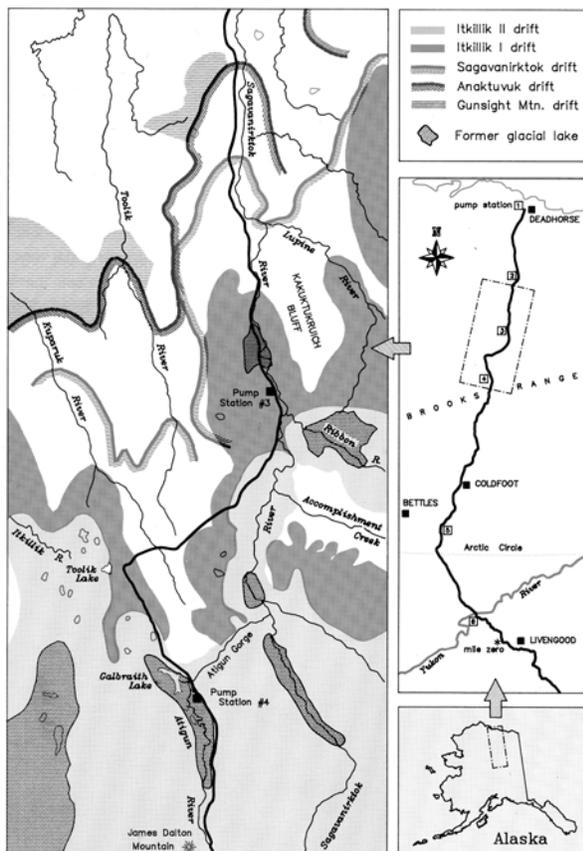
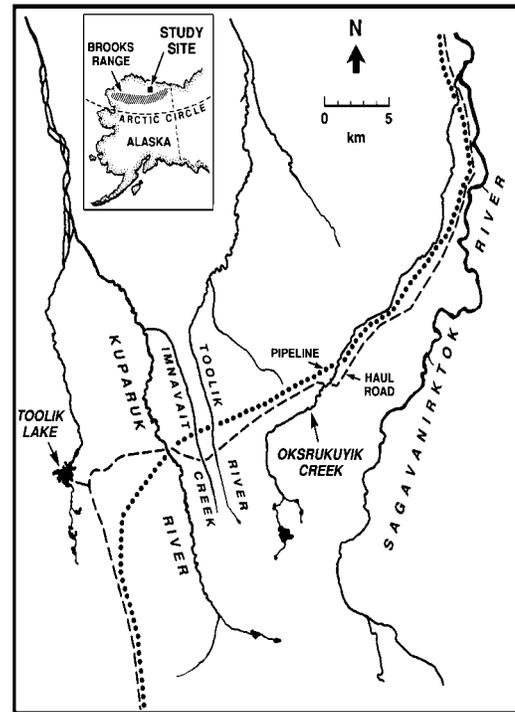
**Table 2-4.** Experimental Designs for Terrestrial Research of the Arctic LTER Project.

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 2002 Sedge 1994, 2001 Heath 1996
	1994	Acidic tussock Dry heath	Snowfence	Annual point-frame monitoring
	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 2004	Wet sedge (2001) Acidic Tussock (2002) Acidic tussock	<sup>14</sup> C addition, control and N+P fert Low-level NxP Soil water flushing	2001, 2002, 2003
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

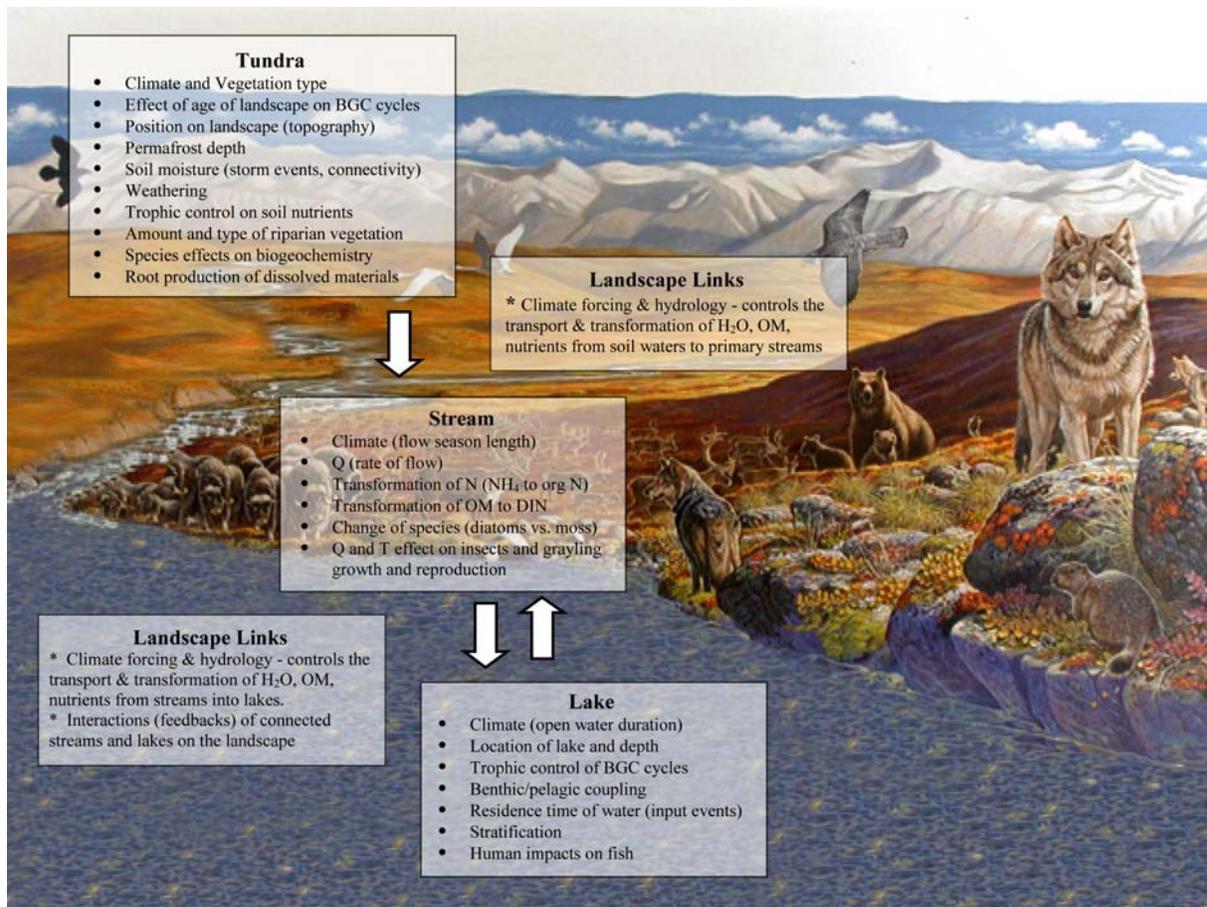
**Table 2-5.** Research locations and approaches used to gather information on landscape interactions. Each of these approaches, and the resulting data, relates back to a major research question and the conceptual model of the important controls on land-water interactions shown in Figure 2-15.

Land-Water Interactions Research		Observations Experiments Synthesis
Location	Ecosystem Type	Measurements
Terrestrial Experimental plots	Moist Acidic Tussock, Wet Sedge, Nonacidic Tussock	Soil water chemistry, C and nutrient production Water additions to tundra <sup>14</sup> CO <sub>2</sub> labeling
Tussock Watershed	Moist Acidic Tussock, Primary Stream	Stream flow and chemistry, rain events Soil water chemistry Hydrology and biogeochemistry model
Inlet Series of Lakes in the Toolik Basin	Lakes and Streams	Lake and stream chemistry Lake mixing and primary production Hydrology and biogeochemistry model
Toolik Lake, Lake E5	Lakes and their inlet streams	Ecological and chemical impacts of storm events (major inflows) on lakes

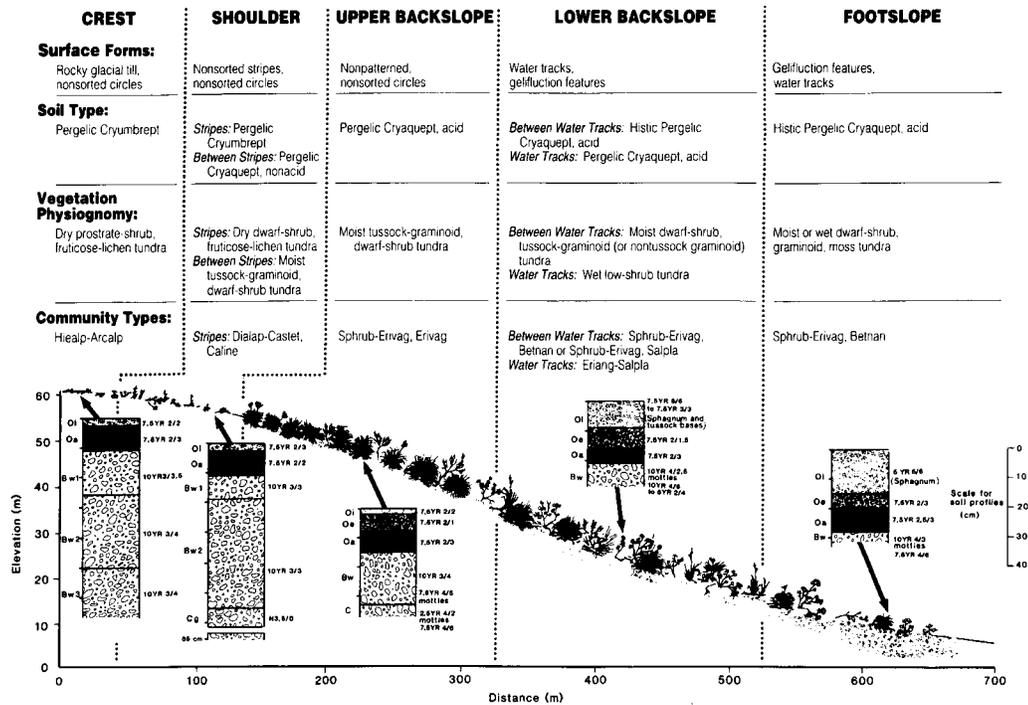
Figure 2-1. Major research sites and place names in the Toolik Lake region. The Arctic LTER research site formally includes the drainage basin enclosing the two branches of the headwaters of the Kuparuk River (Toolik Lake and its drainage basin, the upper Kuparuk River, and Innavaik Creek). The Arctic LTER research also includes sections of Oksrukuyik Creek and sites along the Sagavanirktok River, and lakes and springs.



**Figure 2-2.** Glacial limits of the area between James Dalton Mountain and Sagwon Bluff. (Bureau of Land Management, 1993). As described by Hamilton (2003), Itkillik II and Itkillik I surfaces are Late Pleistocene (11,500-25,000 y and ~60,000 y, respectively, at Toolik Lake); Sagavanirktok surfaces are Middle Pleistocene (~300,000 y at Innavaik Creek); Anaktuvuk River surfaces are Early Pleistocene (1-2 M y); Gunsight Mountain surfaces are Late Tertiary (2-4 M y).

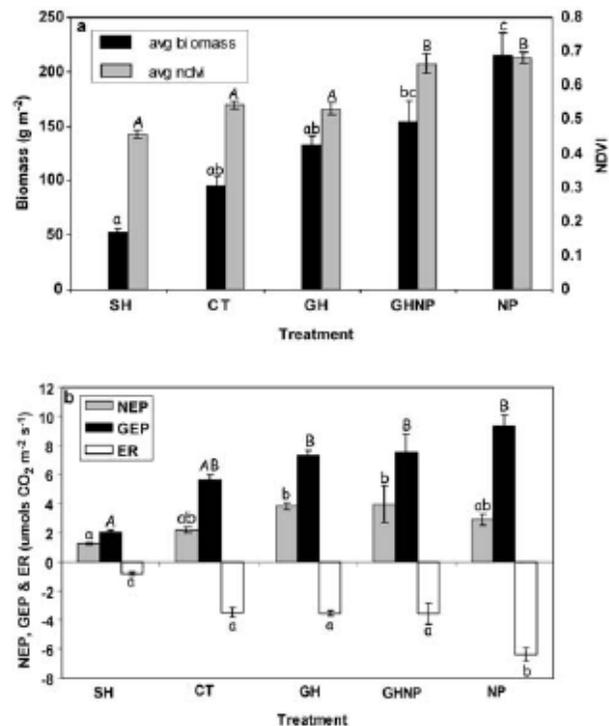


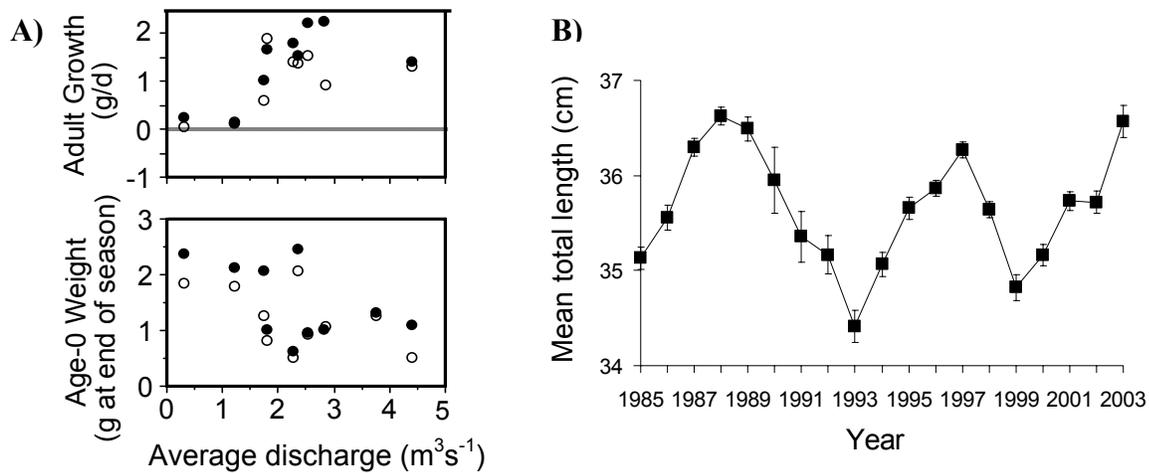
**Figure 2-3.** The conceptual framework of the Arctic LTER project with a background of the foothills and mountains at Toolik Lake, Alaska (modified from the U.S. Postal Series Number 5, Nature of America). The large boxes are the three components of the landscape. The bullets inside the boxes are the 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.



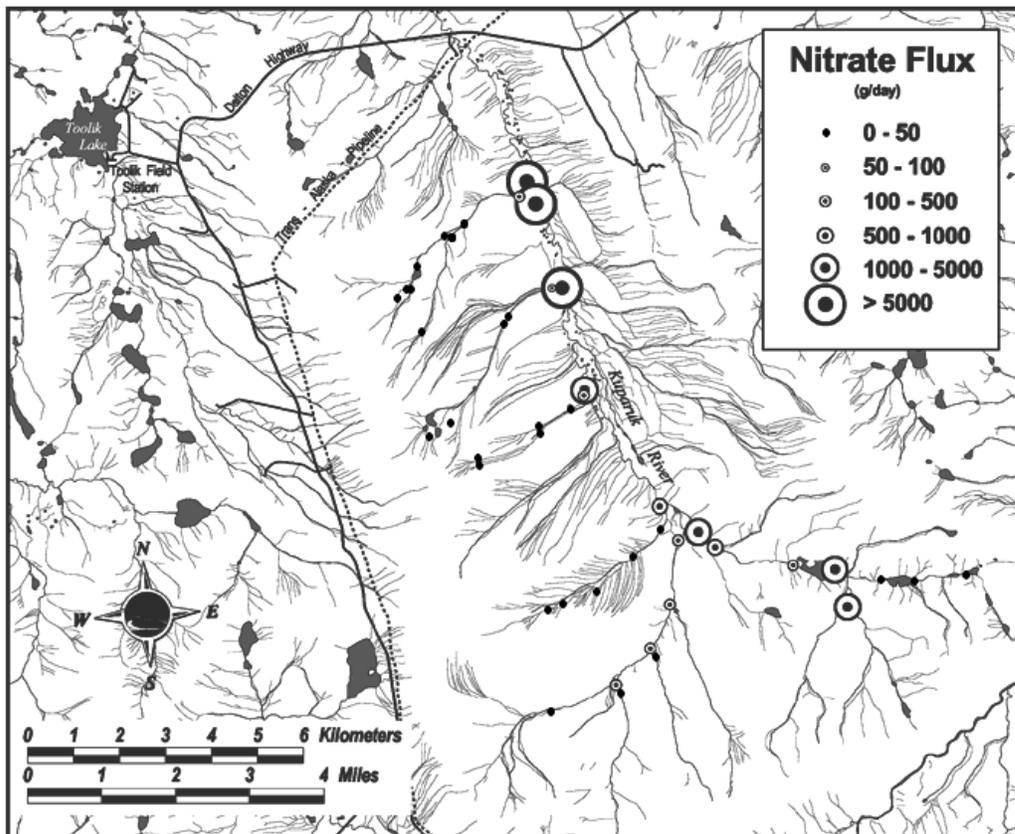
**Figure 2-4.** A typical toposequence of Sagavanirktok age (~300,000 y), in the Imnavait Creek drainage (Walker et al. 1989). This is one of the toposequences to be studied intensively by the Terrestrial and Landscapes Interactions groups, focusing on downslope water and element movement. It is underlain by permafrost at a depth of 30-150 cm

**Figure 2-5.** Effects of experimental treatments on aboveground biomass, NDVI, and CO<sub>2</sub> fluxes in wet sedge tundra at Toolik Lake. The plots were harvest in July 2001, in the 13<sup>th</sup> summer of treatment. SH=shade; CT=control; GH=greenhouse; GHNP=greenhouse plus N+P fertilizer; NP=N+P fertilizer. NEP=net ecosystem production or net CO<sub>2</sub> flux; GEP=gross ecosystem photosynthesis; ER=ecosystem respiration. Details reported in Boelman et al. 2003.

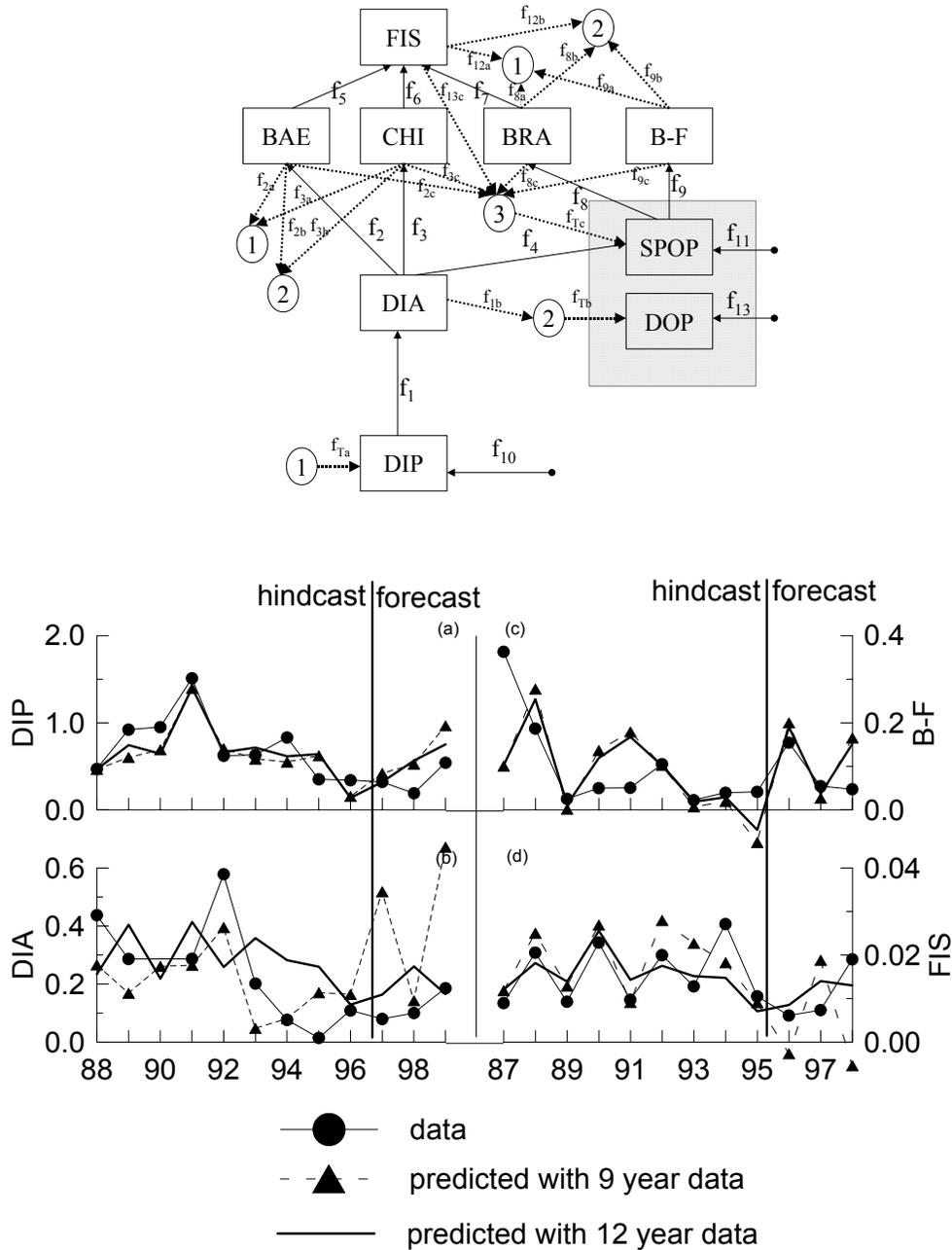




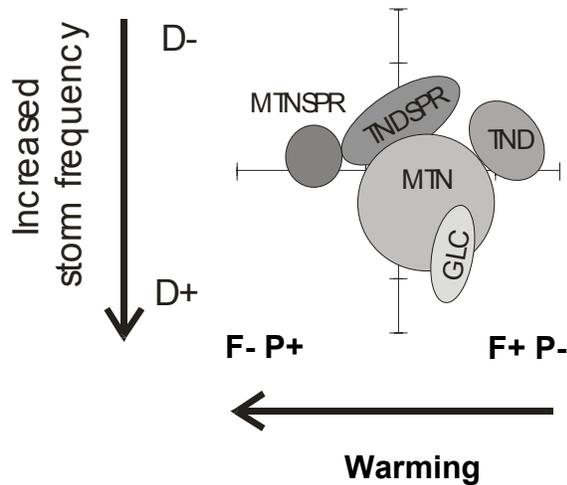
**Figure 2-6 A)** Adult and young-of-the-year (YOY) grayling growth versus mean summer river discharge in the Kuperuk River. Adult fish growth is higher when discharge is high, whereas YOY grow best during low flow summers. **B)** Mean total length ( $\pm$  SE) of Kuperuk River grayling over time. Changes in mean length reflect the recruitment resulting from favorable years for YOY growth and survival.



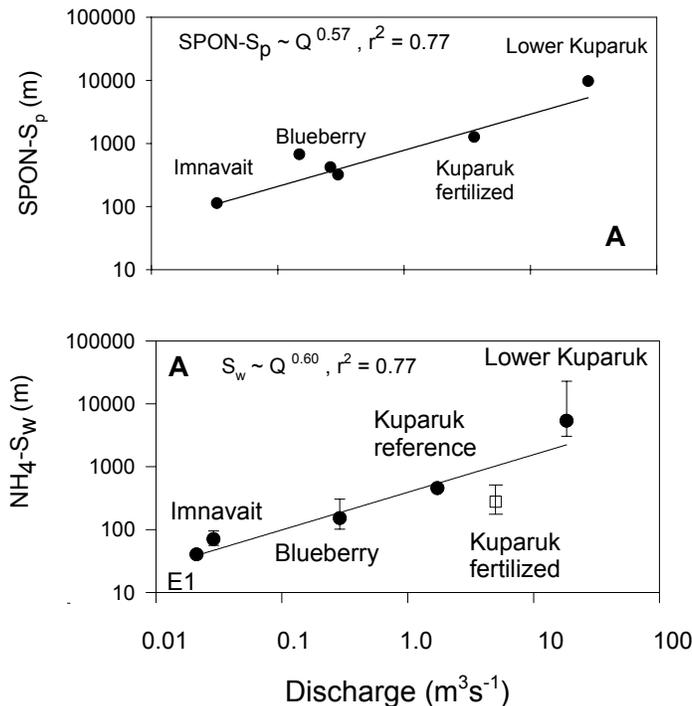
**Figure 2-7.** Synoptic sampling of streams in the Upper Kuperuk watershed was conducted for discharge and water chemistry on July 6, 2003. Figure shows the distribution of nitrate flux throughout the stream network. Most tributaries show low nitrate export but there are both source and sink hotspots that dominate nitrate dynamics in the watershed.



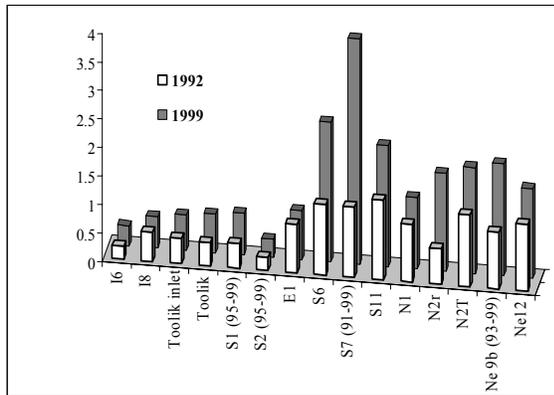
**Figure 2-8. Top:** The structure of the Tundra River Ecosystem Model (TREM) developed for the purpose of predicting changes in the stream community structure and P cycling from climate drivers. **Bottom:** TREM model prediction compared to data from the fertilized reach of the Kuparuk River. This example compares model predictions based on either 12 or 9 years of calibration data. In general, predictions improve as calibration data sets encompass more years and thereby include more of the natural year-to-year climate variability. DIP = dissolved inorganic phosphorus, DIA = diatom biomass, BF= blackfly abundance, FIS = grayling growth, SPOP = sestonic particulate organic phosphorus, DOP = dissolved organic phosphorus.



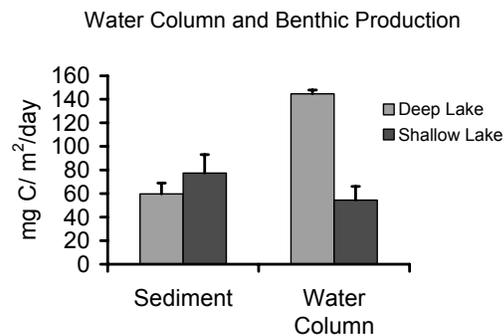
**Figure 2-9.** Distribution of macroinvertebrate communities from different stream types (mountain spring, tundra spring, mountain, tundra, glacier) within a 2-D habitat template. Y-axis represents substratum disturbance intensity (D+ = high, D- = low). X-axis represents probability of winter freezing (F) and phosphorus (P) supply (+ = high, - = low). Community positions are based on DCA analysis. Predicted changes in habitat attributes in response to expected climate change are indicated by the direction of the arrows.



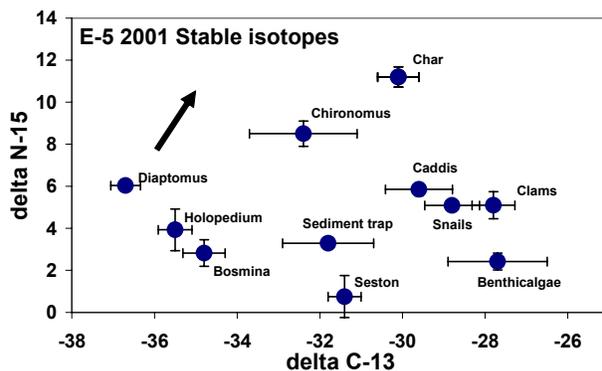
**Figure 2-10.** The uptake and travel distances of both ammonium ( $\text{NH}_4\text{-S}_w$ ) and sestonic particulate organic nitrogen ( $\text{SPON-S}_p$ ) are clearly related to stream discharge. These data from prior research will be used for calibrating the transport of nutrients and particulates in different order streams (Wollheim et al. 2001).



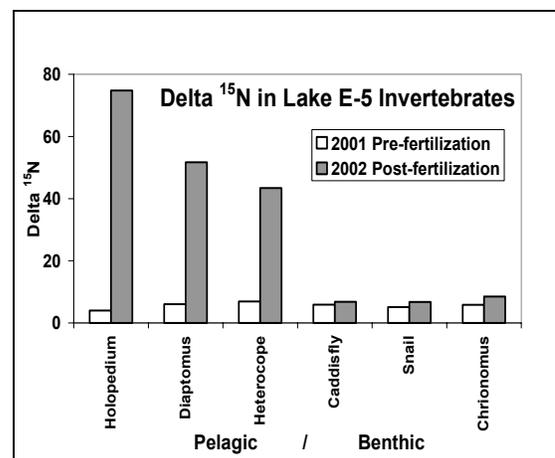
**Figure 2-11.** Alkalinity (mEq/L) in Toolik area lakes in 1992 and 1999. Lakes showed an average increase of 80% during this time period. Note the high alkalinity values for the seepage dominated lakes (S-6, S-7 and Ne-9b).



**Figure 2-12.** Mid-summer primary production in water column and benthic sediments of lakes E-5 (mean depth 6.2m) and E-6 (mean depth 1.7m). Pattern is typical among lakes in Toolik region where benthic production exceeds pelagic production in shallow lakes.

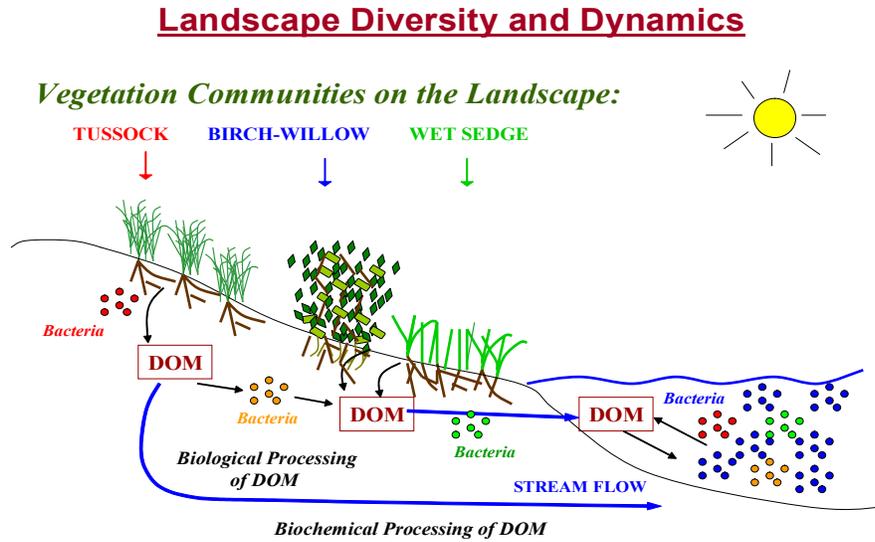


**Figure 2-13.** Stable isotopes of nitrogen and carbon for organisms collected in Lake E-5 in 2001 prior to fertilization. Note that seston and zooplankton demonstrate a pelagic affinity with delta <sup>13</sup>C values less than -30. Benthic algae and most benthic invertebrates produce delta <sup>13</sup>C values greater than -30 reflecting benthic resources. The lighter <sup>13</sup>C values for Chironomus indicates a mixing of sedimenting phytoplankton and benthic algal resources. Char values reflect a mixing of Chironomus and other benthic invertebrates.



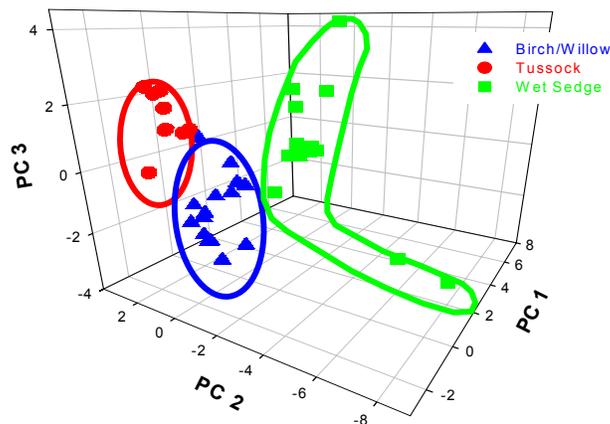
**Figure 2-14.** Changes in delta <sup>15</sup>N values of pelagic and benthic invertebrates after fertilization. <sup>15</sup>N was added as a tracer in the nutrient addition. Results indicate a separation in pelagic and benthic food webs with pelagic invertebrates demonstrating tight linkages to increases in nutrients, whereas benthic invertebrates demonstrate little ability to respond to initial nutrient additions.

**Figure 2-15** Overall diagram showing linkages between production of dissolved materials in different vegetation communities on a heterogeneous landscape, to processing of materials as they move downslope, to transfers of materials and organisms to aquatic systems.

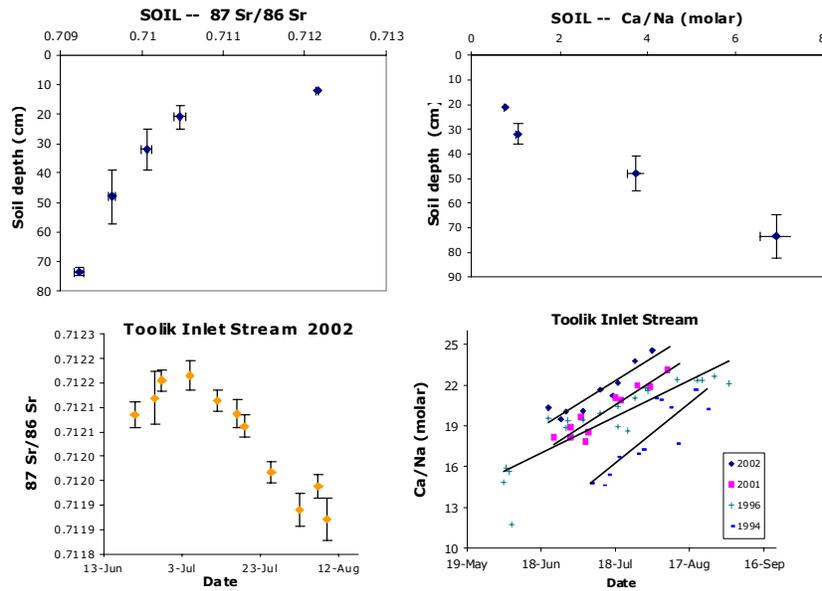


**Figure 2-16.** Plot showing that microbial soil communities (identified by PLFA analysis) group consistently under different terrestrial vegetation types. Soil-water chemistry is also consistently different under vegetation types of upland tussock, birch-willow (riparian), and lowland wet sedge (K. Judd and G. Kling, unpublished). Additional evidence (Crump et al. 2003) indicates that these soil water microbes are transported to lakes and can form persistent communities.

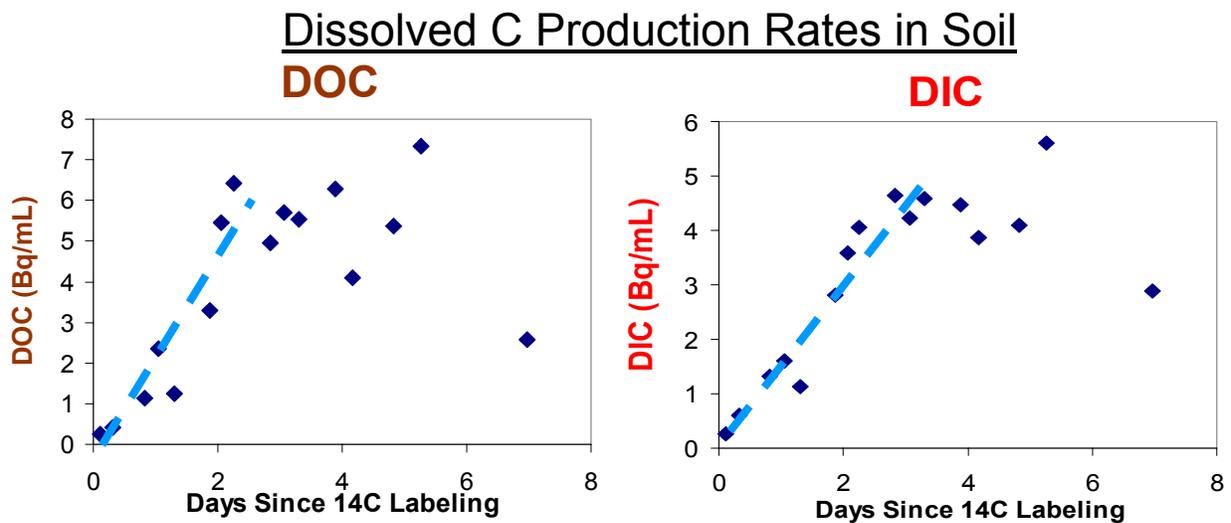
***Microbial Communities Group by Vegetation***  
PCA of PLFAs in Soils



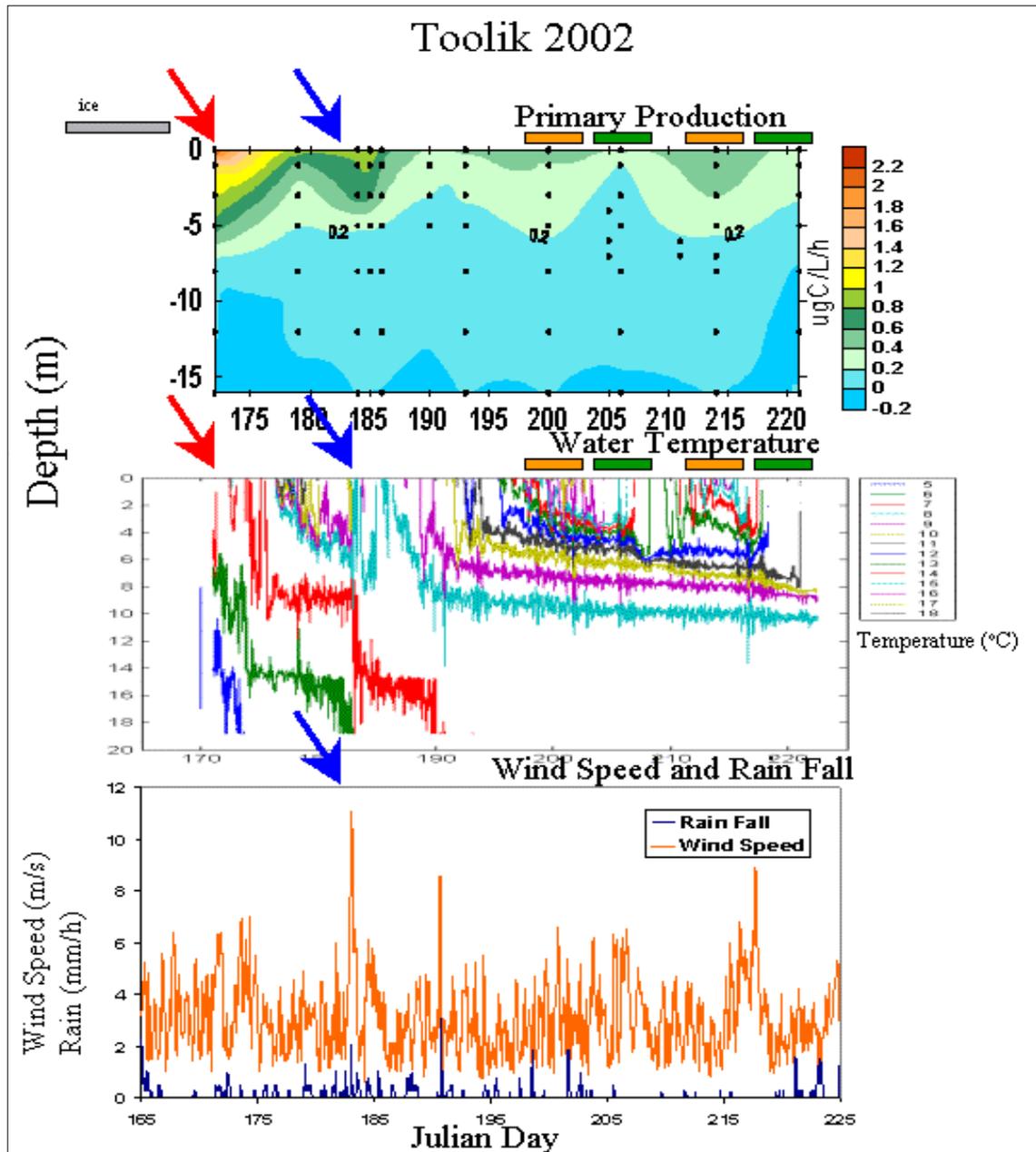
**Figure 2-17.** Top panels show changes in strontium isotopic composition (left) and Ca/Na ratios (right) with depth in tundra soils. Bottom panels show (1) how strontium isotope ratios decrease in stream water as thaw deepens in summer (left), exposing more soil with lower isotope ratios (top left panel), and (2) how Ca/Na ratios in stream water increase each summer as thaw deepens and exposes more soil with higher Ca/Na ratios to weathering (K. Keller, G. Kling, J. Blum, unpublished).



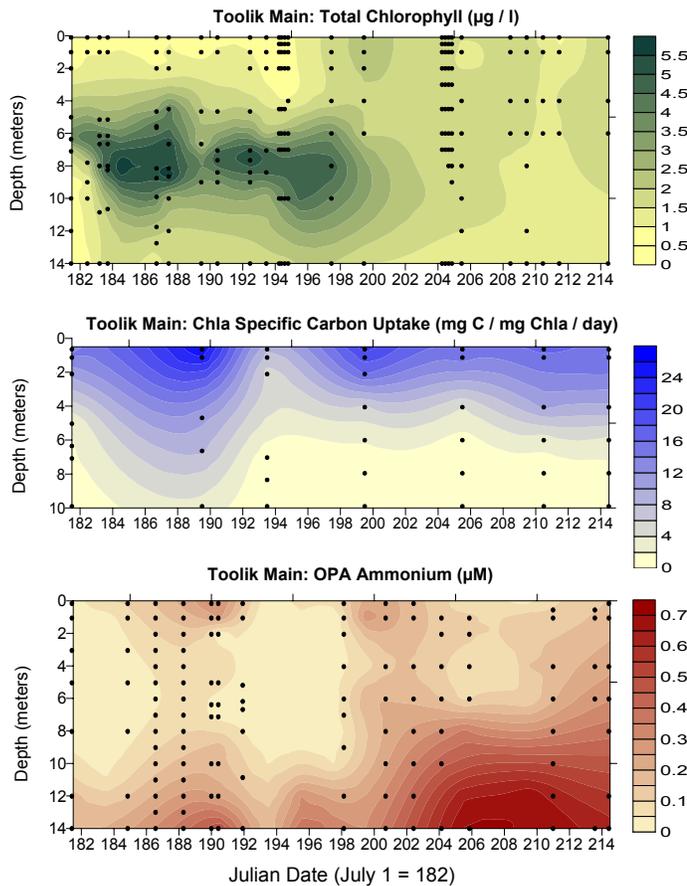
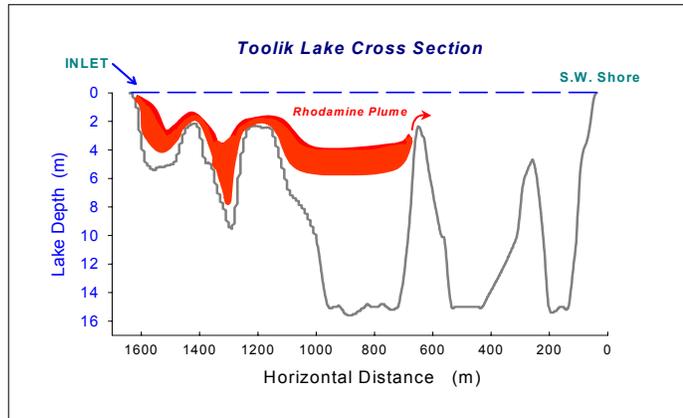
**Figure 2-18.** Rates of soil-water C production as estimated by following a  $^{14}\text{C}$ - $\text{CO}_2$  tracer applied to wet sedge tundra plants. The slope of radioactivity increase shows the rate of root production of dissolved organic and inorganic carbon (DOC, DIC), and dissolved  $\text{CO}_2$  and  $\text{CH}_4$  (G. Kling, M. Sommerkorn, K. Nadelhoffer, unpublished).



**Figure 2-19.** Illustration of a storm-driven event and its impact on Toolik Lake. Primary production (top) increased when a wind event (bottom) caused mixing of deeper waters with nutrients into the surface euphotic zone (middle – temperature isotherms show mixing). The initial high productivity is caused by ice-off and mixing in the lake (first arrow from left), while the second arrow indicates the impact of the storm event. Similar increases in primary production have been observed due to rainstorm inflows into the lake – our new activities in this grant will be to compare the relative strengths of the climate linkage versus the stream input linkage in determining the response of lakes to such perturbations.



**Figure 2-20.** Illustration of a storm-driven inflow event and its long-term impact on Toolik Lake. The top figure shows the path of the inflow water traced by rhodamine. The bottom 3 panels show the impact of the storm event which occurred on Julian Day 199. Chla concentrations were diluted dramatically (top), but the rate of C uptake per unit Chla stayed the same (middle), probably due to the increase in ammonium concentrations in surface waters brought in by the storm (bottom).



Interpolation Method: Kriging

data4/toolik99/lake\_chemistry/TM1.srf

## SECTION 3: SITE MANAGEMENT

**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.

An Executive Committee consisting of the lead PI (Hobbie), representatives of each of the four research groups (currently Shaver, Peterson, O'Brien, 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 to ensure continuity in our network participation; both Shaver and Hobbie have served or are currently serving on the Network Executive Committee.

Key project personnel include the four full-time, senior assistants associated with each of the four research areas, and a part-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.

**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 (Fig. 3-2). 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); projects without OPP support, including the LTER project, pay a per diem fee that includes room and board, lab space, and limited logistic support. 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. One important service that has developed over the past three summers is the GIS service provided by an in-residence GIS manager. LTER scientists also attend annual winter planning meetings as members of the TFS Steering Committee; M.S. Bret-Harte, an LTER scientist at the University of Alaska, is Associate Scientific Director of TFS.

**Collaborating projects, diversity, and interactions with LTER Network.** The Arctic LTER project encourages collaborations with other scientists and institutions. A complete list of collaborating projects in 1998-2004 is provided in the Budget Justification section. Perhaps the best measure of the LTER project's success at attracting others to the site is the fact the user-days at TFS have increased more than twofold since 1990 (Fig. 3-1). This growth includes both projects that work directly on LTER sites and experiments and projects that use the facilities at TFS and often collaborate in synthesis papers (e.g., Arft et al. 1999). Often the LTER project will encourage a particular interaction by inviting visitors with supplemental or core research funds, who eventually acquire independent funding (an example is the relationship we have built with J. Moore over the past 6 years).

The project has been particularly successful in attracting female investigators in the past 6 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 (Syndonia Bret-Harte, Loretta Johnson, Sarah Hobbie, and Laura Gough have all followed this route; in addition Gough has an NSF ADVANCE grant from OPP).

Cross-site and Network collaborations are encouraged in diverse ways. Over the past five 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, Sheffield, and Edinburgh; this has led to several publications, theses and a metaanalysis of responses to tundra experiments (van Wijk et al. 2003). Shaver was awarded an LTER Cross-Site grant (NSF-DEB-0087046) to develop comparisons with Abisko, leading to several review papers written with Abisko researchers, and to a metaanalysis of results of long-term experiments at the two sites (van Wijk et al. 2003). A new award to Shaver (NSF-OPP 0352897) will support research at Abisko, Zackenberg (Greenland), and on Svalbard (Norway) starting on summer 2004.

**Anticipated changes, 2004-2010.** Our current management system has worked well since 1987 and we plan no major changes in the next six years. One issue that does need careful forethought is the rotation of personnel in project leadership. After more than 30 years, John Hobbie will step down as project PI. Over the next six years, the current plan is that Gus Shaver will gradually assume this role, with a complete changeover by 2010. A similar transition is planned for the position of Lakes group coordinator and Executive Committee member, with John O'Brien being replaced by Chris Luecke.

Figure 3-1. Total Userdays 1990 to 2003  
Toolik Field Station

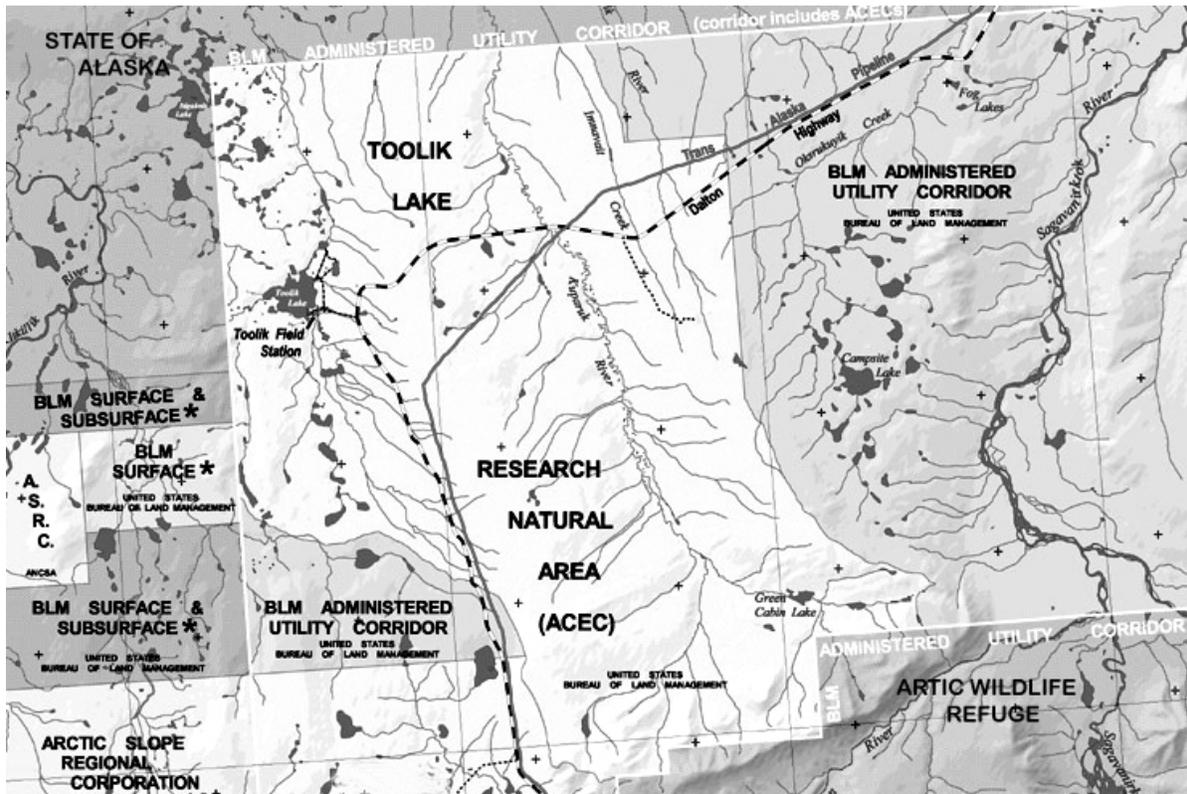
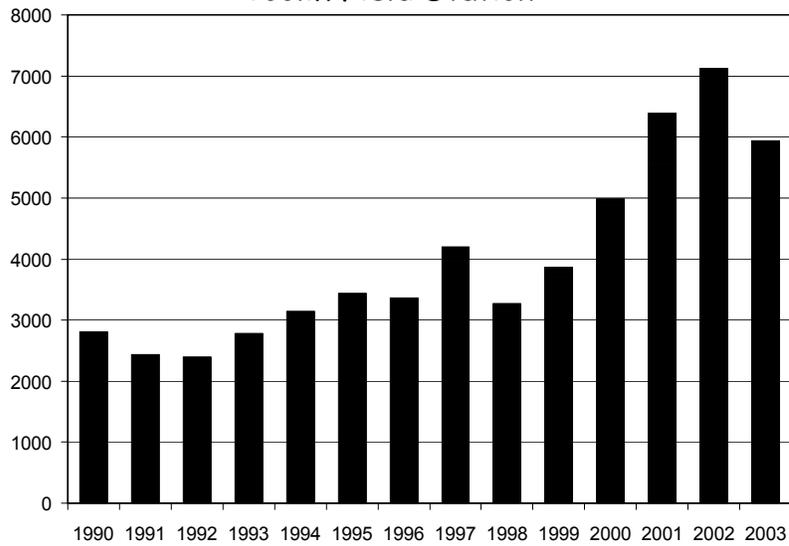


Fig. 3-2. Land ownership near Toolik Lake Field Station, from the Toolik Field Station GIS

## SECTION 4. INFORMATION MANAGEMENT AND TECHNOLOGY

**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 through careful development of metadata, but more importantly it is achieved as a result of the fact that multiple kinds of measurements are made 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 made at the same or nearby sites.

The structure of our information management system parallels the overall management structure of the project (Proposal Section 3). 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 (Section 3) 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 also 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.

**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/default.htm>). We only ask that the principal investigator of 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.

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.

**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 data sets are submitted in plain ASCII and in the required Arctic LTER formats (see <http://ecosystems.mbl.edu/arc/dataprotocol/datapro.html>). The metadata must follow our structured text-base format and the data are submitted in comma delimited files. 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 server by these research assistants. A Perl script is used to add the document file to an index file and to create an HTML version of the document file with a link to the data file.

**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 data base 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 data bases are provided on the Arctic LTER web site at <http://ecosystems.mbl.edu/arc/database1.html>; these include:

- The *Circumpolar Geobotanical Atlas*, developed by Dr. Donald (Skip) Walker and colleagues at the Alaska Geobotany Center, University of Alaska (<http://www.geobotany.uaf.edu/arcticgeobot/index.html>), features a nested, hierarchical series of maps of arctic ecosystems at scales ranging from 1:10 (1 m<sup>2</sup>) 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 km<sup>2</sup>), 1:5000 (25 km<sup>2</sup>), and of the Kuparuk River basin at 1:25,000 and 1:250,000. This Atlas was recently featured in Science magazine's "Netwatch" (2 January 2003, vol. 303 p. 21)
- The *Toolik Field Station GIS* (<http://www.uaf.edu/toolik/>) 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 Balsler, 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; [http://nrm.salrm.uaf.edu/~abalsler/projects\\_new.html](http://nrm.salrm.uaf.edu/~abalsler/projects_new.html)). 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. A recent addition to this GIS is 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.

- A GIS focused on *Landscape Control of Arctic Alaskan Food Webs* is available at the [Natural Resources Research Institute](#), University of Minnesota, Duluth (A. Hershey, C. Richards, et al.). This GIS focuses on food webs of lakes in the Toolik Lake area and their variation in relation to geology, bathymetry, and chemistry

**General site information and publications.** General information about the Arctic LTER project is provided on our web site (<http://ecosystems.mbl.edu/arc/default.htm>) 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.

**Future Plans.** We are currently working with the LTER Network Office and with the Information Manager's group to add Ecological Metadata Language (EML) formatted metadata files to our database. EML, a subset of XML, is a specification for structuring metadata, allowing automated processing, searching and retrieval of information from within a metadata file (see <http://knb.ecoinformatics.org/software/eml/>). The LTER Network Office is providing tools to convert our structure text base metadata into EML format. We plan to store these files on Metacat, an XML database (<http://knb.ecoinformatics.org/software/metacat/>), either locally or at the LTER network office. The EML formatted metadata files will not replace our structured text base files. The metadata and data will continue to be archived in ASCII. The EML format will enable better searching of data and also standardize metadata across the LTER network. The conversion tool along with web style sheets will replace our Perl script for formatting metadata for our online data access. Using a database like Metacat will enable easier searching and retrieval of datasets.

Table 4-1. For the year 2003, each column shows month-by-month sums of hits on all Arctic LTER web pages and on data files only (not including web-crawler hits). Hits from addresses outside the Marine Biological Laboratory (MBL) are also listed.

Month	Hits on Arctic LTER Web Site		Hits on Arctic LTER Data Files	
	All Hits	Outside MBL	All Hits	Outside MBL
1	87,764	35,974	2,876	2,756
2	80,225	33,868	1,539	1,517
3	89,156	37,928	1,252	1,184
4	82,968	33,563	1,307	1,214
5	85,851	34,730	1,384	1,357
6	82,606	33,515	346	341
7	85,599	34,751	824	738
8	79,552	29,166	1,141	1,141
9	83,594	32,224	550	537
10	127,553	41,838	1,303	1,263
11	109,239	38,582	187	59
12	103,992	29,104	239	222

Table 4-2. Journal publications of the Arctic LTER project, 1998-2003

<i>Journal</i>	<i>Published or accepted</i>	<i>Submitted</i>
1 Ecology	9	
2 Journal of Geophysical Research	8	
3 Global Change Biology	7	
4 Journal of the North American Benthological Society	7	
5 BioScience	6	
6 Journal of Ecology	6	1
7 Ecosystems	5	1
8 Global Biogeochemical Cycles	5	
9 Freshwater Biology	4	1
10 Oikos	4	
11 Biogeochemistry	3	
12 Limnology and Oceanography	3	
13 Plant And Soil	3	
14 Arctic, Antarctic, and Alpine Research	2	2
15 Canadian Journal of Fisheries and Aquatic Sciences	2	2
16 Journal of Evolutionary Biology	2	
17 Journal of Hydrometeorology	2	1
18 Nature	2	1
19 New Phytologist	2	
20 Oecologia	2	2
21 Science	2	
22 Soil Biology and Biochemistry	2	
23 Advances in Water Research	1	
24 Annual Reviews of Ecology and Systematics	1	
25 Applied and Environmental Microbiology	1	
26 Archiv für Hydrobiologie	1	
27 Boundary Layer Meteorology	1	
28 Canadian Journal of Forest Research	1	
29 Ecological Applications	1	1
30 Ecological Modeling	1	2
31 Ecological Monographs	1	
32 Environmental Biology of Fishes	1	
33 Geophysical Research Letters	1	
34 Global Change Science	1	
35 Hydrobiologia	1	
36 Journal of North American Fisheries Management	1	
37 Journal of Plankton Research	1	
38 Polar Geography	1	
39 Polar Research	1	
40 Transactions American Fisheries Society	1	
41 Verh. Int. Verein. Limnol.	1	
42 Water Resources Research	1	1
43 Soil Biology and Biochemistry	1	
44 Ecology Letters		1
45 Hydrological Processes		1

## SECTION 5: EDUCATION AND OUTREACH

The Arctic LTER project maintains a multifaceted education and outreach program. In addition to the training of over 50 graduate and undergraduate students in 1998-2003 (Table 5-1), every summer we bring 1-3 journalists to Toolik Lake as part of the Marine Biological Laboratory's Science Journalism Program (Table 5-2). Over the past two summers we have developed a very popular Schoolyard LTER program based at Barrow, Alaska, in association with the Barrow Arctic Science Consortium, and in 2003 we established a new field course for students and journalists, "Arctic Ecology and Modeling" (Table 5-3). 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), under the auspices of the International Arctic Research Committee (IARC).

All of these activities will be continued and expanded in 2004-2010. We particularly hope to expand our program of support for graduate students as a result of a new agreement (signed September 2003) between Brown University and the Marine Biological Laboratory, which for the first time ever will allow 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 will continue to support at least 2 REU students each year with LTER supplemental funds, and 2-6 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 1). We will continue to promote the training of graduate students with support on collaborating grants, and we will 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 2-3 weeks of "hands on" field experience. A wide range of newspaper, magazine, radio, and film media are represented (Table 2). A list of articles produced is included in Supplementary Documents as part of our publications list.
- *Arctic ecology course:* In 2004, the course based on the NSF BioComplexity project, "Land-water Interaction at the Catchment Scale: Linking Biogeochemistry and Hydrology" will again be offered, but this time as a joint effort of the International Arctic Research Center (University of Alaska Fairbanks) and the Marine Biological Laboratory ([http://www.mbl.edu/education/courses/other\\_programs/arctic.html](http://www.mbl.edu/education/courses/other_programs/arctic.html)). The course, *Arctic*

*Climate and Terrestrial Ecosystems*, is 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. It will also give students an understanding of the scientific underpinnings of the controls and feedbacks of climate-related changes in Arctic ecosystems, and it will include first-hand exposure to ongoing research. The first week of the workshop, to be spent in the Fairbanks area, will consist of lectures and discussions at the International Arctic Research Center (IARC), together with visits to various research sites in and near Fairbanks. During the second week, the group will travel to the North Slope and will visit the Toolik LTER site.

- *Schoolyard LTER*: The Arctic LTER Schoolyard project, based in Barrow, AK, began in May 2002 and has had two very successful years. Directed by the Barrow Arctic Science Consortium, 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. In 2002, Suzanne Randazzo of the Arctic LTER set up the greenhouses and treatments in late June, maintained contact with project personnel at Barrow via email from Toolik, and returned in September to make final measurements and discuss results and plans for the academic year. Gus Shaver visited the site in August to coordinate experiments at the Schoolyard site with the research at Toolik Lake. In 2003, the greenhouse warming experiment continued, and an automatic weather station was installed for year-round observations. A gift from BP Exploration Alaska helped fund a trip to Toolik Field Station for several of the program’s student field participants and their science teacher, where they were able to see the Arctic LTER’s tundra warming experiments. Forty sessions of the Schoolyard Saturday lecture series have been held since 2002; total attendance has been about 1,300 students and adults. Future plans include a Schoolyard pond site, which has already been set up at the Barrow Environmental Observatory by Heidi Wilcox of the Arctic LTER; the Schoolyard Saturday series and the greenhouse experiment also will continue.
- *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 policies, and DNR has developed a dialog with Marc Stieglitz about modeling the timing of the freeze and thaw of the tundra to ensure better regulation of oil exploration machinery. Each year we invite representatives from these agencies to attend our winter meeting; in recent years Harry Bader of DNR and David Payer of ANWR have attended.
- *Research planning and organization*: We will 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 will continue to help with the long-term management and organization of the University of Alaska’s Toolik Field Station.

Table 5-1. Undergraduate and graduate students associated with the Arctic LTER, 1998-2003

<i>Academic level</i>	<i># students</i>	<i>College or University</i>
Research Experience for Undergraduates	34 (24 female, 10 male)	Alabama, Appalachian State, Beloit, Brown, California (Santa Barbara), Central Arkansas (2), Central Michigan, Clark, Clarkson, Connecticut, Cornell (3), Gettysburg, Lycoming, Marietta, Maryland, Michigan, Michigan State, Michigan Tech, Middlebury (2), Northern Colorado, Notre Dame, Penn State (2), Pomona, Utah State (2), Vermont (2), Wellesley, Western Washington
Master's degree in progress	9 (7 male, 2 female)	Maine, Minnesota, North Carolina (Greensboro) (3), Northern Colorado, Texas (Arlington), Vermont, Utah State
Master's degree recipients	4 (3 female, 1 male)	Kansas, Michigan, Minnesota, Northern Colorado
Ph.D. degree in progress	8 (female)	Columbia, Cornell, Michigan (4), Minnesota, Utah State
Ph.D. degree recipients	2 (male)	Arizona State, Columbia
Foreign students	5 (3 female, 2 male)	Kyoto (Japan), Copenhagen (Denmark), Cordoba (Argentina), Wageningen (Netherlands) (2)

Table 5-2. Science Journalism Program and other media interactions, 1998-2003:

<i>Year</i>	<i>Name and Media</i>
2003	Amanda Onion, ABCNews.com; Nicola Jones, New Scientist Magazine, now Nature
2003	"Hot Times in Alaska" documentary filmed at Toolik Lake by Chedd-Angier Production Company for Scientific American Frontiers, featuring Alan Alda, to be broadcast in 2004
2002	Jennifer Bogo, Audubon Magazine; Bob King, Palm Beach Post
2001	Chris Anderson, San Antonio Express-News
2000	David Poulson, Booth Newspapers; Dan Fagin, Newsday; Michael Mansur, Kansas City Star; Dan Grossman, freelance radio producer
1999	Michael Burns, Baltimore Sun; Cheryl Hogue, Bureau of National Affairs; Gretel Schueller, Audubon Magazine
1998	Diedra Henderson, Seattle Times; Angela Swafford, Mas Vida/CBS Telenoticias

Table 5-3. Participants in the 2003 field course, "Arctic Ecology and Modeling":

<i>Occupation</i>	<i># in course</i>
Teacher – elementary	1
Teacher – high school	2
Research assistant	2
Journalist	2
Graduate student	1
Scientist	1

## SECTION 6: REFERENCES

- Arndt, S.K.A., R. A. Cunjak, and T. J. Benfey. 2002. Effect of summer floods and spatial-temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams. *Transactions of the American Fisheries Society* 131:607-622.
- Arscott, D. B. 1997. Primary production in a fourth-order arctic stream. Masters Thesis, Univ. of New Hampshire, 178pp.
- Band, L.E., C.L. Tague, P. Groffman, and K. Belt, Forest ecosystem processes at the watershed scale: hydrological and ecological controls of nitrogen export, *Hydrological Processes*, 15 (10), 2013-2028, 2001.
- Beaulac, M., and K. Reckhow. 1982. An examination of land use-nutrient export relationships. *Water Resources Bulletin* 18:1013-1024.
- Benstead, J.P., L.A. Deegan, B.J. Peterson, A.D. Huryn, W.B. Bowden, K. Suberkropp, K.M. Buzby, A.C. Green, and J. Vacca. 2004. Responses of a beaded Arctic stream to short-term N and P fertilization. Submitted to *Freshwater Biology*.
- Biggs, B. J. F., R. J. Stevenson, and R. L. Lowe. 1998. A habitat matrix conceptual model for stream periphyton. *Archiv für Hydrobiologie* 143:21-56.
- Billings, W.D. 1973: Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience* 23:697-704
- Boelman, N. T., M. Steiglitz, H. Rueth, M. Sommerkorn, K.L. Griffin, G.R. Shaver, J. Gamon (2003). "Response of NDVI, Biomass, and Ecosystem Gas Exchange to Long-Term Warming and Fertilization in Wet Sedge Tundra." *Oecologia* 135: 414-421.
- Bret-Harte, M. S., G. R. Shaver, F.S. Chapin. (2002). "Primary and secondary stem growth in Arctic shrubs: Implications for community response to environmental change." *Journal of Ecology* 90: 251-267.
- Bret-Harte, M. S., G. R. Shaver, J.P. Zoerner, J.F. Johnstone, J.L. Wagner, A.S. Chavez, R.F. Gunkelman, S.C. Lippert, J.A. Laundre, (2001). "Developmental plasticity allows *Betula Nana* to dominate tundra subjected to an altered environment." *Ecology* 82(1): 18-32.
- Bret-Harte, M.S., E.A. García, V.M. Sacré, J.R. Whorley, J.L. Wagner, S.C. Lippert, and F. Stuart Chapin, III. In review. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology*
- Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150: 28-35.
- 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, pp. *In* J. Brown K. M. Hinkel F. E. Nelson (Eds.), *The circumpolar active layer monitoring (CALM) program: Research designs and initial results.* *Polar Geography* 24 (2):165-258.
- Carpenter, S.R., J.F. Kitchell and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634-639.

- Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694-711.
- Chapin, F.S., III, and G.R. Shaver. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77:822-840.
- Chinn, C. 2001. Estimating microbial biomass in low-production ecosystems. Undergraduate Honors Thesis, Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639.
- Clein, J. S., B. L. Kwiatkowski, A.D. McGuire, J.E. Hobbie, E.B.Rastetter, J.M. Melillo, D.W. Kicklighter. (2000). Modeling carbon responses of tundra ecosystems to historical and project climate: A comparison of a plot- and a global-scale ecosystem model to identify process-based uncertainties. *Global Change Biology* 6(s1): 127-140.
- Cole, J. J., S. R. Carpenter, J. F. Kitchell and M. L. Pace. 2002. Pathways of organic carbon utilization in small lakes: results from a whole-lake <sup>13</sup>C addition and coupled model. *Limnol. Oceanogr.* 47:1664-1675.
- Cosby, B.J., G.M. Hornberger, J.N. Galloway, and R.F. Wright. 1985. Modeling the effects of acid deposition: assessment of a lumped-parameter model of soil water and stream chemistry. *Water Resources Res.* 21:51-63.
- Crocker, R.L., and J. Major. 1955. Soil development in relation to vegetation and surface at Glacier Bay, Alaska. *Journal of Ecology* 43: 427-448.
- Crump, B. C., G. W. Kling, M. Bahr, J. E. Hobbie. 2003. Bacterioplankton community shifts in an Arctic lake correlate with seasonal changes in organic matter source. *Applied Environmental Microbiology* 69:2253-2268.
- Cyr, H. and M.L/ Pace 1992. Grazing by zooplankton and its relationship to community structure. *Can. J. Fish. Aquat. Sci.* 49:1455-1465.
- Deegan L.A., H.E. Golden, C.J. Harvey, B.J.Peterson. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. *Transactions of the American Fisheries Society*.128:1163-1175.
- Dent C.L., G.S. Cumming, S.R.Carpenter. 2002. Multiple states in river and lake ecosystems. *Philosophical Transactions of the Royal Society London Series Biological Sciences.* 357: 635-645.
- Dent, C.L., N.B. Grimm, and S.G. Fisher. 2001. Multiscale effects of surface-subsurface exchange on stream water nutrient concentrations *Journal of the North American Benthological Society* 20:162-181.
- Doles, J. 2000. A survey of soil biota in the arctic tundra and their role in mediating terrestrial nutrient cycling. Masters Thesis, Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639.
- Edwardson, K. J., W. B. Bowden, C. Dahm, J. Morrice. 2003. The hydraulic characteristics and geochemistry of hyporheic and parafluvial zones in arctic tundra streams, North Slope, Alaska. *Advances in Water Resources* 26:907-923.

- Elwood, J.W., J.D. Newbold, R.V. O'Neill, and W. Van Winkle. 1983. Resource spiralling: An operational paradigm for analyzing lotic ecosystems. P. 3-29. In T.D. Fontaine III and S.M. Bartell (ed)s, Dynamics of lotic ecosystems. Ann Arbor, MI: Ann Arbor Science.
- Eugster, W., G. W. Kling, T. Jonas, J. McFadden, A. Weust, S. MacIntyre, F. S. Chapin. 2003. CO<sub>2</sub> exchange between air and water in an arctic Alaskan and mid-latitude Swiss lake: the importance of convective mixing. *J. Geophysical Research* 108:ACL7-1 – 7-14.
- Evans, M.A., S. MacIntyre, and G. W. Kling. *In Prep.* Physical and chemical controls on primary production in arctic lakes.
- Fausch KD, C.E. Torgersen, C.V. Baxter, H.W.Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* 52:483-498.
- Fisher, T.R., D. Correll, R. Costanza, J. Hollibaugh, C. Hopkinson, R. Howarth, N. Rabalais, J. Richey, C. Vorosmarty, and R. Wiegert. 2000. Synthesizing drainage basin inputs to coastal systems. Pp. 81-106, *In* J. Hobbie (Ed.), *Estuarine Science*. Island Press, Washington D.C.
- Georgian, T., J.D. Newbold, S.A. Thomas, M.T. Monaghan, G.W. Minshall, and C.W. Cushing. 2003. Comparison of corn pollen and natural fine particle matter transport in streams: can pollen be used as a seston surrogate. *Journal of the North Benthological Society* 22:2-16.
- Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre and A. J. McKerrow. 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecological Monographs* 61:415-436.
- Gold, W.G. 1998. The influence of cryptogamic crusts on the thermal environment and temperature relations of plants in a high arctic polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research* 30: 108-120.
- Gold, W.G., and L.C. Bliss. 1995. Water limitations and plant community development in a polar desert. *Ecology* 76: 1558-1568.
- Gomi, T., R.C. Sidle, and J.S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. *Bioscience*. 52 (10): 905-916.
- Gough, L., and S. E. Hobbie. 2003. Responses of moist non-acidic arctic tundra to altered environment: Productivity, biomass and species richness. *Oikos* 103:204-216
- Gough, L., G. R. Shaver, J. Carroll, D. L. Royer, and J. A. Laundre (2000). Vascular plant species richness in Alaskan arctic tundra: The importance of soil pH. *Journal of Ecology* 88(1): 54-66.
- Gough, L., P. A. Wookey, G.R. Shaver (2002). Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arctic, Antarctic and Alpine Research* 34: 211-218.
- Grattan, R.M. and K. Suberkropp. 2001. Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. *Journal of the North American Benthological Society* 20:33-43.
- Grimm, N.B., S.E. Gergel, W.H. McDowell, E.W. Boyer, C.L. Dent, P. Groffman, S.C.Hart, J.Harvey, C. Johnston, E. Mayorga, M.E. McClain, and G. Pinay, 2003. Merging aquatic and terrestrial perspectives of nutrient biogeochemistry. *Oecologia* 137: 485-501.

- Gupta, A. and V. Cvetkovic. 2002. Material transport from different sources in a network of streams through a catchment. *Water Resources Research* 38:1098.
- Hamilton, T.D. 2003. Glacial geology of the Toolik Lake and upper Kuparuk River regions. *Biological Papers of the University of Alaska*, number 26. Institute of Arctic Biology, University of Alaska. ISSN 0568-8604
- Harvey, C.J., B.J. Peterson, W.B. Bowden, A.E. Hershey, M.C. Miller, L.A. Deegan, and J.C. Finlay. 1998. Biological responses of Oksrukuyik Creek, a tundra stream, to fertilization. *Journal of the North American Benthological Society* 17:190-209.
- Hedin, L.O., P.M. Vitousek, and P.A. Matson. 2003. Nutrient losses over four million years of tropical forest development. *Ecology* 84: 2231-2255.
- Henderson-Sellers, B. 1985. New formulation of eddy diffusivity thermocline models. *Appl. Math. Modeling* 9:441-446.
- Herbert, D.A., E.B. Rastetter, G.R. Shaver, and G. Ågren. 1999. Effects of plant growth characteristics on biogeochemistry and community composition in a changing climate. *Ecosystems* 2:367-382.
- Herbert, D.A., E.B. Rastetter, L. Gough, and G.R. Shaver. In press. Species diversity along nutrient gradients: An analysis of resource competition in model ecosystems. *Ecosystems*.
- Hinzman, L., D.L. Kane, C.S. Benson, and K.R. Everett. 1996. Energy balance and hydrological processes in an arctic watershed. Pp. 131-154 In: Reynolds, J. F., and J.D. Tenhunen. (eds.) *Landscape Function and Disturbance in Arctic Tundra*. Springer Verlag, Ecological Studies Series Volume 120. Springer-Verlag, New York. 437 pp.
- Hinzman, L.D., D.J. Goering, and D.L. Kane. 1998. A distributed thermal model for calculating soil temperature profiles and depth of thaw in permafrost regions. *Journal of Geophysical Research* 103: 28975-28992.
- Hobbie, E.A., S.A. Macko, and M. Williams. 2000. Correlations between foliar  $\delta^{15}\text{N}$  and nitrogen concentrations may indicate plant-mycorrhizal interactions. *Oecologia* 122: 273-283.
- Hobbie, J. E., B. L. Kwiatkowski, E. B. Rastetter, D.A. Walker, R.B. McKane. 1998. Carbon cycling in the Kuparuk Basin: Plant production, carbon storage, and sensitivity to future changes. *Journal of Geophysical Research* 103: 29,065-29,073.
- Hobbie, J.E., G. Shaver, J. Laundre, K. Slavik, L. Deegan, J. O'Brien, S. Oberbauer and S. MacIntyre. 2003. Climate forcing at the Arctic LTER Site. In: D. Greenland, D. Goodin and R. Smith (eds.) *Climate Variability and Ecosystem Response at Long-Term Ecological Research (LTER) Sites*. Oxford University Press, New York. pp. 74-91.
- Hobbie, S. E. and L. Gough (2002). Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in Northern Alaska. *Oecologia* 131(3): 453-462.
- Hobbie, S. E., A. Shevtsova, and F. S. I. Chapin. 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos* 84:417-434.

- Hobbie, S. E., T. A. Miley, and M. S. Weiss. 2002. Carbon and nitrogen cycling in soils from different glacial surfaces in northern Alaska. *Ecosystems* 5:761-774
- Hornberger, G.M., K.E. Bencala, and D.M. McKnight, Hydrological Controls On Dissolved Organic-Carbon During Snowmelt in the Snake River Near Montezuma, Colorado, *Biogeochemistry*, 25 (3), 147-165, 1994.
- Hughes, N.F. 1992. Selection of positions by drift feeding salmonids in dominance hierarchies: Model and test for arctic grayling in subarctic mountail streams. *Can J. Fish. Aquat. Sci.* 49:1999-2008.
- Huryn, A. D., K. A. Slavik, R. L. Lowe, D. S. Anderson, S. M. Parker and B. J. Peterson. 2004. Landscape heterogeneity and the biodiversity of arctic stream communities: a habitat template analysis. Submitted to Canadian Journal of Fisheries and Aquatic Sciences.
- Jenny, H. 1980. *The Soil Resource: Origin and Behavior*. Springer-Verlag Ecological Studies Series #37. Springer-Verlag, New York. 377.
- Johnson, L. C., G. R. Shaver, D.H. Cades, E. Rastetter, K. Nadelhoffer, A. Giblin, J. Laundre, A. Stanley. (2000). Plant carbon-nutrient interactions control CO<sub>2</sub> exchange in Alaskan wet sedge tundra ecosystems. *Ecology* 81(2): 453-469.
- Jonasson, S., F. S. I. Chapin, G.R. Shaver. (2001). Biogeochemistry in the Arctic: Patterns, processes and controls. In *Global Biogeochemical Cycles in the Climate System*. E.-D. Schulze, S. P. Harrison, M. Heimann et al., (eds). Academic Press: 139-150.
- Judd, K. E. and G. W. Kling. 2002. Production and export of dissolved C in arctic tundra mesocosms: the roles of vegetation and water flow. *Biogeochemistry* 60:213-234.
- Judd, K., and G. W. Kling. *In Prep*. Chemical composition and microbial species communities – which is most important in determining DOM transformations on the landscape?
- Kane, D.L., L.D. Hinzman, C.S. Benson, and K.R. Everett. 1989. Hydrology of Imnavait Creek, an arctic watershed. *Holarctic Ecology* 12: 262-269.
- King, J. Y., W. S. Reeburgh, K. K. Thieler, G. W. Kling, W. M. Loya, L. C. Johnson, and K. J. Nadelhoffer. 2002. Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: the contribution of photosynthates to methane emission. *Global Biogeochemical Cycles* 16: 1062, doi:10.1029/2001GB001456.
- Kling, G. W. 1995. Land-water linkages: the influence of terrestrial diversity on aquatic systems. pp. 297-310 *In*, F. S. Chapin and C. Korner (eds.), *The Role of Biodiversity in Arctic and Alpine Tundra Ecosystems*, Springer-Verlag, Berlin. 320pp.
- Kling, G. W., G. W. Kipphut, and M. C. Miller. 1991. Arctic lakes and rivers as gas conduits to the atmosphere: implications for tundra carbon budgets. *Science* 251:298-301.
- Kling, G. W., G. W. Kipphut, and M. C. Miller. 1992. The flux of carbon dioxide and methane from lakes and rivers in arctic Alaska. *Hydrobiologia* 240:23-36.
- Kling, G. W., G. W. Kipphut, M. C. Miller, and W. J. O'Brien. 2000. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. *Freshwater Biology* 43:477-497.

- Kling, G. W., G. W. Kipphut, M. C. Miller, and W. J. O'Brien. 2000. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. *Freshwater Biology* 43:477-497.
- Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573-592.
- Le Dizès, S., B.L. Kwiatkowski, E.B. Rastetter, A. Hope, J.E. Hobbie, D. Stow, S. Daeschner. 2003. Modeling biogeochemical responses of tundra ecosystems to temporal and spatial variations in climate in the Kuparuk River Basin (Alaska). *Journal of Geophysical Research-Atmospheres* 108(D2), 8165, doi:10.1029/2001JD000960.
- Lee, K-Y, T. R. Fisher, T. E. Jordan, D. L. Correll, and D. E. Weller. 2000. Modeling the hydrochemistry of the Choptank River Basin using GWLF and Arc/Info: 1. Model calibration and validation. *Biogeochemistry* 49:143-173.
- Lewis, W.M., and J.F. Saunders. 1989. Concentration and transport of dissolved and suspended substances in the Orinoco River. *Biogeochemistry* 7:203-240.
- Likens, G.E., and F.H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. *BioScience* 24:447-456.
- Likens, G.E., F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1967. The calcium, magnesium, potassium and sodium budgets for a small forested ecosystem. *Ecology* 48:772-785.
- Lowrance, R., R. Todd, J. Fail, O. Hendrickson, R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *BioScience*, 34:374-377.
- Loya, W. M., L. C. Johnson, G. W. Kling, J. Y. King, W. S. Reeburgh, K. J. Nadelhoffer. 2002. Pulse-labeling studies of carbon cycling in arctic tundra ecosystems: the contribution of photosynthates to soil organic matter. *Global Biogeochemical Cycles* 16 (4): 1101; doi:10.1029/2001GB001464.
- Luecke, C., W.A. Wurtsbaugh, P. Budy, H.P. Gross, and G. Steinhart. 1996. Simulated growth and production of endangered Snake River sockeye salmon: assessing management strategies for the nursery lakes. *Fisheries* 21:18-25.
- MacIntyre, S., W. Eugster, and G. W. Kling. 2002. The critical importance of buoyancy flux for gas flux across the air-water interface. pp. 135-139 *In* Gas Transfer at Water Surfaces, M.A. Donelan, W.M. Drennan, E.S. Saltzman, and R. Wanninkhof (Eds.), American Geophysical Union, Geophysical Monograph 127.
- McClain, M.E., E.W. Boyer, C.L. Dent, S.E. Gergel, N.B. Grimm, P.M. Groffman, S.C. Hart, J.W. Harvey, C.A. Johnston, E. Mayorga, W.H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301-312.
- McKane, R. B., E. B. Rastetter, G. R. Shaver, K. J. Nadelhoffer, A. E. Giblin, and J. A. Laundre. 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology* 78: 1170-1187.

- McKane, R. B., E. B. Rastetter, G. R. Shaver, K. J. Nadelhoffer, A. E. Giblin, and J. A. Laundre. 1997. Reconstruction and analysis of historic changes in carbon storage in arctic tundra. *Ecology* 78: 1188-1198.
- Meybeck, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. *American Journal of Science* 282: 401-450.
- Michaelson, G. J., C. L. Ping, G. W. Kling and J. E. Hobbie. 1998. The character and bioactivity of dissolved organic matter at thaw and in the spring runoff waters of the arctic tundra North Slope, Alaska. *Journal of Geophysical Research* 103:28,939-28,946.
- Moore, J.C. and P.C. de Ruiter. (2000). Invertebrates in detrital food webs along gradients of productivity. *In: Invertebrates as Webmasters in Ecosystems*. D.C. Coleman and P.F. Hendrix (eds.), CABI Publishing, Oxford, UK.
- Moore, J.C., K. McCann, H. Setälä and P.C. de Ruiter (2003). Top-down is bottom-up: Does predation in the rhizosphere regulate aboveground production. *Ecology* 84:84-857.
- O'Brien, W.J. and J.J. Showalter. 1993. Effects of current velocity and suspended debris on the drift feeding of arctic grayling. *Trans. Am. Fish. Soc.* 122:609-615.
- Oechel, W.C., 1989. Nutrient and water flux in a small arctic watershed: an overview. *Holarctic Ecology* 12:229-237.
- Oswald, W.W., L.B. Brubaker, F.S. Hu, and D.G. Gavin. 2003a. Pollen-vegetation calibration for tundra communities in the arctic foothills, northern Alaska. *Journal of Ecology* 91: 1022-1033
- Oswald, W.W., L.B. Brubaker, F.S. Hu, and G.W. Kling. 2003b. Holocene pollen records from the central arctic foothills, northern Alaska. Testing the role of substrate in the response of tundra to climate change. *Journal of Ecology* 91: 1034-1048.,
- Oswood M.W., A.M. Milner, and J.G. Irons III. 1992. Climate change and Alaskan rivers and streams. *In: Global climate change and freshwater ecosystems* (Eds P. Firth & S.G. Fisher), pp. 192-210. Springer-Verlag, Berlin.
- Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, J. R. Hodgson, M. C. Van de Bogert, D. L. Bade, E. S. Kritzberg, and D. Bastviken. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427:240-243.
- Perakis, S.S. and L.O. Hedin. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416-419.
- Peterjohn, W.T., and D.L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology* 65: 1466-1475.
- Peterson, B. J., J. E. Hobbie, A. Hershey, M. Lock, T. Ford, R. Vestal, M. Hullar, R. Ventullo and G. Volk. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. *Science* 229:1383-1386.
- Poole, G.C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47: 641-660
- Power, M.E., Dietrich, W.E. 2002. Food webs in river networks. *Ecological Research* 17: 451-471.

- Rastetter, E. B. and G. R. Shaver. 1992. A model of multiple element limitation for acclimating vegetation. *Ecology* 73:1157-1174.
- Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neill and J. E. Hobbie. 1992a. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications* 2:55-70.
- Rastetter, E. B., J. D. Aber, D. P. C. Peters, D. S. Ojima, and I. Burke. 2003. Using Mechanistic Models to Scale Ecological Processes Across Space and Time. *BioScience* 53(1): 68-76.
- Rastetter, E. B., J. D. Aber, D. P. C. Peters, D. S. Ojima, and I. Burke. 2003. Using mechanistic models to scale ecological processes across space and time. *BioScience* 53:68-76.
- Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie and J. D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO<sub>2</sub>, climate, and N deposition. *Tree Physiology* 9:101-126.
- Rastetter, E.B., and G. I. Ågren. 2002. Changes in individual allometry can lead to species coexistence without niche separation. *Ecosystems* 5:789-801
- Rastetter, E.B., B. L. Kwiatkowski, S. Le Dizes, and J.E. Hobbie. In Press. The role of down-slope water and nutrient fluxes in the response of arctic hill slopes to climate change. *Biogeochemistry*.
- Rastetter, E.B., B. L. Kwiatkowski, S. Le Dizes, and J.E. Hobbie. In Press. The Role of Down-Slope Water and Nutrient Fluxes in the Response of Arctic Hill Slopes to Climate Change. *Biogeochemistry*.
- Rastetter, E.B., Göran I. Ågren, and G.R. Shaver. 1997. Responses of N-limited ecosystems to increased CO<sub>2</sub>: Application of a balanced-nutrition, coupled-element-cycles model. *Ecological Applications* 7: 444-460.
- Rastetter, E.B., S.S. Perakis, G.R. Shaver, and G. Ågren. In Review. Dissolved organic nitrogen losses could attenuate responses of terrestrial ecosystems to elevated CO<sub>2</sub>. *Ecological Applications*.
- Reeburgh, W.S., J.Y. King, S.K. Regli, G.W. Kling, N.A. Auerbach, D.A. Walker. 1998. A CH<sub>4</sub> emission estimate for the Kuparuk River Basin, Alaska. *Journal of Geophysical Research* 103:29,005-2,9013.
- Reiners W.A., and K.L. Driese. 2001. The Propagation of Ecological Influences through Heterogeneous Environmental Space. *Bioscience* 51:939-950.
- Reynolds, J. F., and J.D. Tenhunen. (eds.) 1996. *Landscape Function and Disturbance in Arctic Tundra*. Springer Verlag, Ecological Studies Series Volume 120. Springer-Verlag, New York. 437 pp.

- Rouse W.R., M.S.V. Douglas, R.E. Hecky, A.E. Hershey, G.W. Kling, L. Lesack P. Marsh, M. McDonald, B. J., Nicholson, N. T. Roulet, and J.P. Smol. 1997. Effects of climate change on the freshwaters of Arctic and Subarctic North America. *Hydrological Processes* 11:873-902.
- Sarnelle, O. 1999. Zooplankton effects on vertical particulate flux: testable models and experimental results. *Limnol. Oceanogr.* 44:357-370.
- Scarsbrook, M.R. and C.R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology* 29:395-410.
- Schindler, D. W., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. *Trans. Am. Fish. Soc.* 122:756-772.
- Shaver, G. R. 1996. Integrated ecosystem research in northern Alaska, 1947-1994. In: J. Reynolds and J. Tenhunen, eds. Landscape Function and Disturbance in Arctic Tundra. Springer-Verlag Ecological Studies Series, Volume 120. Springer-Verlag, Heidelberg. pp.19-34.
- Shaver, G. R., and F. S. Chapin, III. 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. *Arctic and Alpine Research* 18:261-268.
- Shaver, G. R. and F. S. Chapin, III. 1991. Production/biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs* 61:1-31.
- Shaver, G. R., F. S. Chapin III and B. L. Gartner. 1986. Factors limiting growth and biomass accumulation in Eriophorum vaginatum L. in Alaskan tussock tundra. *Journal of Ecology* 74:257-278.
- Shaver, G. R., K. J. Nadelhoffer and A. E. Giblin. 1991. Biogeochemical diversity and element transport in a heterogeneous landscape, the North Slope of Alaska. pp. 105-126 In: M. G. Turner and R. H. Gardner (eds.), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York.
- Shaver, G. R., L. C. Johnson, D. H. Cades, G. Murray, J. A. Laundre, E. B. Rastetter, K. J. Nadelhoffer and A. E. Giblin. 1998. Biomass accumulation and CO<sub>2</sub> flux in three Alaskan wet sedge tundras: Responses to nutrients, temperature, and light. *Ecological Monographs* 68:75-97.
- Shaver, G. R., M. S. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin, III. (2001). Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82(3163-3181).
- Shaver, G. R., N. Fetcher and F. S. Chapin, III. 1986. Growth and flowering in Eriophorum vaginatum: Annual and latitudinal variation. *Ecology* 67:1524-1525.
- Shaver, G. R., W. D. Billings, F. S. Chapin, III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel and E. B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. *BioScience* 42:433-441.
- Shaver, G.R., and F.S. Chapin, III. 1995. Long-term responses to factorial NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* 18: 259-275.

- Shaver, G.R., J.A. Laundre, A.E. Giblin, and K.J. Nadelhoffer. 1996. Changes in vegetation biomass, primary production, and species composition along a riverside toposequence in arctic Alaska. *Arctic and Alpine Research* 28:363-379.
- Slavik, K., B. J. Peterson, L.A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. In press. *Ecology*.
- Smith, TR and L.J. Buckley. 2003. RNA-DNA ratio in scales from juvenile cod provides a nonlethal measure of feeding condition. *Transactions of the American Fisheries Society* 132:9-17.
- Soranno, P. A., K. E. Webster, J.L. Riera, T.K. Kratz, J.S. Baron, P.A. Bukaveckas, G.W. Kling, D.S. White, N. Caine, R.C. Lathrop and P.R. Leavitt. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. *Ecosystems* 2:395-410.
- Southwood, T.R.E. 1988. Tactics, strategies and templates. *Oikos* 52:3-18.
- Stelzer R.S., J. Heffernan and G.E. Likens. 2003. The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshwater Biology* 48:1925-1937.
- Stieglitz, M. J. Hobbie, A. Giblin, G. Kling. 1999. Hydrologic modeling of an arctic tundra watershed: Toward Pan-Arctic predictions *J. Geophys. Res.* Vol. 104 , No. D22 , p. 27,507 (1999JD900845)
- Stieglitz, M., A. Giblin, J. Hobbie, M. Williams, and G. Kling. 2000. Simulating the effects of climate change and climate variability on carbon dynamics in Arctic tundra. *Global Biogeochemical Cycles* 14:1123-1136.
- Stieglitz, M., A. Giblin, J. Hobbie, M. Williams, G. Kling. 2000. Simulating the effects of climate change and climate variability on carbon dynamics in Arctic tundra. *Global Biogeochem. Cycles* Vol. 14 , No. 4 , p. 1123 (1999GB001214)
- Stieglitz, M., J. Hobbie, A. Giblin, and G. Kling. 1999. Hydrologic modeling of an arctic watershed: Towards Pan-Arctic predictions. *Journal of Geophysical Research* 104, D22, 27507-27518.
- Stieglitz, M., J. Shaman, J. McNamara, G.W. Kling, V. Engel, J. Shanley 2003. “ An approach to understanding hydrologic connectivity on the hillslope and the implications for nutrient transport.” *Global Biogeochemical Cycles*. 17 (4), 1105, doi:10.1029/2003GB002041.
- Stieglitz, M., J. Shaman, J. McNamara, V. Engel, J. Shanley, and G. W. Kling. 2003. An approach to understanding hydrologic connectivity on the hillslope and the implications for nutrient transport. *Global Biogeochemical Cycles* 17:1105,doi:10.1029/2003GB002041.
- Stieglitz, M., S. J. Déry, V.E. Romanovsky, T.E. Osterkamp. (2003). “The role of snow cover in the warming of arctic permafrost.” *GRL* 30(13): 1721, doi:10.1029/2003GL017337.

- Vadeboncoeur, D.M. Lodge and S.R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic pathways. *Ecology* 82:1065-1077.
- Vadeboncoeur, Y., M.J. Vander Zanden and D.M. Lodge. 2002. Putting it all back together: Reintegrating benthic pathways into lake food web models. *BioScience* 52:1-11.
- Van der Peijl, M.J., and J.T.A. Verhoeven. 2000. Carbon, nitrogen and phosphorus cycling in river marginal wetlands; a model examination of landscape geochemical flows. *Biogeochemistry* 50:45-71.
- Vander Zanden, M. J. and Y. Vadeboncoeur. 2002. Fishes as intergrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152-2161.
- Vander Zanden, M. J., J. B. Rasmussen. 1999. Primary consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and the trophic position of aquatic consumers. *Ecology* 80:1395-1404.
- Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Ann. Rev. Ecol. Syst.* 33:341-370.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Jour. Fish. Aquatic Sci.* 37: 130-137.
- Vitousek, P.M. 2003. Stoichiometry and flexibility in the Hawaiian model system. pp. 117-133 IN: J.M. Melillo, C.B. Field, and B. Moldan, eds. *Interactions of the Major Biogeochemical Cycles: Global Change and Human Impacts*. Island Press, Washington.
- Vörösmarty, C.J. and B.J. Peterson. 2000. Macro-scale models of water and nutrient flux to the coastal zone, p. 43-79. In J. Hobbie (Ed.), *Estuarine Science*. Island Press, Washington D.C.
- Walker, D.A., N.A. Auerbach, J.G. Bockheim, F. S. Chapin, W. Eugster, J. Y. King, J. P. McFadden, G. J. Michaelson, F. E. Nelson, W. C. Oechel, C. L. Ping, W. S. Reeberg, S. Regli, N. I. Shiklomanov, G. L. Vourlitis. 1996. Energy and trace-gas fluxes across a soil pH boundary in the Arctic *Nature* 394, 469 - 472
- Walker, M.D., D.W. Walker, and N.A. Auerbach. 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* 5: 843-866.
- Wan, Z. and J. Vallino. An inverse ecosystem model of year-to-year variations with first order approximation to the annual mean fluxes. Submitted to *Ecological Modeling*.
- Wan, Z., J. J. Vallino, and B. J. Peterson. Study of the inter-annual dynamics in the Kuparuk River with a first order approximation inverse model. Submitted *Journal of the North American Benthological Society*.
- Weintraub, M., and J.P. Schimel. 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems* 6: 129-143.
- Wiens, J. A.. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47:501-515.

- Williams, M., E. B. Rastetter, D. N. Fernandes, M. L. Goulden, G. R. Shaver and L. C. Johnson. 1997. Predicting gross primary productivity in terrestrial ecosystems. *Ecological Applications* 7:882-894.
- Williams, M., E. B. Rastetter, G. R. Shaver, J. E. Hobbie, E. Carpino and B. L. Kwiatkowski. (2001). "Primary production of an arctic watershed: An uncertainty analysis." *Ecological Applications* 11(6): 1800-1816.
- Williams, M., W. Eugster, E. B. Rastetter, J. P. McFadden, and F. S. Chapin. 2000. The controls on net ecosystem productivity along an Arctic transect: a model comparison with flux measurements. *Global Change Biology* 6(s1): 116-126.
- Wollheim, W.M., B.J. Peterson, L.A. Deegan, J.E. Hobbie, B. Hooker, W.B. Bowden, K.J. Edwardson, D.B. Arscott, A.E. Hershsey, and J. Finlay. 2001. Influence of stream size on ammonium and suspended particulate nitrogen processing. *Limnology and Oceanography* 46:1-13.